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Genetic Evaluation of Growth Traits in Nellore Cattle through Multi-trait and Random Regression Models

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ABSTRACT

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We aimed to evaluate different orders of fixed and random effects in random regression models (RRM) based on Legendre orthogonal polynomials as well as to verify the feasibility of these models to describe growth curves in Nellore cattle. The proposed RRM were also compared to multi-trait models (MTM). Variance components and genetic parameters estimates were performed via REML for all models. Twelve RRM were compared through Akaike (AIC) and Bayesian (BIC) information criteria. The model of order three for the fixed curve and four for all random effects (direct genetic, maternal genetic, permanent environment, and maternal permanent environment) fits best. Estimates of direct genetic, maternal genetic, maternal permanent environment, permanent environment, phenotypic and residual variances were similar between MTM and RRM. Heritability estimates were higher via RRM. We presented perspectives for the use of RRM for genetic evaluation of growth traits in Brazilian Nellore cattle. In general, moderate heritability estimates were obtained for the majority of studied traits when using RRM. Additionally, the precision of these estimates was higher when using RRM instead of MTM. However, concerns about the variance components estimates in advanced ages via Legendre polynomial must be taken into account in future studies.

Keywords: body weight; genetic parameters; growth curves

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Traditionally, in breeding programs, variance components and genetic parameters estimation for growth traits are performed via multi-trait models (MTM) (Arango et al. 2002). In these models, observed weights are usually pre-adjusted for standard ages. Random regression models (RRM) might be an alternative for modelling traits that are repeatedly measured, and change gradually and continuously over time (Schaeffer 2004). The application of RRM to growth traits allows (co)variance components and genetic parameters estimation at any age of interest, even those that have not been measured. Furthermore, there is no need to create classes of ages or use any pre-adjustment weights. These models allow the efficient use of all available information, generally implying in accuracy increase (Meyer 2004).

According to Meyer (2005a) and Silva et al. (2013), orthogonal polynomials are the most appropriate to estimate covariance functions of growth traits, and Legendre is the most commonly used due to correlation reduction between estimated regression coefficients. Although a previous study has been reported comparing RRM and MTM to describe growth traits in Nellore cattle (Nobre et al. 2003a), the authors assumed a constant residual variance over time. Probably, it might be not true due to great difference between environments in Brazil. Additionally, in the cited study, there was no comparison between different MTM, since the authors used only one model. In this context, more general comparisons involving heteroscedastic RRM and different MTM would confer new insights on genetics of growth traits in Nellore cattle.

Toward this orientation, we aimed to identify the best RRM to estimate (co)variance components and genetic parameters as well as to verify RRM feasibility as an alternative of MTM in genetic evaluations of growth traits in Nellore cattle.

MATERIAL AND METHODS

Pedigree and phenotypic data. The dataset used in this study was provided by the National Association of Breeders and Researchers (Associação Nacional dos Criadores e Pesquisadores – ANCP). A total of 247 818 animals remained after pedigree pruning for the numerator relationship matrix calculation.

The studied traits were body weights of Nellore cattle from 308 farms in Brazil. Weights records were obtained from 60–499-day-old animals born between 2005 and 2012, and raised exclusively on pasture.

Two data sets were further used for statistical analyses; one for multi-trait models (pre-adjusted weights; DS1), and another for random regression models (non-adjusted weights; DS2). DS1 was composed of adjusted weights at 120 (W_{120}), 210 (W_{210}), 365 (W_{365}), and 450 (W_{450}) days of age. These weights corresponded, respectively, to age intervals of 60–149, 150–299, 300–419, and 420–499 days. The weights were pre-adjusted as follows:

$$PAW_i = W_0 + SA_i (W_i - W_0)/RA_i \qquad (1)$$

where:
PAW_i = pre-adjusted weight at age i
W_0 = birth weight
W_i = observed weight
RA_i = real age at W_i
SA_i = standard age i (i = 1 (120 days), …, 4 (450 days)).

The data consistency was performed via SAS software (Statistical Analysis System, Version 9.4, 2014). DS1 contained 10 002 observations from 2501 animals originating from 530 sires and 2433 cows after consistency (Table 1). DS2 contained the same weight records as DS1, but they were not pre-adjusted. The number of weight records for each animal varied from two to four.

Estimation of (co)variance components and genetic parameters was performed via the restricted maximum likelihood (REML) method developed by Patterson and Thompson (1971) and implemented in Wombat software (Meyer 2007).

Maternal effect. In order to verify the importance of maternal effects, single-trait analyses were performed for W_{120}, W_{210}, W_{365}, and W_{450}. For this, we fitted three different models: M_1: direct genetic and fixed effects; M_2: direct genetic, maternal genetic, and fixed effects; M_3: direct genetic, maternal genetic, maternal permanent

Table 1. Number of records (N), phenotypic means ($\overline{X}$), standard deviations (σ), coefficients of variation (CV), and standard errors (SE) for weights along the growth curve

Age (days)	N	$\overline{X}$ (kg)	σ (kg)	CV (%)	SE (kg)
60–149	2501	127.98	24.88	19.44	0.50
150–299	2501	190.51	22.95	12.05	0.46
300–419	2500	222.67	30.07	13.50	0.60
420–499	2500	264.17	35.65	13.50	0.71

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environment, and fixed effects. The MTM animal models (M_1 to M_3) considered as fixed effect the contemporary groups (CG), defined by animals in the same sex, year, herd, and season of birth (January to March, April to June, July to September, and October to December).

In matrix notation, M_1, M_2, and M_3 can be described, respectively, as follows:

$$y = \mathbf{X}\beta + \mathbf{Z_1}g + e \qquad (2)$$

$$y = \mathbf{X}\beta + \mathbf{Z_1}g + \mathbf{Z_2}m + e \qquad (3)$$

$$y = \mathbf{X}\beta + \mathbf{Z_1}g + \mathbf{Z_2}m + \mathbf{Z_3}c + e \qquad (4)$$

where:
y = vector of observations
$\mathbf{X}$ = incidence matrix for fixed effects
$\mathbf{Z_1}, \mathbf{Z_2}, \mathbf{Z_3}$ = incidence matrices of random effects
β = vector of fixed effects
g = vector of direct genetic effects
m = vector of maternal genetic effects
c = vector of maternal permanent environment effects
e = vector of residuals.

The likelihood ratio test (LRT) was used to compare these models and obtained by the following equation:

$$LRT = 2lnL_i - 2lnL_j \qquad (5)$$

where:
lnL_i = maximum likelihood function for the complete model i
lnL_j = maximum likelihood function for the reduced model j.

The LRT statistics was compared to tabulated chi-square value (χ^2), with V degrees of freedom and significance of 1%, where n is the difference between the number of parameters from the complete and reduced models.

Multi-trait model (MTM). Based on the maternal effect results, we carried out bivariate analyses by using the best fit MTM, i.e. M_1, M_2 or M_3. Bi-trait analyses were performed because the convergence criterion was not achieved when fitting the full multi-trait model. Therefore, to estimate (co)variance components and genetic parameters, $a = t (t - 1)/2$ bi-trait analyses were carried out in which t is the number of traits ($t = 4$) and a is the number of performed analyses, i.e. $a = 6$

analyses combinations ($W_{120-210}$, $W_{120-365}$, $W_{120-450}$, $W_{210-365}$, $W_{210-450}$, $W_{365-450}$). The means of bi-trait analyses were used as heritability estimates.

In matrix notation, the best fit MTM can be equally defined as equations 2 (M_1), 3 (M_2) or 4 (M_3).

The following assumptions were made:

$$E\begin{bmatrix} y \\ g \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{X}\beta \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ and } V\begin{bmatrix} g \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{G_g} \otimes \mathbf{A} & 0 & 0 & 0 \\ 0 & \mathbf{G_m} \otimes \mathbf{A} & 0 & 0 \\ 0 & 0 & \mathbf{G_c} \otimes \mathbf{I_q} & 0 \\ 0 & 0 & 0 & \mathbf{R} \otimes \mathbf{I_n} \end{bmatrix} \qquad (6)$$

where:
$\mathbf{G_g}$ = (co)variances matrix of direct genetic effects
$\mathbf{G_m}$ = (co)variances matrix of maternal genetic effects
$\mathbf{G_c}$ = (co)variances matrix of maternal permanent environment effects
$\mathbf{R}$ = matrix of residual effects of (co)variances
$\mathbf{A}$ = numerator relationship matrix
$\mathbf{I_q}$ = identity matrix with order q (q = number of dams)
$\mathbf{I_n}$ = identity matrix with order n (n = number of observations)
$\otimes$ = Kronecker product operator.

Note that the use of assumptions for maternal effects depends upon the maternal effect results.

Random regression models (RRM). The RRM via Legendre Orthogonal Polynomials (LOP) fitted contemporary groups and mean growth curve (fixed curve of order k_β) as fixed effects, and direct genetic (order k_g), maternal genetic (order k_m), permanent environment (order k_w), maternal permanent environment (order k_c) and residual as random effects. For fixed curve modelling, we used LOP of order three or four. Random curves were modelled assuming k_g, k_m, k_w, k_c from two to four. The tested models were named as RRM_CL, where RRM is the model number and CL the classes of residual variances, e.g. model 6_2 represents model number 6 and two classes of residual variance.

The RRM were described as follows:

$$y_{ij} = F_{ij} + \sum_{m=0}^{k_\beta-1} \beta_m \phi_m(s_i) + \sum_{m=0}^{k_g-1} g_{im} \phi_m(s_i) + \sum_{m=0}^{k_m-1} m_{im} \phi_m(s_{ij}) + \\ + \sum_{m=0}^{k_w-1} w_{im} \phi_m(s_{ij}) + \sum_{m=0}^{k_c-1} c_{im} \phi_m(s_{ij}) + e_{ij} \qquad (7)$$

where:
y_{ij} = weight on the jth day of the ith animal
F_{ij} = set of fixed effects

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β_m = m^{th} fixed regression coefficient of the mean growth curve of the population

g_{im}, m_{im}, w_{im}, c_{im} = random regression coefficients of direct genetic, maternal genetic, maternal permanent environment, and permanent environment effects, respectively, for the ith animal

k_g, k_m, k_w, k_c = orders of covariance functions used to describe the direct genetic, maternal genetic, maternal permanent environment, and permanent environment effects, respectively

s_{ij} = age j of animal i

$\phi_m(s_{ij})$ = LOP evaluated for s_{ij} for fixed regression and direct genetic, maternal genetic, maternal permanent environment, and permanent environment random effects, considering their respective orders k_g, k_m, k_w, and k_c

e_{ij} = residual

Residual variances were modelled considering the following classes: CL_1 for homogeneous; CL_2 60–149 and 150–499 days; CL_3 60–149, 150–299, and 300–499 days; CL_4 60–149, 150–299, 300–419, and 420–499 days. These classes were obtained from previous pilot studies aimed only at the identification of the best variance structure for the studied dataset based on likelihood ratio test.

RRM were compared via Akaike (AIC) and Bayesian (BIC) information criteria. The AIC and BIC were obtained via Wombat software (Meyer 2007). AIC and BIC imply penalties according to the number of parameters to be estimated and are defined as follows:

$$AIC = -2lnL + 2p \tag{8}$$

$$BIC = -2lnL + plnL(n - r(\beta)) \tag{9}$$

where:
−2lnL = model deviance
p   = number of parameters
n   = number of observations
r(β) = rank of β (fixed effect incidence matrix)
lnL   = maximum likelihood function logarithm

The covariance between direct genetic and maternal effects in MTM and RRM was assumed to be zero. The residual variance used in RRM was the sum of permanent environment and residual variances, which is equivalent to the residual variance obtained by MTM (Mota et al. 2013). The standard errors for the variance components estimates were calculated using the approximated method presented in Mrode (2014).

RESULTS AND DISCUSSION

Descriptive statistics. Age-wise descriptive statistics such as mean ($\overline{X}$), standard deviation (σ), coefficient of variation (CV), and standard error (SE) are presented in Table 1. Classes of 60–149, 150–299, 300–419, and 420–499 days old are normally the chosen intervals to adjust weight records in different beef cattle breeds such as Nellore (Nobre et al. 2003a), Simmental (Mota et al. 2013), and Tabapua (Menezes et al. 2013). It was observed that the first class (60–149 days) had the highest coefficient of variation. In fact, it is known that in the initial stage of life the animal tends to present higher stress factors which may lead to higher weight variations. The standard deviation and standard error, in general, tend to increase as the age increases, i.e. scale effect.

Maternal effect with multi-trait model. The complete multi-trait model (M_3) was significant ($P < 0.01$) for all traits. These results also suggested that after weaning, the maternal effects continue to affect the animal weight. Mota et al. (2013) working with similar models for pre-adjusted weights at 100, 205, 365, 450, 550, and 730 days old in Simmental cattle, reported significant results ($P < 0.01$) for these traits, except at 550 days. These authors also observed that the influence of maternal effects continues even after weaning, and the inclusion of these effects is indeed important. Meyer (2004) stated that the maternal permanent environment might affect the calf at both pre-weaning and growing phases, in which the effect can be modified due to the management. Menezes et al. (2013), working with Tabapua cattle, reported the importance and influence of maternal permanent environment from birth to 600 days of age. According to Meyer (2005a), models that do not consider maternal effects lead to over estimation of direct heritability. Therefore, it is recommended to fit maternal effects on the evaluation model in order to seek more accurate estimates even for the post-weaning phase.

Random regression models. In general, more parameterized models provided low AIC and BIC values (Table 2). Based on AIC and BIC, it can be seen that the model number 6 with $K_\beta = 3$, $K_g = 4$, $K_m = 4$, $K_w = 4$, and $K_c = 4$ best fit to dataset. Mota et al. (2013) studying RRM in Simmental beef cattle, verified similar results. However, in their study some models with higher orders and number of parameters presented lower AIC and BIC values.

The model with homogeneity of residual variance (6_1) had the worst fit among all heterocedastic models number 6 (Table 2). It indicated that the residual variance has different behaviours along the growth curve. These results were similar to those reported by Mota et al. (2013) and Menezes et al. (2013). According to these authors, assuming homogeneity of residual variance may create considerable distortions in the total variance, i.e. the residual variance can be affected by many factors along the growth. As the number of residual classes increased, an improvement was observed. The model 6_4 presented lower AIC and BIC values (Table 2).

This point forward, for better illustration, model 6_4, the best model of fit through random regression analyses, will be referred to as RRM and the best fit multi-trait model M_3 as MTM.

Variance components and genetic parameters (MTM and RRM). Figure 1 presents estimates of direct genetic variance (σ_g^2 – Figure 1A), maternal genetic (σ_m^2 – Figure 1B), maternal permanent environment (σ_c^2 – Figure 1C), composite residual (σ_{RC}^2 – Figure 1D), and phenotypic (σ_p^2 – Figure 1E) for MTM and RRM (Model 6_4).

In general, according to Meyer (2004) and Ghafouri-Kesbi et al. (2008), genetic evaluations for growth traits could be improved by replacing MTM with RRM because the latter is more appropriate to estimate genetic parameters due to avoidance of age pre-adjustment, and possibility of taking into account the specific environmental effects on the time of recording. These advantages of RRM allow to explain more amount of variances in genetic evaluations. In the present study, the ability of RRM to capture and explain variances over time is remarkable in Figure 1, mainly in terms of genetic and phenotypic variances.

Estimates of σ_g^2 increased along the curve in both models (MTM and RRM; Figure 1A). These results were similar to those observed by Dias et al. (2005) who identified increasing estimates of σ_g^2 via MTM and RRM from birth to 450 days of age in Tabapua cattle. Boligon et al. (2009), in a similar study of Nellore cattle, reported that estimates of σ_g^2 increased. According to these authors, the scale effect is one of the main factors that contribute to σ_g^2 increase, since at older ages, weights have greater magnitude.

Estimates of maternal genetic variances were divergent between RRM and MTM (Figure 1B). From 120 to 210 days, there was a slight increase

for MTM and slight decrease for RRM. These results were different from Meyer (2005b) who observed increase of σ_m^2 for both models. This author justified it by a greater maternal influence, directly affecting both models.

In general, an increase of σ_m^2 in both models after weaning was observed. Similar results were reported by Laureano et al. (2011), i.e. a slight increase from 210 days of age in MTM. Nobre et al. (2003b) also verified estimates of σ_m^2 similar to those observed in this study via RRM. These authors reported a slight increase from 210 to 365 days of age with a plateau afterwards.

Table 2. Polynomial orders (OP), number of parameters (NP), Akaike (AIC) and Bayesian (BIC) information criteria for random regression models

RRM_CL	OP					NP	AIC	BIC
	k_β	k_g	k_m	k_w	k_c			
1_1	3	3	2	2	2	27	134 899.3	134 810.1
2_1	3	3	3	3	2	29	134 743.2	134 287.2
3_1	3	2	4	3	3	28	133 697.1	134 241.8
4_1	3	2	3	4	3	32	134 099.3	134 010.6
5_1	3	2	4	4	4	33	134 043.4	134 087.0
6_1	3	4	4	4	4	40	**133 338.4**	**133 716.8**
7_1	4	3	2	2	2	27	134 594.9	134 902.6
8_1	4	2	2	3	2	28	134 299.7	134 510.2
9_1	4	2	2	3	3	29	134 143.8	134 287.1
10_1	4	3	3	4	4	30	134 097.5	134 040.1
11_1	4	2	4	4	4	33	134 194.1	134 058.2
12_1	4	4	4	4	4	41	134 038.3	134 001.4
6_2	3	4	4	4	4	41	133 270.2	133 699.3
6_3	3	4	4	4	4	42	133 222.3	133 512.6
6_4	3	4	4	4	4	43	**133 118.7**	**133 477.9**

k_β, k_g, k_m, k_w, k_c = orders of covariance functions used to describe the fixed curve, direct genetic, maternal genetic, maternal permanent environment, and permanent environment effects, respectively; RRM_CL = model number (RRM) and classes of residual variances (CL)

values in bold indicate the best fit model

Estimates of σ_c^2 presented increasing in RRM, especially after 365 days (Figure 1C). The abrupt results after 365 days are not biologically consistent and may happen due to a low number of offspring per cow ($\overline{X}$ = 1.02 on average). Menezes et al. (2013) reported 1.55 offspring per cow, and also observed increase in σ_c^2 from 360 days. On the other hand, Mota et al. (2013) and Rosa et al. (2000) verified estimates of maternal permanent environment close to zero. Schaeffer (2004) observed estimates tending to zero for maternal permanent environment effect with a number of offspring per cow equal to two or less. In summary, working with a low number of offspring per cow could lead to biased maternal permanent environment estimates.

Estimates of σ_{RC}^2 for both models were similar for 365 days (Figure 1D). For MTM, composite residual variances increased up to 210 days, slightly decreased up to 365 days, and increased again from 365 days. For RRM, σ_{RC}^2 decreased between pre-weaning and weaning, and abruptly increased after this period. Cyrillo et al. (2004) and Martins et al. (2000) observed similar behaviour, i.e., a slight decrease during initial period followed by an increase afterwards.

As can be observed in Figure 1E, there was an increase of phenotypic variance along the growth
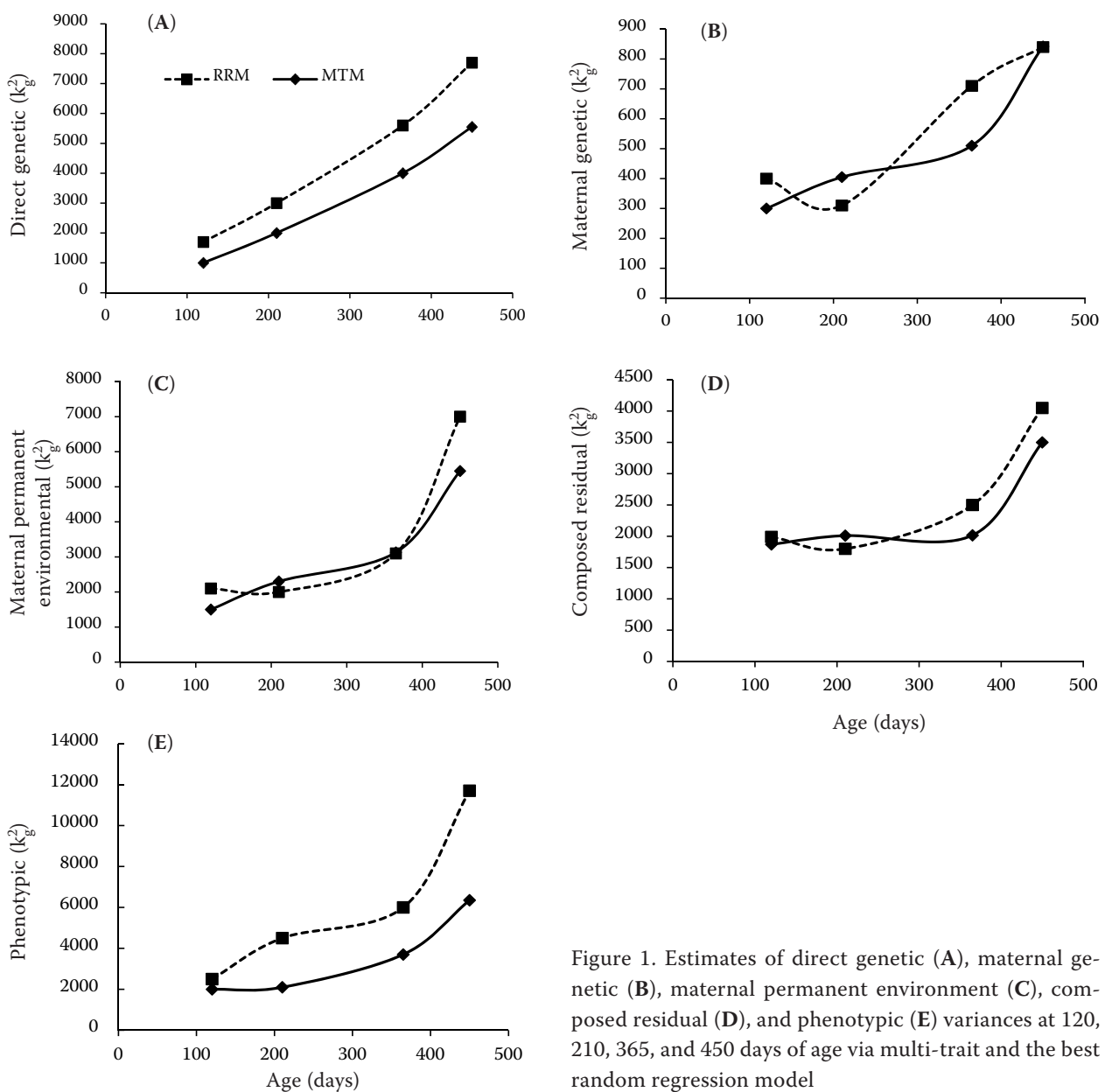

Figure 1. Estimates of direct genetic (**A**), maternal genetic (**B**), maternal permanent environment (**C**), composed residual (**D**), and phenotypic (**E**) variances at 120, 210, 365, and 450 days of age via multi-trait and the best random regression model

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Table 3. Direct genetic (h_g^2) and maternal genetic (h_m^2) heritabilities, maternal permanent environment (h_c^2), and composed residual (σ_{RC}^2) variance ratio for multi-trait and random regression models (in italics)

Weight(ages)	h_g^2*	h_m^2*	h_c^2*	σ_{RC}^2*
W_{120}	0.09 ± 0.03	0.02 ± 0.01	0.08 ± 0.04	0.79 ± 0.23
	0.15 ± 0.03	*0.08 ± 0.02*	*0.02 ± 0.01*	*0.68 ± 0.12*
W_{210}	0.13 ± 0.04	0.03 ± 0.01	0.07 ± 0.02	0.74 ± 0.21
	0.16 ± 0.03	*0.11 ± 0.04*	*0.05 ± 0.02*	*0.65 ± 0.09*
W_{365}	0.23 ± 0.06	0.01 ± 0.01	0.08 ± 0.03	0.68 ± 0.19
	0.31 ± 0.09	*0.09 ± 0.03*	*0.07 ± 0.03*	*0.43 ± 0.10*
W_{450}	0.28 ± 0.09	0.01 ± 0.02	0.11 ± 0.04	0.60 ± 0.19
	0.39 ± 0.11	*0.08 ± 0.03*	*0.08 ± 0.02*	*0.39 ± 0.11*

W_{120}, W_{210}, W_{365}, W_{450} = adjusted weights at 120, 210, 365, and 450-day-old animals, respectively

*values are means of bi-trait analyses for the multi-trait model

curve in both models. This increase can be attributed to the increase of genetic variance along the growth curve, and also to the scale effect since weights are commonly of greater magnitude at adulthood. Similar results were reported in the literature (Nobre et al. 2003b; Meyer 2004).

In summary, according to Fischer et al. (2004), the variance estimates in advanced ages obtained through Legendre polynomial, mainly in the presence of low number of records, tend to be overestimated. This behaviour was observed in Figure 1 for all variance components. In order to verify if this increase in variance is really due to the use of Legendre polynomial, more research must be done by using other functions such as splines.

Direct heritability estimates (h_g^2) ranged from 0.09 to 0.28 and 0.15 to 0.39 for MTM and RRM, respectively (Table 3). Higher values were observed in advanced ages indicating that greater annual genetic gains could be achieved if selection is performed considering weights measured later in life. These results are in agreement with literature

(Garneiro et al. 2001; Araujo et al. 2006; Laureano et al. 2011; Souza et al. 2011; Silva et al. 2013). Maternal heritability estimates (h_m^2) obtained at 120, 210, 365, and 450 days of age were low, ranging from 0.01 to 0.03 and 0.08 to 0.11 for MTM and RRM, respectively (Table 3). In both models, heritability increased from pre-weaning to weaning phase, with a slight decrease after 365 days. However, this behaviour was persistent along the curve for RRM. It indicates that this model can continuously detect the point from which maternal effects stop acting or decrease. It cannot be done in MTM in which this information is discrete and restricts to ages in which weights were observed. Souza et al. (2011) and Silva et al. (2013) observed similar results, being the maximum estimates of h_m^2 from weaning to adult phase (± 400 days), and further decrease up to the end of the growth curve. These results also highlight the importance to take into account these heritability estimates on beef cattle breeding, especially during the growing phase.

Table 4. Direct genetic (above diagonal) and phenotypic (below diagonal) correlations via multi-trait and random regression models (in italics)

Weight(ages)	120 days	210 days	365 days	450 days
W_{120}	–	0.91 ± 0.38	0.94 ± 0.39	0.71 ± 0.29
		–0.33 ± 0.09	*–0.39 ± 0.09*	*–0.42 ± 0.13*
W_{210}	0.73 ± 0.24	–	0.94 ± 0.32	0.95 ± 0.41
	0.32 ± 0.08		*0.79 ± 0.12*	*0.80 ± 0.12*
W_{365}	0.40 ± 0.12	0.57 ± 0.12	–	0.91 ± 0.39
	0.22 ± 0.04	*0.60 ± 0.04*		*0.93 ± 0.19*
W_{450}	0.49 ± 0.13	0.55 ± 0.20	0.93 ± 0.39	–
	0.11 ± 0.02	*0.61 ± 0.12*	*0.82 ± 0.13*	

W_{120}, W_{210}, W_{365}, W_{450} = adjusted weights at 120, 210, 365, and 450-day-old animals, respectively

Maternal permanent environment variances were estimated as the proportion of increasing phenotypic variance. The values ranged from 0.07 to 0.11 and 0.02 to 0.08 for MTM and RRM, respectively (Table 3). Meyer (2005a) observed similar and increasing estimates throughout animal's life using random regression models. The residual variances estimated as proportion of phenotypic variance were from 0.60 to 0.79 and from 0.39 to 0.68 for MTM and RRM, respectively (Table 3). Studies in beef cattle also obtained similar estimates as those observed in the present study (Araujo et al. 2006; Laureano et al. 2011).

Estimates of genetic correlations $W_{120} \times W_{210}$, $W_{120} \times W_{365}$, and $W_{120} \times W_{450}$ via RRM were negative, varying from –0.42 to –0.33 (Table 4). Meyer (2005b) obtained similar results, in which negative estimates were observed between similar ages. These low and negative results may be due to problems arising from the polynomial function since correlations between these measures are predominantly positive, resulting from the cumulative sum of body weight gain during lifetime, creating structural dependence between them. These same correlations obtained by MTM were positive and high magnitude (from 0.71 to 0.94). Estimates of genetic correlations $W_{210} \times W_{365}$, $W_{210} \times W_{450}$, and $W_{365} \times W_{450}$ were positive and high magnitude for RRM (0.79 to 0.93) and MTM (0.91 to 0.95). The results are within the values range reported in literature (Sakaguti et al. 2002; Siqueira et al. 2003; Souza et al. 2011).

Phenotypic correlations obtained from RRM were low to medium magnitude (0.11 to 0.82) while from MTM were medium to high (0.40 to 0.93), and generally larger at closest ages. Meyer (2005a), Boligon et al. (2010), and Goncalves et

al. (2011) verified that correlations increased at closer ages.

Maternal genetic correlations presented similar estimates, medium to high magnitudes in both models, RRM (0.76 to 0.93) and MTM (0.74 to 0.93) (Table 5). These estimates are similar to those observed by Araujo et al. (2006) and Silva et al. (2013). In both models, maternal genetic correlations were above 0.90 between 120 × 210, 120 × 365, 210 × 365 days old, and similar to values obtained by Menezes et al. (2013), who observed values above 0.92. These authors explained that the same genes might influence maternal genetic effects at these ages.

The estimates of maternal permanent environment correlations between 120, 210, 365, and 450 days are presented in Table 5. The estimates were high magnitude, from 0.80 to 0.93 and from 0.86 to 0.96, respectively, for RRM and MTM. As expected, these correlations were smaller in distant ages. Garneiro et al. (2001), Meyer (2005b), and Mota et al. (2013) reported similar estimates. These authors stated that high values indicate that effects generated by the environment provided by the cow during the pre-weaning phase have an important role during the animal's life. In fact, it confirms the importance of cows with good maternal ability in beef cattle production systems.

In summary, results via MTM differed from those via RRM. This fact was expected due to pre-adjusted or non-adjusted data. This difference makes the statistical comparisons between these methodologies difficult, even from biological viewpoint. However, it is clear that random regression models may be a good alternative to Nellore breeding programs in order to identify the best age for selection and higher genetic gain based on the presented results.

Table 5. Maternal genetic (above diagonal) and maternal permanent environment (below diagonal) correlations via multi-trait and random regression models (in italics)

Weight$_{(ages)}$	120 days	210 days	365 days	450 days
W$_{120}$	–	0.93 ± 0.36 *0.91 ± 0.19*	0.89 ± 0.39 *0.86 ± 0.19*	0.74 ± 0.30 *0.76 ± 0.16*
W$_{210}$	0.95 ± 0.25 *0.91 ± 0.18*	–	0.91 ± 0.34 *0.93 ± 0.17*	0.79 ± 0.40 *0.80 ± 0.11*
W$_{365}$	0.94 ± 0.22 *0.92 ± 0.14*	0.96 ± 0.22 *0.93 ± 0.17*	–	0.80 ± 0.37 *0.89 ± 0.18*
W$_{450}$	0.86 ± 0.23 *0.80 ± 0.12*	0.93 ± 0.40 *0.91 ± 0.22*	0.94 ± 0.38 *0.90 ± 0.15*	–

W$_{120}$, W$_{210}$, W$_{365}$, W$_{450}$ = adjusted weights at 120, 210, 365, and 450-day-old animals, respectively

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CONCLUSION

The study presented perspectives for the use of RRM for genetic evaluation of growth traits in Brazilian Nellore cattle. In general, moderate heritability estimates were obtained for the majority of studied traits when using RRM. Additionally, the precision of these estimates was higher when using RRM instead of MTM. However, concerns about the variance components estimates in advanced ages via Legendre polynomial must be taken into account in future studies.

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