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# Covariance functions for body weight from birth to maturity in Nellore cows<sup>1</sup>

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**ABSTRACT:** The objective of this study was to estimate (co)variance functions using random regression models on Legendre polynomials for the analysis of repeated measures of BW from birth to adult age. A total of 82,064 records from 8,145 females were analyzed. Different models were compared. The models included additive direct and maternal effects, and animal and maternal permanent environmental effects as random terms. Contemporary group and dam age at calving (linear and quadratic effect) were included as fixed effects, and orthogonal Legendre polynomials of animal age (cubic regression) were considered as random covariables. Eight models with polynomials of third to sixth order were used to describe additive direct and maternal effects, and animal and maternal permanent environmental effects. Residual effects were modeled using 1 (i.e., assuming homogeneity of variances across

all ages) or 5 age classes. The model with 5 classes was the best to describe the trajectory of residuals along the growth curve. The model including fourth- and sixth-order polynomials for additive direct and animal permanent environmental effects, respectively, and third-order polynomials for maternal genetic and maternal permanent environmental effects were the best. Estimates of (co)variance obtained with the multi-trait and random regression models were similar. Direct heritability estimates obtained with the random regression models followed a trend similar to that obtained with the multi-trait model. The largest estimates of maternal heritability were those of BW taken close to 240 d of age. In general, estimates of correlation between BW from birth to 8 yr of age decreased with increasing distance between ages.

**Key words:** growth curve, longitudinal data, Nellore cattle, random regression

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## INTRODUCTION

The growth trajectory of beef cattle can be represented by points that associate BW with age. Body weights obtained along a time scale can be evaluated using random regression models. These models have some advantages over traditional multi-trait models [e.g., allow the inclusion of records that would normally be discarded; Meyer (2004)], describe in a continuous

manner the structure of covariances over time, and allow the estimation of breeding values for a trait at any age within the data interval (Albuquerque and Meyer, 2001; Tier and Meyer, 2004).

Random regression models have been widely used for the estimation of genetic parameters of growth traits in beef cattle. Some authors only considered records after 2 yr of age (Meyer, 1999; Arango et al., 2004; Nephaw, 2004), whereas others used BW records obtained from birth to weaning or to approximately 2 yr of age (Meyer, 2000, 2004, 2005). In Brazil, studies using random regression models include BW records of animals from birth to approximately 700 d of age (Albuquerque and Meyer, 2001, 2005; Nobre et al., 2003; Sakaguti et al., 2003). At present, there are not studies available that include BW at older ages, such as mature weight of cows.

The estimation of covariance functions including BW until adult age can be used for developing functions that permit selection to modify the shape of growth

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curves. Such functions would allow producers to select desired market point and select animals based on this choice, including records that would normally be discarded in a multi-trait approach (Meyer, 2004).

The objective of this paper was to identify the most adequate model to describe the changes of (co)variances

of BW with age, from birth to maturity, using (co) variance functions of different orders for additive direct and maternal genetic effects, and animal and maternal permanent environmental effects.

## MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database (Nellore Cattle Breeding Program).

### Data

The data analyzed were obtained from the Nellore Brazil Program, including animals from 8 herds located in São Paulo State. This genetic evaluation program started in 1987.

Animals participating in the program are weighed every 90 d from birth to 550 d of age, and those remaining in the herds for reproduction are weighed routinely in the same interval. Births occurred throughout the year but were more frequent in spring and summer. Animals were weaned at 240 d of age, on average. Animals were included in the analyses if they were products of AI (corresponding to 96% of the total data), raised on pastures without supplementation, and nursed by their biological mothers.

The contemporary group for records from birth to 3 yr of age was defined including animals born on the same farm, year, and season of birth, and belonging to the same group of age at recording (birth and every 45 d of age). As a result, the age variation within contemporary group was not larger than 45 d. The contemporary group for records taken after 3 yr of age was defined by farm, year and season of birth, and year and season of recording. Body weight records out of the range given by the mean of the contemporary group  $\pm$  3 SD were excluded. Contemporary groups with less than 8 animals were also excluded, leaving 2,693 groups. All animals had at least 5 BW records. On average, there were 10.07 records per animal, with a maximum of 43. There were 813, 2,133, 1,243, 1,138, 528, 282, and 2,008 animals with 5, 6, 7, 8, 9, 10, and 11 to 43 BW records, in that order. This corresponds to 63.83, 48.57, and 34.60% animals with at least 7, 8, and 9 records, respectively.

Regression was on Legendre polynomials of animal age at recording, from birth to 2,920 d. The data set analyzed had 82,064 records from birth to 8 yr of age of 8,145 females, daughters of 470 sires and 5,186 dams. The relationship matrix contained information of all generations available and had 12,596 animals.

### Analysis

The analyses were performed using a fourth-order Legendre polynomials to model trends in the population mean. Four random effects modeled by polynomials of different orders ( $k$ ) were considered, resulting in 8 different models. Quadratic and cubic polynomials were used for additive direct ( $a$ ), maternal genetic ( $m$ ), and maternal permanent environmental effects ( $c$ ), i.e.,  $k_a = k_m = k_c = 3$  and 4, respectively. Because environmental effects are separated from residual effects by using multiple measures over time, environmental effects can be estimated for an animal at any given age within the range of the data. These animal environmental effects ( $p$ ), also called animal permanent environmental effects, were modeled using quadratic, cubic, quartic, and quintic polynomials (i.e.,  $k_p = 3, 4, 5$ , and 6, respectively). Residual variances were modeled considering one (i.e., assuming homogeneity of variances across all ages) or 5 age classes divided as follows: 0, 1 to 216, 217 to 660, 661 to 960, and 961 to 2920 d of age. In addition, contemporary group was included as a fixed effect and dam age at calving (in days) as a covariate (linear and quadratic effects). The random regression model can be described as

$$y_{ij} = F + \sum_{m=0}^{k_b-1} \beta_m \phi_m(t_i) + \sum_{m=0}^{k_a-1} \alpha_{jm} \phi_m(t_{ij}) + \sum_{m=0}^{k_m-1} \gamma_{jm} \phi_m(t_{ij}) + \sum_{m=0}^{k_p-1} \delta_{jm} \phi_m(t_{ij}) + \sum_{m=0}^{k_c-1} \rho_{jm} \phi_m(t_{ij}) + E_{ij},$$

where  $y_{ij}$  is the BW at  $i$ th age of animal  $j$ ;  $F$  is the set of fixed effects;  $\beta_m$  are regression coefficients to model the average trajectory of the population;  $\phi_m(t_i)$  is the  $m$ th Legendre polynomial according to age of the animal ( $t_i$ );  $\phi_m(t_{ij})$  are regression functions describing the trajectories of each individual  $j$  according to age ( $t_i$ ) for the following random effects: direct genetic, maternal genetic, animal permanent environmental, and maternal permanent envi-

ronmental effects;  $\alpha_{jm}$ ,  $\gamma_{jm}$ ,  $\delta_{jm}$ ,  $\rho_{jm}$  are individual random coefficients of direct and maternal genetic, and animal and maternal permanent environmental effects;  $kb$ ,  $ka$ ,  $km$ ,  $kp$ , and  $kc$  are the order of polynomials used for the effects described above, and  $E_{ij}$  is a random error associated with each age  $i$  of animal  $j$ . The matrix representation of the model is

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{W}_1\mathbf{p} + \mathbf{W}_2\mathbf{c} + \mathbf{e},$$

where  $\mathbf{y}$  is the vector of observations,  $\mathbf{b}$  is the vector of fixed effects (including  $F_{ij}$  and  $\beta_m$ ),  $\mathbf{a}$  is the vector of random coefficients for additive direct effects,  $\mathbf{m}$  is the vector of random coefficients for additive maternal effects,  $\mathbf{p}$  is the vector of random coefficients for animal environmental effects,  $\mathbf{c}$  is the vector of random coefficients for maternal permanent environmental effects,  $\mathbf{e}$  is the vector of residual effects, and  $\mathbf{X}$ ,  $\mathbf{Z}_1$ ,  $\mathbf{Z}_2$ ,  $\mathbf{W}_1$ , and  $\mathbf{W}_2$  are the corresponding incidence matrices. The model is based on the following assumptions:

$$\begin{bmatrix} \mathbf{y} \\ \mathbf{a} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{c} \end{bmatrix} = \begin{bmatrix} \mathbf{X}\mathbf{b} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} = \mathbf{V} \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{K}_a \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{K}_m \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{K}_p \otimes \mathbf{I}_{N_A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{K}_c \otimes \mathbf{I}_{N_M} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix},$$

where  $\mathbf{K}_a$ ,  $\mathbf{K}_m$ ,  $\mathbf{K}_p$ , and  $\mathbf{K}_c$  are (co)variance matrices between random regression coefficients for additive direct, additive maternal, and animal and maternal permanent environmental effects, respectively;  $\mathbf{A}$  is the relationship matrix;  $\mathbf{I}$  is an identity matrix;  $N_A$  is the number of animals for which records are available;  $N_M$  is the number of dams;  $\otimes$  is the Kronecker product between matrices; and  $\mathbf{R}$  is a block diagonal matrix containing residual variances. Correlations between random regression coefficients for different effects were set to zero. On the basis of the random regression model and assumptions presented, the mixed model equations are

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}_1 & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z}_2 & \mathbf{X}'\mathbf{R}^{-1}\mathbf{W}_1 & \mathbf{X}'\mathbf{R}^{-1}\mathbf{W}_2 \\ \mathbf{Z}_1'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}_1'\mathbf{R}^{-1}\mathbf{Z}_1 + \mathbf{K}_a \otimes \mathbf{A}^{-1} & \mathbf{Z}_1'\mathbf{R}^{-1}\mathbf{Z}_2 & \mathbf{Z}_1'\mathbf{R}^{-1}\mathbf{W}_1 & \mathbf{Z}_1'\mathbf{R}^{-1}\mathbf{W}_2 \\ \mathbf{Z}_2'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}_2'\mathbf{R}^{-1}\mathbf{Z}_1 & \mathbf{Z}_2'\mathbf{R}^{-1} + \mathbf{K}_m \otimes \mathbf{A} & \mathbf{Z}_2'\mathbf{R}^{-1}\mathbf{W}_1 & \mathbf{Z}_2'\mathbf{R}^{-1}\mathbf{W}_2 \\ \mathbf{W}_1'\mathbf{R}^{-1}\mathbf{X} & \mathbf{W}_1'\mathbf{R}^{-1}\mathbf{Z}_1 & \mathbf{W}_1'\mathbf{R}^{-1}\mathbf{Z}_2 & \mathbf{W}_1'\mathbf{R}^{-1} + \mathbf{K}_p \otimes \mathbf{I}_{N_A} & \mathbf{W}_1'\mathbf{R}^{-1}\mathbf{W}_2 \\ \mathbf{W}_2'\mathbf{R}^{-1}\mathbf{X} & \mathbf{W}_2'\mathbf{R}^{-1}\mathbf{Z}_1 & \mathbf{W}_2'\mathbf{R}^{-1}\mathbf{Z}_2 & \mathbf{W}_2'\mathbf{R}^{-1}\mathbf{W}_1 & \mathbf{W}_2'\mathbf{R}^{-1} + \mathbf{K}_c \otimes \mathbf{I}_{N_M} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{a} \\ \mathbf{m} \\ \mathbf{p} \\ \mathbf{c} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}_1'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}_2'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{W}_1'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{W}_2'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}.$$

The covariance components were estimated by REML using the WOMBAT software (Meyer, 2006). The models with polynomials of different orders were compared using the following criteria:

Akaike information criterion (**AIC**; Akaike, 1974),  $AIC = -2\log L + 2p$ , where  $L$  is the likelihood and  $p$  is the number of parameters;

Schwarz Bayesian information criterion (**BIC**, Schwarz, 1978),  $BIC = -2\log L + p\log(N - r)$ , where  $N$  is the number of observations and  $r$  is rank of the incidence matrix for fixed effects;

information-theoretic measure of complexity (**ICOMP**, Bozdogan, 2000),  $ICOMP = -2\log L + 2[C_1(K_{Model})]$ ,

where  $C_1(K_{Model}) = C_1(K_a) + C_1(K_m) + C_1(K_p) + C_1(K_c)$ , and  $C_1(K_{a,m,p \text{ and } c}) = \frac{p}{2} \log \left[ \frac{\text{trace}(K)}{p} \right] - \frac{1}{2} \log |K|$ ;

$K_a$  and  $K_m$  are additive direct and maternal (co)variance matrices, respectively;  $K_p$  and  $K_c$  are animal and maternal permanent environmental (co)variance matrices.

The AIC and BIC test the fit of the model considering the number of parameters and can be used to compare models with the same fixed effects but different (co)variance structures. The BIC attributes a greater penalty for additional parameters than AIC does. The ICOMP criterion relates the complexity of the model to the degree of interdependence between its parameters. Smaller values of AIC, BIC, and ICOMP are preferred.

To compare the results obtained with the random regression models and a standard analysis, the same data set was analyzed with a multi-trait model. The traits evaluated were birth weight, weaning weight, BW at 550 d, and BW at 2, 3, and 5 yr of age. For all traits, genetic additive direct and maternal, and maternal permanent environmental were considered as random effects. Contemporary group (farm, year, and season of birth) was included in

the model as a fixed effect. Linear and quadratic effects of age of the animal at recording (except for birth weight), and dam age at calving were included as covariables.

Next, the specification of polynomial order in different random regression models follows the pattern  $Mk_a k_m k_p k_c r$ , which means: the order of the covariance function for additive direct effect ( $k_a$ ), additive maternal effect ( $k_m$ ), animal permanent environmental effect ( $k_p$ ), maternal permanent environmental effect ( $k_c$ ), and structure of residual variances ( $r$ ).

## RESULTS AND DISCUSSION

The number of records in each age and the corresponding mean BW are shown in Figure 1. The BW increased with age, as expected. After weaning, the growth velocity decreased and a linear tendency was observed after 800 d of age. In addition, a strong decrease in the number of records was observed after 600 d of age, suggesting the occurrence of selection at young ages. Figure 2 shows the SD and CV for records from birth to 8 yr of age. The SD followed the growth trend, especially at the beginning of the data interval. However, the CV remained almost constant up to 700 d of age and showed greater oscillations at subsequent ages. This indicates a strong correlation between the mean and the SD.

A summary of results from analysis with random regression models is shown in Table 1. When maternal permanent environmental was considered, the model assuming homogeneity of residual variances presented the worst fit. This indicates that residual variances are increasing along the trajectory. In addition to the models presented in Table 1, other models including a larger number of parameters for random effects were tested. However, the increase in the polynomial order impaired the convergence of analysis. Convergence problems were greater when 1 or more eigenvalues of the (co)variance matrices were close to zero. In some cases, the process stabilized at a local maximum and the global maximum could not be reached. Using mature weight re-

cords of females, Meyer (1999) and Arango et al. (2004) reported the same problem (i.e., convergence could not be reached when models included a large number of parameters). Other authors that used random regression models for the evaluation of BW in beef cattle also reported lack of convergence when using high-degree polynomials and inconsistent fitting along the growth curve, especially at the boundaries (Sakaguti et al., 2003; Meyer, 2005).

According to AIC, model M4454\_5 that includes 50 parameters gave the best fit to the data. On the other hand, BIC and ICOMP indicated that model M4363\_5, including a total of 48 parameters, was sufficient to model variance in the data. The more parsimonious specification, with polynomials of order 3 for genetic and environmental maternal effects, resulted in the same fit as M4454\_5. The estimates of (co)variance components between random regression coefficients, and between them, and the matrix eigenvalues obtained with models M4363\_5 and M4454\_5 are shown in Table 2. There is evidence that model M4454\_5 is overfitted given the near-zero eigenvalues for additive direct and both maternal effects. For all of the random effects, the greatest variance was at the intercept. The correlations between the intercept and the linear regression coefficients were positive for both models. On the other hand, the correlations between the intercept and the quadratic regression coefficients were negative for all effects. Similar results were reported by Meyer (2001b) and Albuquerque and Meyer (2001) for

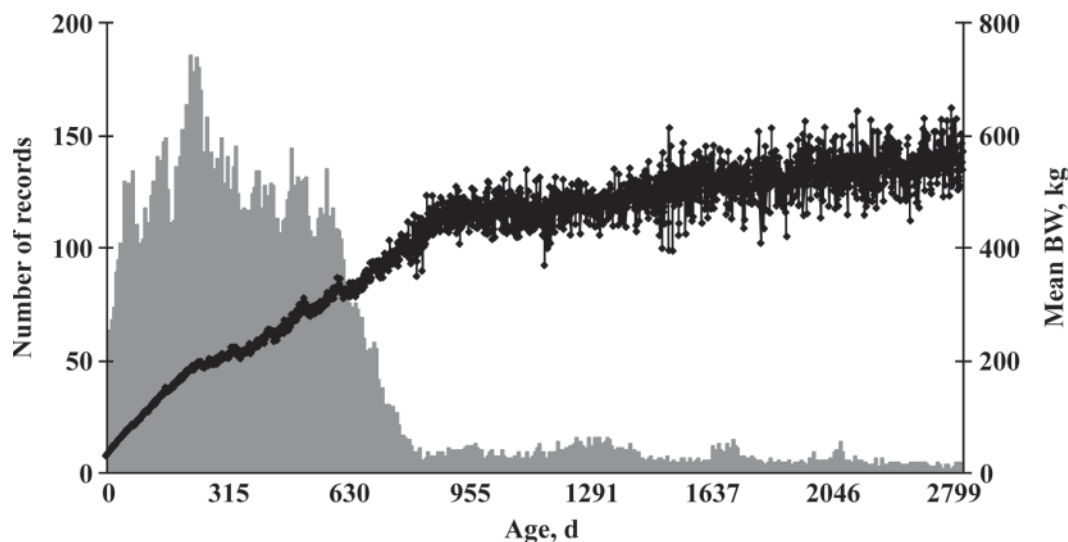
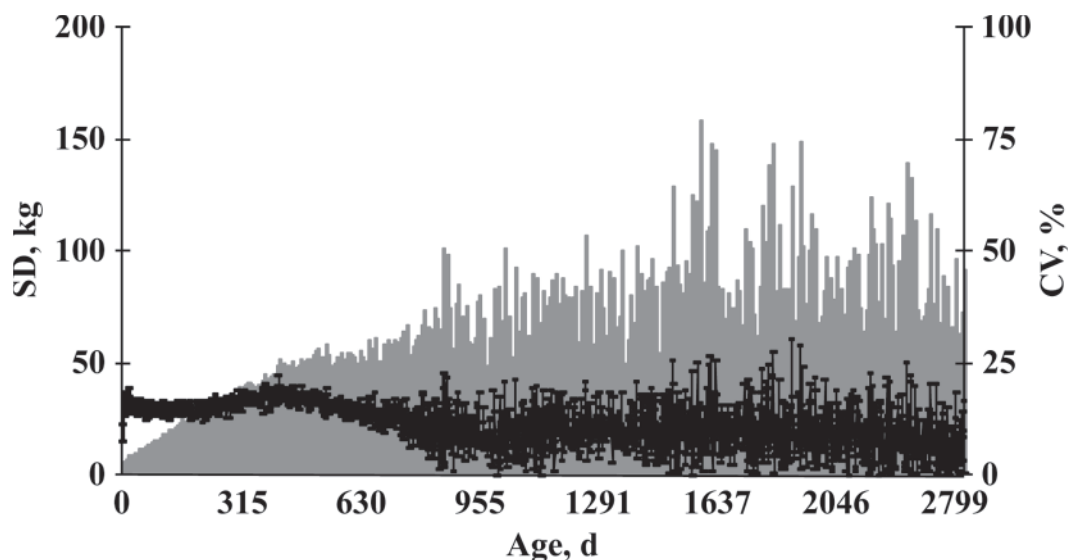


Figure 1. Number of records (gray bars) and mean BW (black lines) according to age.





**Figure 2.** Standard deviations (gray bars) and CV (black lines) for BW according to age.

BW from birth to weaning and from birth to 630 d of age, respectively. The variance estimates for BW from birth to adult age obtained with models M4363\_5 and M4454\_5, and with the multi-trait model, are shown in Figure 3. Phenotypic variances strongly increased until 2,000 d of age, and smaller differences were observed thereafter. Meyer (2001a, 2005) reported greater phenotypic variances estimates using random regression models for BW at 250 d of age of Australian cattle and 820 d of age of Angus cattle, respectively. Using random regression models to analyze BW from 2 to 8 yr of age of Angus, Hereford, and  $F_1$  females, Arango et al. (2004) also reported variance estimates increasing with age, but estimates at older ages were different from those obtained using standard 2-trait models.

The estimates of additive direct variance obtained with different models were similar (Figure 3). Greater estimates of animal permanent environmental variance were obtained with model M4363\_5 than with model M4454\_5. Also, after increasing the order of polynomials for animal environmental effect from 5 to 6, a small increase in the additive direct variance, especially at intermediate ages, was observed. Animal environment variance increased with age. This trend was stronger

before 800 d of age, and a faster increase was observed with model M4363\_5. This difference between models can be observed in phenotypic variance estimates as well. The random regression models differ mainly with respect to the maternal variances (Figure 3). By using fourth-order polynomials for maternal effects, greater variance estimates were obtained for maternal permanent environmental. The maternal variance components were closer to those obtained with the multi-trait model when lower order polynomials were used for maternal effects. The greatest maternal variance was observed close to 260 d of age.

Some studies using random regression models for BW at different ages showed large increases of variance for BW at extreme ages (Albuquerque and Meyer, 2001; Nobre et al., 2003; Meyer, 2005). Random regression models with Legendre polynomials are poorly fit at extremes where small amounts of data are available (Meyer, 2001b; Iwaisaki et al., 2005). One alternative to fitting Legendre polynomials could be the use of certain functions, such as spline functions (Huisman et al., 2002; Meyer, 2005). Recently, in several studies, linear spline functions have been used to estimate covariance functions for growth in beef cattle (Bohmanova et al.,

**Table 1.** Order of fit of additive direct ( $k_a$ ) and maternal ( $k_m$ ) effects and animal ( $k_p$ ) and maternal ( $k_c$ ) permanent environmental effects, number of residual classes ( $r$ ), number of parameters ( $np$ ), log-likelihood value ( $\log$ ), Akaike information criterion (AIC), Bayesian information criterion (BIC), and information complexity (ICOMP)

| Model   | $k_a$ | $k_m$ | $k_p$ | $k_c$ | $r$ | $np$ | Log      | AIC     | BIC     | ICOMP   |
|---------|-------|-------|-------|-------|-----|------|----------|---------|---------|---------|
| M3333_1 | 3     | 3     | 3     | 3     | 1   | 25   | -249,080 | 498,212 | 498,443 | 498,177 |
| M3330_5 | 3     | 3     | 3     | 0     | 5   | 23   | -256,338 | 512,723 | 512,936 | 512,683 |
| M3333_5 | 3     | 3     | 3     | 3     | 5   | 29   | -236,236 | 472,531 | 472,799 | 472,483 |
| M3343_5 | 3     | 3     | 4     | 3     | 5   | 33   | -230,463 | 460,993 | 461,300 | 460,942 |
| M3353_5 | 3     | 3     | 5     | 3     | 5   | 38   | -229,871 | 459,818 | 460,171 | 459,739 |
| M4453_5 | 4     | 4     | 5     | 3     | 5   | 46   | -223,209 | 446,419 | 446,938 | 458,709 |
| M4363_5 | 4     | 3     | 6     | 3     | 5   | 48   | -221,382 | 442,860 | 443,305 | 453,830 |
| M4454_5 | 4     | 4     | 5     | 4     | 5   | 50   | -221,378 | 442,856 | 443,320 | 453,857 |

**Table 2.** Estimates of variances (diagonal), covariances (below the diagonal), and correlations (above the diagonal) between random regression coefficients and eigenvalues ( $\lambda$ ) of the (co)variance matrix obtained with models M4363\_5 and M4454\_5 for direct and maternal genetic effects and animal and maternal permanent environmental effects

| Effect                           | Order of fit | 0      | 1     | 2      | 3     | 4     | 5     | $\lambda$ |
|----------------------------------|--------------|--------|-------|--------|-------|-------|-------|-----------|
| <b>M4363_5</b>                   |              |        |       |        |       |       |       |           |
| Additive direct                  | 0            | 285.43 | 0.78  | -0.34  | 0.03  |       |       | 317.85    |
|                                  | 1            | 86.79  | 43.45 | -0.16  | -0.25 |       |       | 21.26     |
|                                  | 2            | -37.28 | -4.36 | 16.60  | 0.47  |       |       | 9.40      |
|                                  | 3            | 1.48   | -4.87 | 5.71   | 9.03  |       |       | 2.46      |
| Additive maternal                | 0            | 72.67  | 0.86  | -0.28  |       |       |       | 80.04     |
|                                  | 1            | 15.92  | 4.74  | -0.15  |       |       |       | 1.36      |
|                                  | 2            | -16.73 | -3.26 | 3.98   |       |       |       | 0.27      |
| Animal permanent environmental   | 0            | 200.77 | 0.79  | -0.35  | 0.04  | 0.01  | -0.11 | 571.32    |
|                                  | 1            | 99.36  | 86.68 | 0.12   | -0.03 | -0.23 | 0.13  | 94.46     |
|                                  | 2            | -2.54  | 19.39 | 34.95  | -0.48 | -0.26 | 0.33  | 42.18     |
|                                  | 3            | 1.51   | -2.89 | -9.17  | 13.07 | 0.52  | -0.04 | 31.19     |
|                                  | 4            | 2.65   | -2.48 | -1.71  | 7.70  | 12.63 | -0.61 | 10.72     |
| Maternal permanent environmental | 5            | -1.42  | 10.47 | 19.93  | -1.06 | -7.65 | 20.74 | 0.08      |
|                                  | 0            | 34.96  | 0.98  | -0.63  |       |       |       | 14.01     |
|                                  | 1            | 9.79   | 6.52  | -0.45  |       |       |       | 3.74      |
|                                  | 2            | -6.69  | -1.19 | 2.28   |       |       |       | 0.19      |
| <b>M4454_5</b>                   |              |        |       |        |       |       |       |           |
| Additive direct                  | 0            | 293.41 | 0.84  | -0.46  | 0.04  |       |       | 308.07    |
|                                  | 1            | 108.39 | 68.49 | -0.03  | -0.09 |       |       | 33.30     |
|                                  | 2            | -40.64 | -1.03 | 22.26  | 0.67  |       |       | 9.49      |
|                                  | 3            | 0.44   | -1.85 | 8.23   | 6.69  |       |       | 0.01      |
| Additive maternal                | 0            | 49.89  | 0.63  | -0.90  | -0.66 |       |       | 47.03     |
|                                  | 1            | 1.93   | 8.77  | 0.48   | 0.71  |       |       | 5.30      |
|                                  | 2            | -4.84  | 1.13  | 2.03   | 0.05  |       |       | 0.47      |
|                                  | 3            | -19.8  | 2.67  | 0.34   | 1.07  |       |       | 0.00      |
| Animal permanent environmental   | 0            | 207.56 | 0.80  | -0.36  | 0.08  | -0.10 |       | 493.65    |
|                                  | 1            | 74.97  | 87.45 | 0.01   | -0.11 | 0.22  |       | 56.92     |
|                                  | 2            | -4.27  | 16.69 | 37.06  | -0.15 | -0.39 |       | 50.48     |
|                                  | 3            | 9.68   | -3.27 | -14.76 | 17.55 | -0.24 |       | 21.86     |
| Maternal permanent environmental | 4            | -1.21  | 8.08  | -1.11  | -6.05 | 9.28  |       | 4.28      |
|                                  | 0            | 34.26  | 0.33  | -0.48  | -0.09 |       |       | 47.03     |
|                                  | 1            | 1.93   | 1.00  | 0.66   | 0.71  |       |       | 5.30      |
|                                  | 2            | -4.84  | 1.13  | 2.90   | 0.05  |       |       | 0.12      |
|                                  | 3            | -19.80 | 2.67  | 0.34   | 4.16  |       |       | 0.00      |

2005; Iwaisaki et al., 2005; Meyer, 2005; Robbins et al., 2005). Compared with Legendre polynomials, a model applying linear spline functions is easier to set up, present superior numerical properties, and is less susceptible problems at the extreme of the growth curve (Arango et al., 2004; Iwaisaki et al., 2005; Meyer, 2005).

The direct heritability estimates obtained in all analysis showed the same trend. However, slightly greater estimates were obtained with random regression models (Figure 4). The estimates obtained with the multi-trait model ranged from 0.25 (birth weight) to 0.35 (BW at 5 yr). Estimates obtained with model M4363\_5 increased from birth (0.34) to 550 d of age (0.42) and remained constant up to 8 yr of age (0.39). Several studies reported a decrease in direct heritability estimates of BW after birth, followed by increases after weaning (Albuquerque and Meyer, 2001; Meyer, 2001a; Dias et al., 2006). Analyzing BW up to adult age, Arango et al. (2004) reported direct heritability estimates ranging from 0.38 (3 yr of age) to 0.78 (7 yr of age). Meyer (1999) also observed greater variation in direct

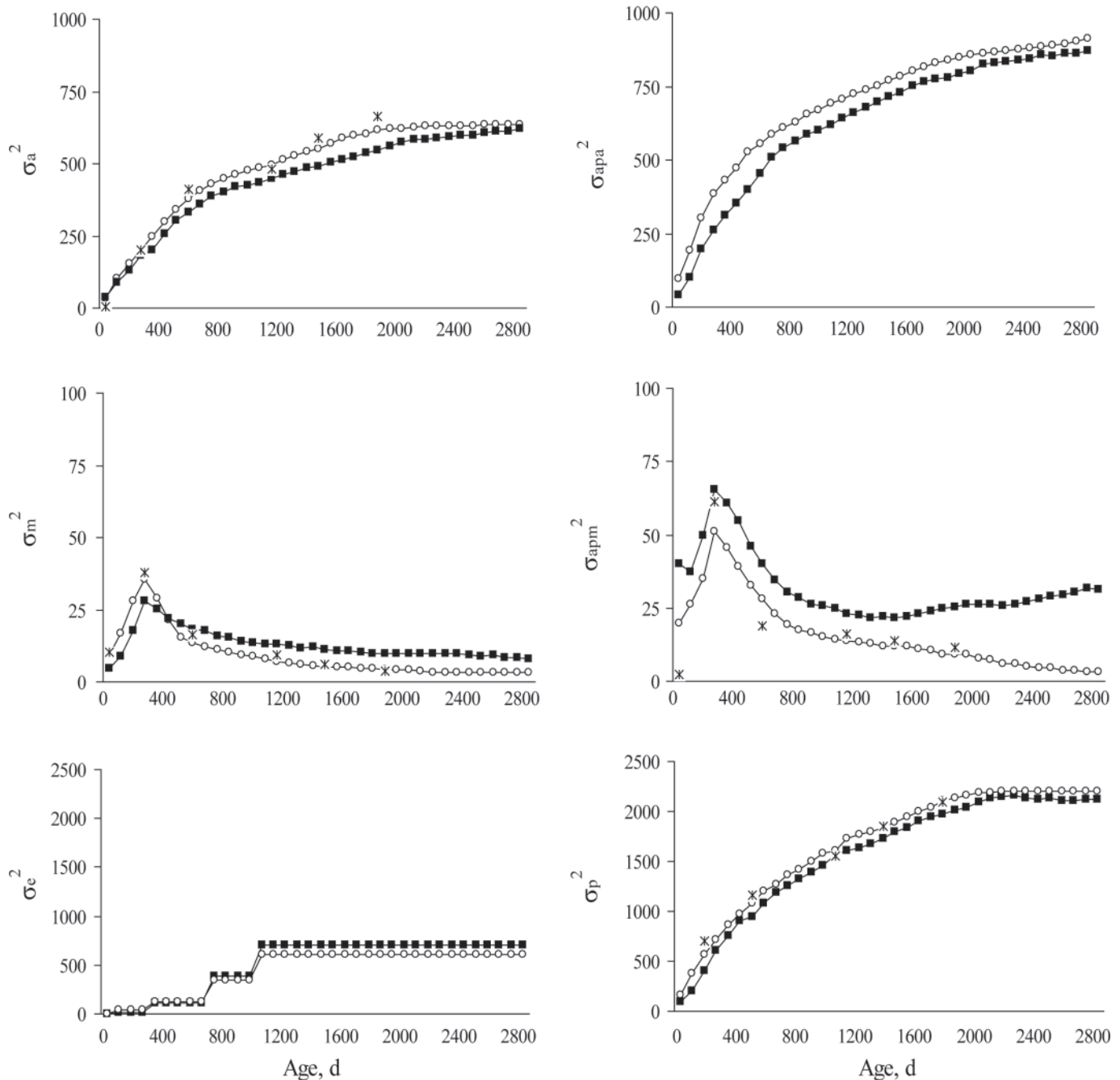
heritability estimates at the boundaries of the age interval, 0.57 and 0.42 (2 yr of age) and 0.37 and 0.49 (10 yr of age) for Polled Hereford and Wokalup females, respectively.

Animal permanent environmental variances as part of phenotypic variances presented smaller variations when model M4363\_5 was used (Figure 4). The permanent environmental variances increased from birth (0.51) to approximately 120 d of age (0.53), followed by a small reduction at about 300 d of age. After that, it tended to increase slightly until the end of the curve. Nephawe (2004) reported estimates of animal environmental effect variances as a proportion of the total variance ranging from 0.30 to 0.42 in a study with Bonsmara females from 2 to 11 yr of age. The author also reported greater variation at the bounds. The maternal heritability estimates from all analysis of weaning weight were similar (Figure 4). The estimates obtained with random regression (model M4363\_5) increased from birth (0.03) to 240 d of age (0.09), followed by a decrease at later ages. However, a greater maternal heritability of

weaning weight was obtained in the multi-trait analysis (0.13). In Brazil, a similar trend was reported by Albuquerque and Meyer (2001), Nobre et al. (2003), and Dias et al. (2006) for maternal heritability estimates in Zebu animals from birth to 630, 683, and 550 d of age, respectively. A great maternal influence until weaning has been reported in Nellore cattle. Greater response to selection for maternal ability can be expected if selection emphasizes greater BW around weaning age. The estimates of maternal permanent environmental variance as part of total variance presented the same trend in random regression and multi-trait analyses,

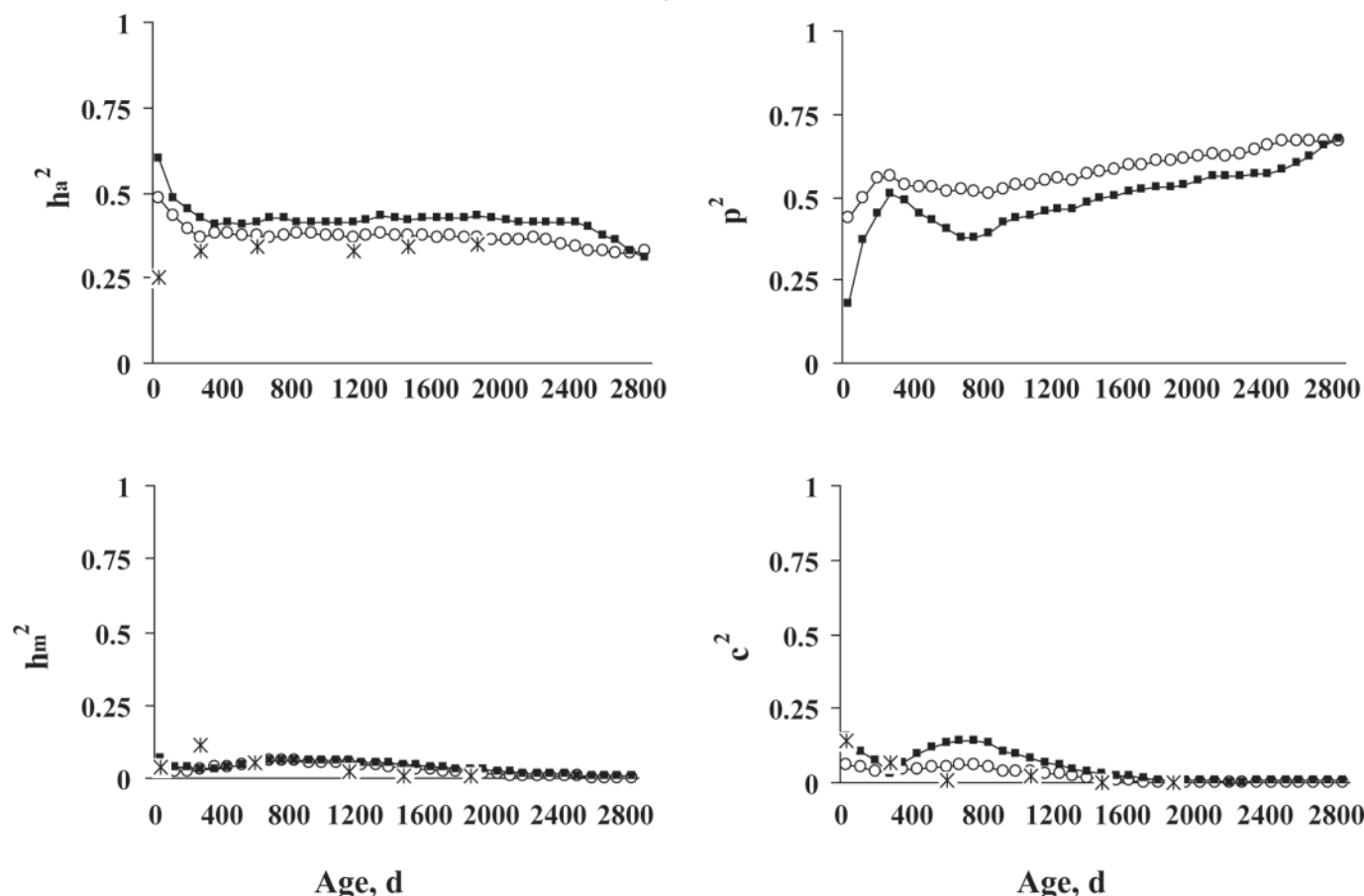
except for the beginning of the growth curve (Figure 4). The estimates obtained with model M4363\_5 decreased from 0.15 at birth to 0.06 at 120 d of age and remained constant thereafter. These results differ from those reported for Nellore cattle by Albuquerque and Meyer (2001), who observed a constant pattern in maternal permanent environmental variance estimates in spite of age.

The direct and maternal genetic correlation estimates between BW from birth to adult age obtained with model M4363\_5 are shown in Table 3. The genetic correlation estimates decreased when distance between



**Figure 3.** Estimates of additive direct ( $\sigma_a^2$ ), additive maternal ( $\sigma_m^2$ ), animal permanent environmental ( $\sigma_{apa}^2$ ), maternal permanent environmental ( $\sigma_{apm}^2$ ), and residual ( $\sigma_e^2$ ) and phenotypic ( $\sigma_p^2$ ) variances obtained with models M4363\_5 (○) and M4454\_5 (■) and with multivariate analysis (\*).





**Figure 4.** Direct ( $h_a^2$ ) and maternal ( $h_m^2$ ) heritability estimates, and animal ( $p^2$ ) and maternal ( $c^2$ ) variance estimates as proportions of phenotypic variances obtained with models M4363\_5 (○) and M4454\_5 (■) and with multivariate analysis (✕).

records increased. The genetic correlations were greater than 0.5 at most ages. Similar estimates, varying from 0.43 to 0.88, were described by Boligon et al. (2009) for the same data using a multi-trait model. These results suggest that selection for greater BW at any age should increase female mature weights. The later the selection is performed, the greater the response in mature weight. Selection is performed using BW from weaning to 550

d of age, mainly. This might increase the adult size of cows, which is not always desired. Arango et al. (2004) also reported strong genetic correlations between BW from 840 to 2,160 d of age (close to 0.84) and between 2,160 and 3,090 d of age (close to 0.90). Nephawe (2004) reported genetic correlation estimates greater than 0.82 for BW from 2 to 11 yr of age. Meyer (1999) obtained genetic correlation estimates close to 1 between BW af-

**Table 3.** Estimates of additive direct (above the diagonal) and additive maternal (below the diagonal) correlations for BW from birth to adult age obtained with model M4363\_5<sup>1</sup>

| BW    | BWt  | W120 | W240 | W365 | W540 | W730 | W1095 | W1460 | W1825 | W2190 | W2555 | W2920 |
|-------|------|------|------|------|------|------|-------|-------|-------|-------|-------|-------|
| BWt   | —    | 0.79 | 0.71 | 0.68 | 0.60 | 0.54 | 0.50  | 0.47  | 0.45  | 0.40  | 0.39  | 0.37  |
| W120  | 0.77 | —    | 0.81 | 0.70 | 0.61 | 0.61 | 0.57  | 0.52  | 0.54  | 0.51  | 0.51  | 0.50  |
| W240  | 0.70 | 0.79 | —    | 0.83 | 0.64 | 0.62 | 0.62  | 0.58  | 0.56  | 0.50  | 0.49  | 0.50  |
| W365  | 0.66 | 0.88 | 0.87 | —    | 0.85 | 0.78 | 0.74  | 0.62  | 0.60  | 0.60  | 0.58  | 0.57  |
| W540  | 0.58 | 0.66 | 0.67 | 0.79 | —    | 0.86 | 0.75  | 0.64  | 0.66  | 0.63  | 0.62  | 0.60  |
| W730  | 0.45 | 0.51 | 0.54 | 0.66 | 0.81 | —    | 0.81  | 0.65  | 0.63  | 0.64  | 0.62  | 0.61  |
| W1095 | 0.40 | 0.40 | 0.45 | 0.57 | 0.67 | 0.79 | —     | 0.85  | 0.78  | 0.78  | 0.69  | 0.64  |
| W1460 | 0.31 | 0.33 | 0.32 | 0.50 | 0.56 | 0.57 | 0.79  | —     | 0.84  | 0.79  | 0.69  | 0.65  |
| W1825 | 0.24 | 0.29 | 0.30 | 0.51 | 0.52 | 0.50 | 0.77  | 0.84  | —     | 0.87  | 0.89  | 0.91  |
| W2190 | 0.23 | 0.28 | 0.29 | 0.53 | 0.56 | 0.56 | 0.76  | 0.76  | 0.87  | —     | 0.92  | 0.93  |
| W2555 | 0.22 | 0.23 | 0.20 | 0.48 | 0.51 | 0.51 | 0.69  | 0.74  | 0.79  | 0.90  | —     | 0.93  |
| W2920 | 0.21 | 0.20 | 0.22 | 0.47 | 0.53 | 0.52 | 0.69  | 0.73  | 0.87  | 0.91  | 0.92  | —     |

<sup>1</sup>Birth weight (BWt) and BW at 120 (W120); 240 (W240); 365 (W365); 540 (W540); 730 (W730); 1,095 (W1095); 1,460 (W1460); 1,825 (W1825); 2,190 (W2190); 2,555 (W2555); and 2,920 (W2920) d of age.

**Table 4.** Estimates of animal environmental (above the diagonal) and maternal permanent environmental (below the diagonal) correlations for BW from birth to adult age obtained with model M4363\_5<sup>1</sup>

| BW    | BWt  | W120 | W240 | W365 | W540 | W730 | W1095 | W1460 | W1825 | W2190 | W2555 | W2920 |
|-------|------|------|------|------|------|------|-------|-------|-------|-------|-------|-------|
| BWt   | —    | 0.79 | 0.67 | 0.65 | 0.60 | 0.47 | 0.40  | 0.41  | 0.36  | 0.34  | 0.35  | 0.32  |
| W120  | 0.49 | —    | 0.73 | 0.71 | 0.69 | 0.58 | 0.49  | 0.50  | 0.48  | 0.49  | 0.47  | 0.45  |
| W240  | 0.56 | 0.67 | —    | 0.73 | 0.70 | 0.66 | 0.64  | 0.63  | 0.65  | 0.59  | 0.60  | 0.54  |
| W365  | 0.54 | 0.62 | 0.63 | —    | 0.72 | 0.69 | 0.68  | 0.70  | 0.66  | 0.64  | 0.65  | 0.60  |
| W540  | 0.49 | 0.60 | 0.54 | 0.58 | —    | 0.64 | 0.65  | 0.60  | 0.58  | 0.56  | 0.53  | 0.52  |
| W730  | 0.47 | 0.52 | 0.50 | 0.60 | 0.59 | —    | 0.78  | 0.77  | 0.69  | 0.68  | 0.64  | 0.62  |
| W1095 | 0.39 | 0.45 | 0.48 | 0.53 | 0.54 | 0.58 | —     | 0.79  | 0.78  | 0.69  | 0.67  | 0.66  |
| W1460 | 0.38 | 0.40 | 0.45 | 0.41 | 0.50 | 0.56 | 0.58  | —     | 0.80  | 0.81  | 0.78  | 0.80  |
| W1825 | 0.34 | 0.47 | 0.46 | 0.43 | 0.48 | 0.55 | 0.56  | 0.61  | —     | 0.84  | 0.81  | 0.82  |
| W2190 | 0.35 | 0.32 | 0.44 | 0.48 | 0.49 | 0.49 | 0.54  | 0.62  | 0.65  | —     | 0.88  | 0.87  |
| W2555 | 0.30 | 0.34 | 0.37 | 0.45 | 0.40 | 0.47 | 0.50  | 0.59  | 0.67  | 0.69  | —     | 0.90  |
| W2920 | 0.29 | 0.31 | 0.39 | 0.41 | 0.41 | 0.48 | 0.49  | 0.57  | 0.64  | 0.68  | 0.71  | —     |

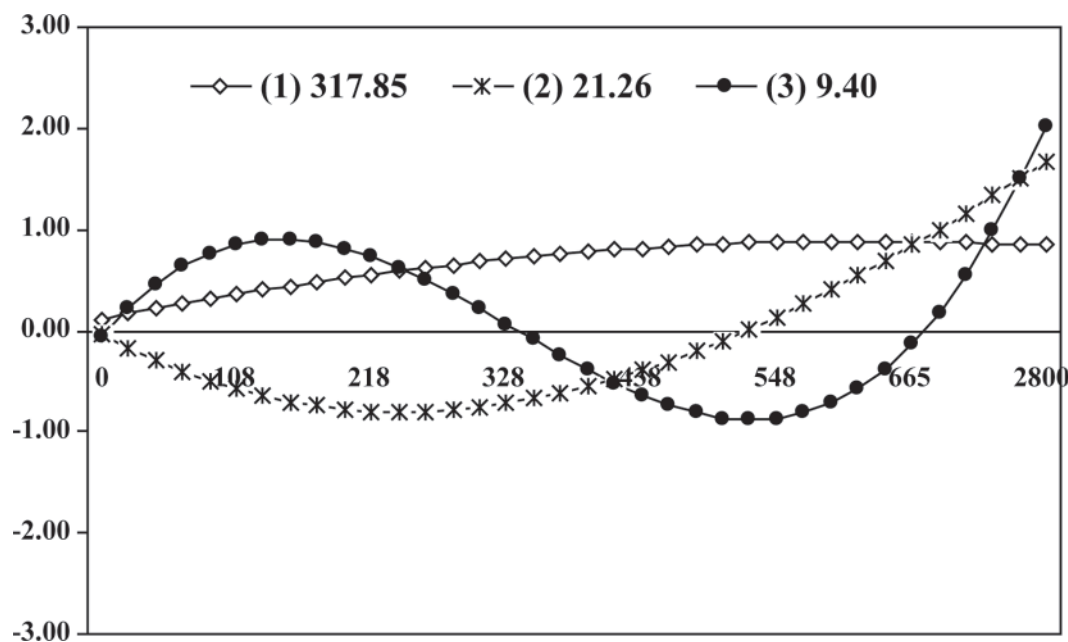
<sup>1</sup>Birth weight (BWt) and BW at 120 (W120); 240 (W240); 365 (W365); 540 (W540); 730 (W730); 1,095 (W1095); 1,460 (W1460); 1,825 (W1825); 2,190 (W2190); 2,555 (W2555); and 2,920 (W2920) d of age.

ter 3 yr of age for Wokalup cattle. Smaller correlations were observed in Polled Hereford data, mainly between BW at 2 and 10 yr of age (0.23).

The maternal genetic correlation estimates between BW from birth to 365 d of age were strong, ranging from 0.66 to 0.88. Moderate to high correlation estimates were also observed between BW after 365 d of age (Table 3). These results suggest that maternal effects on 120, 240, and 365 d BW are, probably, controlled by the same genes. Moreover, the results suggest that these are the same effects because milk production and other aspects of preweaning maternal effects are likely the same or very similar at 120 and 240 d BW. The maternal effect on 365 d BW is probably a carry-over effect from weaning. The high genetic correlation estimates between birth weight and these early (120, 240, and 365 d) BW could be a reflection of the curve fitting to the data rather than of true genetic effects.

Using BW of Nellore cattle in Brazil, Albuquerque and Meyer (2001) and Dias et al. (2006) reported small maternal correlations between birth weight and BW from weaning to 550 d of age, and greater estimates between other ages (from 240 to 550 d). Nobre et al. (2003) reported small maternal genetic correlations between BW from birth to 60 d of age, but estimates greater than 0.70 between BW from 243 to 601 d of age.

Estimates of animal permanent environmental correlations decreased when distance between records increased (Table 4). The least values were observed between BW at birth and after 730 d of age. Strong permanent environmental correlations were observed between BW from birth to 540 d of age, and from 730 d of age to adult age. Smaller correlations than those estimated here were reported by Dias et al. (2006) between birth weight and BW at 240 (0.25), 365 (0.26), and 550 d of age (0.09). Analyzing BW after 570 d of age, Meyer

**Figure 5.** Genetic direct eigenfunctions (1, 2, and 3) and respective eigenvalues (317.85, 21.26, and 9.40) obtained with model M4363\_5.

(1999) and Arango et al. (2004) reported estimates of animal permanent environmental correlations close to 0.60 between intermediate records. However, smaller correlations and greater errors were reported between records in the boundaries. These authors pointed out the need of using polynomials of higher orders to model animal permanent environmental effects if adult BW are available.

The estimates of maternal permanent environmental correlations between birth weight and subsequent BW were moderate to high and increased at the end of the trajectory. These results differ from those reported by Dias et al. (2006), who observed smaller maternal permanent environmental correlations (i.e., 0.32, 0.34, and 0.36 between birth weight and BW at 240, 365, and 550 d of age, respectively). Albuquerque and Meyer (2001) also reported greater correlations; estimates were close to 1.

The 3 main eigenfunctions for additive direct effects obtained with model M4363\_5 are shown in Figure 5. Eigenfunctions are continuous functions whose coefficients are formed by the elements of the eigenvectors of the (co)variance matrices. A specific eigenvalue is attributed to each eigenfunction and corresponds to the proportion of total variation that is explained by such eigenfunction. As emphasized by Kirkpatrick et al. (1990), eigenvalues and eigenfunctions of genetic covariance functions provide an insight into the way selection affects the character under consideration. The 3 main eigenvalues of the additive direct (co)variance matrix explained 99.30% of total additive variance. The first eigenvalue accounted for 90.56%. The first eigenfunctions were all positive; this indicates a positive correlation between BW from birth to 8 yr of age. As discussed before, selection for greater BW at any age will increase other BW. The second eigenfunction was negative up to 400 d of age and positive thereafter. This change indicates that selection for this component will have opposite effects at the beginning and at the end of the trajectory. However, the genetic change due to selection for this component would be small because it was responsible for only 6.06% of additive variance. Similar results were reported by Albuquerque and Meyer (2001) for growth from birth to 630 d of age in Nellore cattle. First eigenvalues explaining most of variation were also reported by Meyer (1999) that found first eigenvalues explaining 91.8 and 97.3% of additive variation in Polled Hereford and Wokulup cattle, respectively. The first eigenvalue explained 96% of additive variance in the study of Arango et al. (2004) of female mature BW. However, in both studies the eigenfunctions associated with the first eigenvalue described curves oscillating more than here.

In random regression models, polynomial order and assumptions about residual variation may affect (co)variance component estimates. In general, a heterogeneous residual structure is more adequate for modeling BW records at different ages because the temporary

environmental does not equally affect all of the growth curve. Regarding the polynomial order, some studies indicated that higher orders provide better fit, but increase computational requirements and can impair convergence (Meyer, 1998). Here, such difficulties were found. Convergence was not reached when higher order polynomials were used and the number of parameters exceeded 50.

The random regression models yielded (co)variance estimates similar to those obtained with the multi-trait model, which included BW records at 6 points. However, the random regression models allowed the use of all data available and not only records obtained at some points. Corrections for standard ages were not required, and errors were avoided. Also, random regression models allowed the estimation of breeding values for any age in the range available in the data set. Both random regression models, M4363\_5 and M4454\_5, adjusted (co)variance patterns equally well, but the former is a more parsimonious specification.

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