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Estimates of covariance functions for growth from birth to 630 days of age in Nelore cattle[1]

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ABSTRACT: Weight records of Brazilian Nelore cattle, from birth to 630 d of age, recorded every 3 mo, were analyzed using random regression models. Independent variables were Legendre polynomials of age at recording. The model of analysis included contemporary groups as fixed effects and age of dam as a linear and quadratic covariable. Mean trends were modeled through a cubic regression on orthogonal polynomials of age. Up to four sets of random regression coefficients were fitted for animals' direct and maternal, additive genetic, and permanent environmental effects. Changes in measurement error variances with age were modeled through a variance function. Orders of polynomial fit from three to six were considered, resulting in up to 77 parameters to be estimated. Models fitting random regressions modeled the pattern of variances in the data adequately, with estimates similar to those from corresponding univariate analysis. Direct heritability estimates decreased after birth and tended to be lowest at ages at which maternal effect estimates tended to be highest. Maternal heritability estimates increased after birth to a peak around 110 to 120 d of age and decreased thereafter. Additive genetic direct correlation estimates between weights at standard ages (birth, weaning, yearling, and final weight) were moderate to high and maternal genetic and environmental correlations were consistently high.

Key Words: Beef Cattle, Growth, Heritability, Maternal Effects, Zebu Breeds

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Introduction

Recently, covariance functions and random regression models (**RRM**) have been proposed as an alternative to model traits that are recorded repeatedly during the animal's life (i.e., longitudinal data; Kirkpatrick et al., 1990, 1994; Schaeffer and Dekkers, 1994). A covariance function gives the (co)variance of traits that are measured at different ages as a function of these ages and is the "infinite dimensional" equivalent to a (co)variance matrix in a multitrait analysis (Kirkpatrick and Heckman, 1989). Meyer and Hill (1997) and Meyer (1998b) showed that random regression models are a special case of covariance functions, and covariance function coefficients can be estimated directly from random regression models by restricted maximum likelihood.

Random regression models provide EBV for the complete growth curve (i.e., in contrast to multitrait models, which provide estimates for given points only) for any target age and for functions of the growth curve. To date, random regression models have been applied mostly for test-day records of dairy cattle (Jamrozik et al., 1997; Van der Werf et al., 1998). In beef cattle, few papers using random regression models have been published, and most dealt with adult weights (Meyer, 1998b, 1999, 2000). Meyer (2001a) estimated genetic direct and maternal covariance functions for growth from birth to weaning of two beef cattle breeds in Australia. Genetic covariance functions from birth to postweaning ages are not available.

Nelore is a Zebu breed (*Bos indicus*) from India that was taken to Brazil at the end of the 19th century. Due to their "easy care" traits, adaptation, and production under an extensive system they became predominant and today represent about 80% of the Brazilian beef cattle population.

The objective of this study was to estimate genetic direct and maternal covariance functions using a random regression model for weights from birth to 630 d of age in Nelore cattle.

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Table 1. Summary of data structure

Number	Data set 1	Data set 2	Data set 3
Records	20,065	21,564	23,581
Animals with records	3,016	3,500	3,450
With 3 records	456	298	258
With 4 records	158	357	169
With 5 records	5	359	222
With 6 records	79	694	206
With 7 records	978	1,057	978
With 8 records	1,340	731	1,614
With 9 records	0	4	3
Sires	87	93	136
Dams	1,903	1,271	1,779
Animals in analysis	5,751	5,114	6,333
Contemporary groups	523	1,901	2,441
Mean, kg	156.2	155.6	178.1
SD, kg	82.9	83.9	95.7

Materials and Methods

Data were supplied by the Brazilian Zebu Breeders Association (**ABCZ**). Since 1974, ABCZ has been running a genetic improvement program considering growth, fertility, and maternal ability traits.

The initial data set consisted of 74,591 weight records on 10,751 Nelore animals, weighed, on average, every 90 d from birth to 730 d of age. Calves were born all year round and were weaned at about 240 d of age. All animals were raised on pasture. Weights recorded after 630 d of age were disregarded. Only records of animals with at least three weights and belonging to contemporary groups (**CG**) of at least four animals were kept. The definition of CG included herd, year and month of birth, sex, weaning state (suckling or weaned), and year and month of record.

The edited data set had 65,210 weight records on 9,966 animals born from 1981 to 1999. This data set was split into three data sets, comprising records from 1, 2, and 3 herds, respectively. A summary of data structure is presented in Table 1. Numbers of records and mean weights for 4-d intervals are shown in Figure 1. Data set 1 (**DS1**) comprised records from a single herd, with a higher concentration of calvings from August to December than for the other two data sets. Numbers of animals with birth weight were 3,016, 3,186, and 3,139 for data sets 1, 2 (**DS2**), and 3 (**DS3**), respectively, and 79, 71, and 81% of animals in each data set had six or more records.

To decrease computer memory requirements, observations were grouped at each 4 d of age, and 159 age classes were created, including birth i.e., (0, 1–4, 5–8, . . ., 628–630 d).

Univariate Analysis

Standard univariate analysis of BW for ages at 0, 1 to 60, 30 to 90, . . ., 570 to 630 d, considering only one record per animal, were carried out. The model of analysis included CG as fixed effects and age of dam, linear and quadratic effects, and linear effect of animal age (except for birth weight) as covariables. Two models of analysis were applied. The first fitted additive genetic direct and permanent environmental effect of dam as random effects. The second considered additive genetic maternal effects in addition. Variance component estimates were obtained by REML using AS-REML (Gilmour et al., 1999).

Random Regression Analysis

Covariances between random regression (**RR**) coefficients were estimated by REML using the program DXMRR (Meyer, 1998a). Fixed effects were the same as for univariate analysis, with an additional cubic regression on orthogonal polynomials of age to model mean age trends. Legendre polynomials of age at recording were used as independent variables.

Previous phenotypic RR analysis of the total data set, including weights from birth to 730 d of age, showed that the log likelihood function increased with order (k) of the polynomial (from 3 to 9), and orders of six or higher were adequate to model the variation in the data. For this data set, 17% of the animals had nine records. Genetic analyses started with k = 6 (quintic) for all random effects in the model using DS1. Different orders of fit were tried only for DS1. Initially, random effects considered in the model of analysis were animal additive genetic effects and animal and maternal permanent environmental effects only (Model A). Model M included additive genetic maternal effects in addition.

The general model can be represented as follows:

$$
\begin{aligned}
y_{ij} = F_{ij} &+ \sum_{m=0}^{3} \beta_m \phi_m(a^*_{ij}) + \sum_{m=0}^{k_A-1} \alpha_{im} \phi_m(a^*_{ij}) \\
&+ \sum_{m=0}^{k_M-1} \gamma_{im} \phi_{im}(a^*_{ij}) + \sum_{m=0}^{k_C-1} \delta_{im} \phi_m(a^*_{ij}) \\
&+ \sum_{m=0}^{k_Q-1} \rho_{im} \phi_m(a^*_{ij}) + \varepsilon_{ij}
\end{aligned}
$$

where y_{ij} is the j^{th} record from the i^{th} animal; a^*_{ij} is the standardized (−1 to +1) age at recording; $\phi_m(a^*_{ij})$ is the m^{th} Legendre polynomial of age; F_{ij} is a set of fixed effects; β_m are the fixed regression coefficients to model the population mean; α_{im}, γ_{im}, δ_{im}, and ρ_{im} are the random regression coefficients for genetic direct, genetic maternal, and animal and maternal permanent environmental effects, respectively; k_A, k_M, k_C, and k_Q denote the corresponding orders of fit; and ε_{ij} is the temporary environmental effect.

In matrix notation:

$$y = XB + Z_1\alpha + Z_2\gamma + W_1\delta + W_2\rho + \varepsilon, \text{ and}$$

$$V\begin{bmatrix}\alpha\\ \gamma\\ \delta\\ \rho\\ \varepsilon\end{bmatrix}=\begin{bmatrix}K_A\otimes A & 0 & 0 & 0 & 0\\ 0 & K_M\otimes A & 0 & 0 & 0\\ 0 & 0 & K_C\otimes I & 0 & 0\\ 0 & 0 & 0 & K_Q\otimes I & 0\\ 0 & 0 & 0 & 0 & R\end{bmatrix}$$

with y the vector of observations; B the vector of fixed effects (including F_{ij} and β_m); α the vector of additive genetic direct random coefficients; γ the vector of additive genetic maternal random coefficients; δ the vector of animal permanent environmental coefficients; ρ the vector of maternal permanent environmental coefficients; X, Z_1, Z_2, W_1, and W_2 are the correspondent incidence matrices; and ε denotes the vector of residuals. K_A, K_M, K_C, and K_Q are the matrices of coefficients of the covariance function for additive direct and maternal effects and animal and permanent environmental effects, respectively. A is the additive numerator relationship matrix and I an identity matrix. Temporary environmental effects (ε) were considered independently distributed, with variances modeled by a quadratic or cubic variance function (VF) assuming a log-linear model, as described by Meyer (2001a):

$$\sigma_j^2 = \sigma_0^2 \exp\left\{1 + \sum_{r=1}^{v-1} b_r (a_{ij}^*)^r\right\},$$

where σ_j^2 is the variance at the j^{th} age, σ_0^2 is the error variance at the mean age, and b_r and v are the coefficients and the number of parameters of the VF, respectively.

To improve convergence of the iterative procedure, eigenvalues of covariance matrix (K) smaller than 0.001 were fixed to an operational zero, forcing estimates of K matrix to have reduced rank. In this case, the number of parameters to be estimated was km − m(m − 1)/2 instead of k(k + 1)/2, with k = order of polynomial fit and m = rank of the coefficient matrix (Meyer, 1998b).

Models with different orders of fitting and random effects were compared by log-likelihood ratio test (**LRT**). The log-likelihood ratio test only allows comparisons between nested models and tends to favor models with higher number of parameters (Olori et al., 1999; Meyer, 2000). Restricted maximum likelihood forms of information criteria such as Akaike's Information Criterion (**AIC**) and Schwarz's Bayesian Information Criterion (**BIC**) (see Wolfinger, 1993), that impose

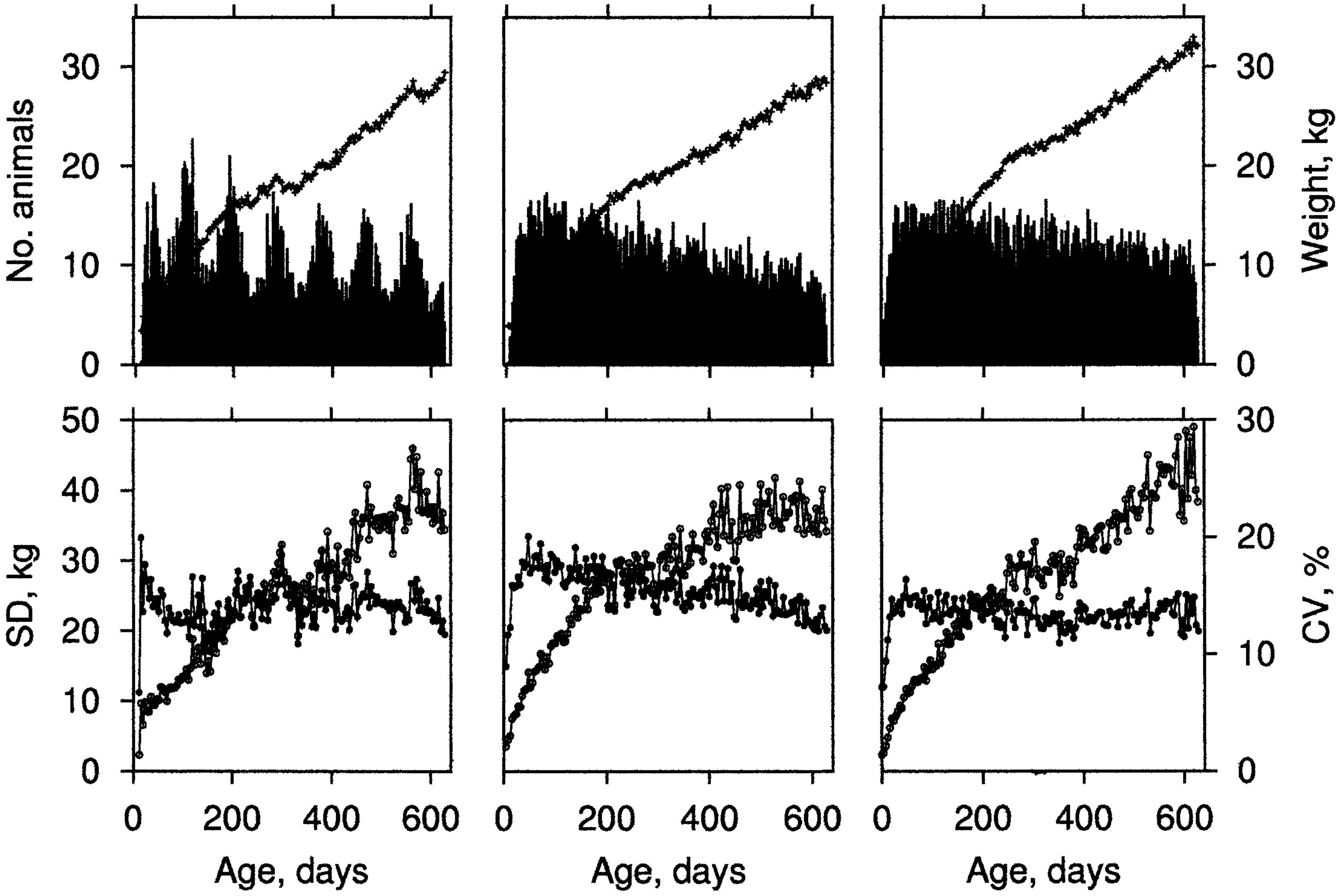

Figure 1. Top: weight means divided by 10 (+) and number of observations divided by 10 (bars). Bottom: standard deviations (○) and coefficient of variation (●), for data sets 1 (left), 2 (middle), and 3 (right), respectively.

penalties according to the number of parameters to be estimated, were also used.

Results and Discussion

Mean weights and SD were 156.1 kg and 82.9 kg for DS1, 155.6 kg and 83.9 kg for DS2, and 178.1 kg and 95.7 kg for DS3, respectively. For the three data sets, weights increased almost linearly with age, with a decrease in growth rate after weaning. Animals from DS3 were heavier than those in the other two data sets (Figure 1). Standard deviations showed the same trend as the means, increasing with age. Coefficients of variation increased until animals were about 30 to 60 d of age and then decreased slightly with age. Birth weight SD and CV in DS2 and DS3 were lower than in DS1.

Due to computational demands different orders of polynomial fit were applied only for DS1. This data set was chosen because it had a smaller number of contemporary groups than the other two and, therefore, a smaller number of equations. Although this data set comprised records of only one herd, estimates of genetic parameters obtained by univariate analysis showed the same trend as estimates obtained previously using a large Nelore data set (Albuquerque and Meyer, 2001).

Preliminary, phenotypic random regression analyses (not shown), considering the three data sets together, indicated that 1) increasing the order of polynomial fit decreased the residual variance; 2) phenotypic SD estimates, using polynomials with order of fit of 6 (quintic) or more, agreed closely with those estimated by univariate analyses except for birth weight; and 3) modeling measurement error variances (σ^2_ε) using a variance function, assuming a log linear model, produced a better fit than assuming homogeneous σ^2_ε.

Initially, an order of fit of 6 for all polynomials was applied. The model included additive direct effect, animal and maternal permanent environmental effects (Model A) with $k_A = 6$, $k_M = 0$, $k_C = 6$, and $k_Q = 6$ (6, 0, 6, 6). Measurement error variances were modeled by a quadratic variance function using a log linear model. For this model, a total of 66 parameters were estimated. Estimates of covariances between RR coefficients indicated that there was little variation for maternal permanent environmental effects quartic and quintic regression coefficients. Fitting a model with k = 6, 0, 6, 4 (55 parameters) did not change the log likelihood function (**log L**) significantly, and all information criteria were smaller for this model than for the previous one (Table 2). A significant change in log L occurred by modeling the measurement error variances as a cubic instead of a quadratic variance function.

A set of models attempting to separate maternal genetic from maternal permanent environmental variances (Model M) was fitted. Adding maternal genetic effects to the model of analysis significantly increased the log L and AIC decreased (Table 2). However, if the number of parameters were equal to 61 or more, a model without maternal genetic effects (k = 6, 0, 6, 4 and v = 4) would be selected by BIC. Both LRT and AIC suggested that a model with k = 6, 6, 6, 4 and v = 4, with a total of 77 parameters, was necessary to model the variances in the data. A more parsimonious model with k = 4, 4, 6, 3, v = 4 and 51 parameters was chosen by BIC.

For DS2 and DS3, only three models were fitted, with k = 6, 0, 6, 4, k = 6, 4, 6, 4, and k = 6, 6, 6, 4, and residual variances were modeled by a log linear cubic variance function. For both data sets, BIC suggested that a model not including additive maternal effects (k = 6, 0, 6, 4), with a total of 56 parameters to be estimated, would suffice to describe the covariance structure in the data. However, LRT and AIC selected models with k = 6, 4, 6, 4, and k = 6, 6, 6, 4 as the "best" to describe variances in DS2 and DS3, respectively. The suggestion of a model with k = 6, 6, 6, 4 for DS3 is clearly a situation in which LRT is favoring the wrong model, because univariate analysis showed little or no variation due to maternal genetic effects in this data set. As expected, LRT and AIC tended to favor models with a higher number of parameters, whereas BIC, which involves a more stringent penalty for number of parameters, selected more parsimonious models.

Estimates of (co)variances and correlations between RR coefficients for models with k = 4, 4, 6, 3, k = 6, 6, 6, 4, and v = 4 for DS1 are presented in Table 3. For all sets of RR the most variable coefficient was the intercept. Correlations between intercept and linear coefficient were positive for all polynomials and moderate to high. However, correlations between intercept and quadratic regression coefficient were negative and ranged from almost zero (genetic direct effect) to almost unity (genetic maternal effect). Meyer (2001a), applying RRM to weights from birth to weaning in two beef cattle breeds in Australia, described similar results.

High correlations between regression coefficients caused some of the eigenvalues to be negligible and set to operational zero, mainly when k = 6, 6, 6, 4. For this model, the variance estimates for quartic and quintic regression coefficients of genetic direct and maternal, and for the third regression coefficient of maternal permanent environmental effects, were smaller than 1.0. For both models, the variance estimates for genetic maternal linear regression coefficient were also smaller than one. This latter result is different from that reported by Meyer (2001a) for weights until weaning but was consistent for the three data sets (models with k = 6, 4, 6, 4 for DS2 and DS3, not shown).

Estimates of (co)variances and correlations between RR coefficients for DS2 and DS3 with a model with k = 6, 0, 6, 4 are presented in Table 4. Similar results as for DS1 were observed, except that the correlation between intercept and linear regression coefficient of

Table 2. Order of fit for animal direct (k_A) and maternal (k_M) genetic effects, animal (k_Q) and maternal permanent (k_C) environmental effects, and residual (v-1), number of parameters (np), log likelihood function (log L +50,000), Akaike's Information Criterion (AIC), and Bayesian Information Criterion (BIC) (all-100,000)

Order of fit								
k_A	k_M	k_Q	k_C	v-1	np	log L	AIC	BIC
Data set 1								
6		6	4	3	56	−1,565	3,242	3,683
6		6	4	2	55	−1,599	3,308	3,741
6		6	6	2	66	−1,592	3,315	3,835
4	4	6	4	3	55	−1,561	3,231	3,665
4	4	6	3	3	51	−1,561	3,224	**3,626**
5	5	6	3	3	61	−1,545	3,213	3,693
6	1	6	3	3	53	−1,574	3,253	3,671
6	4	6	4	3	66	−1,531	3,194	3,714
6	6	6	4	3	77	−**1,515**	**3,184**	3,791
6	6	6	4	2	76	−1,550	3,251	3,850
6	6	6	6	3	88	−1,511	3,198	3,892
Data set 2								
6	0	6	4	3	56	−6,800	13,712	**14,154**
6	4	6	4	3	66	−**6,777**	**13,686**	14,207
6	6	6	4	3	77	−6,772	13,698	14,305
Data set 3								
6	0	6	4	3	56	−11,584	23,280	**23,725**
6	4	6	4	3	66	−11,572	23,276	23,802
6	6	6	4	3	77	−**11,559**	**23,272**	23,885

maternal permanent environmental effects in DS3 was low and negative. Covariance functions for DS1 are presented in Table 5 and for DS2 and DS3 in Table 6.

Variance functions for residuals were as follows:

$$\sigma_j^2 = 14.6146\exp[1 + 0.0487(a_{ij}^*) - 0.9259(a_{ij}^*)^2 + 1.3454(a_{ij}^*)^3]$$

for DS1 with k = 4, 4, 6, 3;

$$\sigma_j^2 = 14.6384\exp[1 + 0.0429(a_{ij}^*) - 0.9378(a_{ij}^*)^2 + 1.3553(a_{ij}^*)^3]$$

for DS1 with k = 6, 6, 6, 4;

$$\sigma_j^2 = 59.9458\exp[1 - 0.3729(a_{ij}^*) - 1.9480(a_{ij}^*)^2 + 3.3847(a_{ij}^*)^3]$$

for DS2 with k = 6, 0, 6, 4; and

$$\sigma_j^2 = 42.5107\exp[1 - 0.1239(a_{ij}^*) - 1.5657(a_{ij}^*)^2 + 2.2750(a_{ij}^*)^3]$$

for DS3 with k = 6, 0, 6, 4.

Variance Component Estimates

Variance component estimates for weights from birth to 630 d of age, obtained with the model chosen by LRT and AIC (k = 6, 6, 6, 4) and by BIC (k = 4, 4, 6, 3) for DS1, are presented in Figure 2. Variance estimates from both RRM were very similar and agreed with those from univariate analyses. Decreasing the order of fit for genetic direct effects from $k_A = 6$ to $k_A = 4$ slightly changed the partitioning of animal effect variances. The difference between the two models was largest after 400 d, with a decrease in genetic direct and an increase in animal permanent environmental variances with k = 4, 4, 6, 3. Variance estimates for DS2 and DS3 (not shown) presented similar trends as for DS1, although phenotypic variances for DS2 tended to be overestimated after 600 d. Regression coefficient estimates are highly influenced by data in the extremes, and birth weight SD for these two data sets were very small (Figure 1). To examine the effect of this small variance on the RRM parameter estimates, birth weights were eliminated from DS2, creating data set 4 (**DS4**), and the same model (k = 6, 0, 6, 4) was applied. Phenotypic variance estimated using DS4 agreed closely with those from univariate analysis even after 600 d of age.

Direct and Maternal Heritability Estimates

Direct and maternal heritability estimates for DS1 are presented in Figure 3. Estimates from both models agreed closely with those obtained by univariate analysis for the same data set. Direct heritability estimates decreased after birth (0.32) until animals were about 120 to 180 d old (0.14), increased slowly until 270 d of age (0.17), and increased faster after that. Maternal heritability estimates increased from birth (0.02) to about 110 to 120 d of age (0.25) and decreased with age thereafter. At weaning (240 d) maternal heritability estimate was 0.20. As Nelore animals were weaned around 240 d of age, results show that maternal genetic effects started to decrease before weaning. These trends are similar to that described by Albuquerque and Meyer (2001) for estimates of direct and maternal heritability obtained using univariate analysis for Nelore cattle. However, they found that the peak in maternal heritability estimates occurred closer to weaning, around 180 to 210 d of age. Meyer (2001a), using RRM for two beef cattle breeds in Australia, also described a decrease in direct heritability estimates after birth. However, the author found that maternal heritability estimates almost did not change with age.

Table 3. Estimates of variances (diagonal), covariances (below diagonal), and correlations (above diagonal) between random regression coefficients and eigenvalues (λ) of coefficient matrix for models with order of fit of 4,4,6,3 and 6,6,6,4 for additive genetic direct and maternal effects and animal and maternal permanent environmental effects, respectively, and fitting a cubic variance function for measurement errors for data set 1

0	1	2	3	4	5	λ
k = 4, 4, 6, 3						
Additive direct effect						
176.44	0.87	–0.05	–0.12			227.84
91.95	62.94	0.36	–0.58			14.03
–0.77	3.40	1.39	–0.84			0.39
–2.02	–5.71	–1.24	1.57			0.07
Animal permanent environmental effect						
245.91	0.70	–0.62	0.20	–0.22	–0.42	280.30
78.15	51.37	–0.12	–0.36	–0.26	–0.32	33.22
–41.37	–3.82	18.32	–0.40	–0.56	0.23	9.62
7.66	–6.51	–4.25	6.24	–0.01	–0.66	4.21
–6.31	–3.49	–4.45	–0.05	3.42	0.14	0.14
–9.78	–3.41	1.49	–2.45	0.37	2.22	0.00
Additive maternal effect						
89.62	0.75	–0.98	0.91			96.22
6.70	0.89	–0.87	0.43			0.95
–19.66	–1.74	4.54	–0.79			0.04
12.63	0.59	–2.47	2.16			0.00
Maternal permanent environmental effects						
59.08	0.98	–0.92				64.54
14.21	3.59	–0.81				0.56
–10.99	–2.38	2.43				0.00
k = 6, 6, 6, 4						
Additive direct effect						
231.04	0.90	–0.16	–0.11	–0.79	–0.82	293.46
116.13	72.88	0.15	–0.49	–0.58	–0.67	13.90
–3.65	1.92	2.36	–0.73	0.15	0.55	1.42
–1.93	–5.02	–1.33	1.42	0.06	–0.08	0.41
–11.13	–4.58	0.22	0.06	0.87	0.66	0.06
–10.34	–4.71	0.70	–0.07	0.51	0.69	0.00
Animal permanent environmental effect						
211.27	0.65	–0.65	0.15	0.04	–0.04	238.99
63.43	44.74	–0.12	–0.45	–0.05	–0.02	31.12
–38.24	–3.28	16.28	–0.35	–0.68	0.06	8.02
5.10	–7.18	–3.33	5.59	–0.03	–0.66	3.41
0.93	–0.49	–4.28	–0.13	2.45	–0.03	0.17
–0.60	–0.14	0.28	–1.83	–0.06	1.38	0.00
Additive maternal effect						
95.75	0.72	–0.95	0.98	–0.09	–0.91	105.11
6.47	0.84	–0.74	0.57	–0.41	–0.87	0.76
–22.82	–1.66	6.02	–0.91	–0.14	0.97	0.56
17.55	0.96	–4.08	3.35	–0.02	–0.82	0.00
–0.36	–0.16	–0.15	–0.01	0.18	0.00	0.00
–4.71	–0.42	1.26	–0.80	0.00	0.28	0.00
Maternal permanent environmental effect						
55.42	0.99	–0.90	–0.28			60.71
12.53	2.89	–0.82	–0.14			0.69
–11.63	–2.44	3.04	0.67			0.00
–0.47	–0.05	0.27	0.05			0.00

Table 4. Estimates of variances (diagonal), covariances (below diagonal), and correlations (above diagonal) between random regression coefficients and eigenvalues (λ) of coefficient matrix for models with order of fit of 6,0,6,4 for additive genetic direct and maternal effects and animal and maternal permanent environmental effects, respectively, and fitting a cubic variance function for measurement errors for data sets 2 and 3

0	1	2	3	4	5	λ
Data set 2						
Additive direct effect						
133.43	0.87	−0.29	0.64	−0.63	−0.47	157.06
53.33	27.92	0.09	0.20	−0.84	−0.67	8.69
−5.66	0.83	2.88	−0.80	−0.28	0.12	1.49
7.23	1.01	−1.32	0.94	0.08	0.06	0.39
−8.25	−5.01	−0.53	0.09	1.29	0.79	0.00
−5.86	−3.82	0.22	0.06	0.96	1.17	0.00
Animal permanent environmental effect						
257.12	0.64	−0.63	0.15	−0.14	−0.03	290.06
79.18	58.82	−0.27	−0.56	0.11	0.05	41.81
−36.92	−7.67	13.38	−0.61	−0.24	0.45	13.90
7.60	−13.35	−6.95	9.84	−0.11	−0.46	12.22
−6.65	2.54	−2.68	−1.12	9.16	0.43	0.00
−1.42	1.18	5.16	−4.50	4.08	9.69	0.00
Maternal permanent environmental effects						
48.83	0.50	−0.99	0.85			52.09
3.59	1.04	−0.56	−0.03			1.37
−8.55	−0.70	1.50	−0.81			0.00
8.56	−0.05	−1.44	2.09			0.00
Data set 3						
Additive direct effect						
294.89	0.85	−0.74	0.50	0.20	−0.53	340.90
107.12	54.32	−0.39	0.02	0.13	−0.30	19.76
−35.62	−8.04	7.88	−0.92	−0.67	0.92	3.46
19.65	0.37	−5.90	5.22	0.57	−0.82	0.00
3.84	1.09	−2.13	1.46	1.27	−0.91	0.00
−6.71	−1.63	1.90	−1.37	−0.75	0.54	0.00
Animal permanent environmental effect						
208.61	0.72	−0.43	−0.16	−0.30	−0.04	249.52
83.03	63.70	0.03	−0.56	−0.28	−0.08	36.05
−25.07	1.01	16.06	−0.17	−0.50	0.03	14.76
−6.92	−13.05	−2.02	8.53	−0.32	−0.67	8.46
−9.78	−5.05	−4.58	−2.15	5.20	0.49	0.28
−1.57	−1.71	0.29	−5.17	2.93	6.96	0.00
Maternal permanent environmental effect						
40.99	−0.16	−0.89	0.36			46.74
−1.26	1.54	−0.11	−0.89			4.73
−14.67	−0.35	6.57	0.04			0.56
3.99	−1.89	0.15	2.92			0.00

Estimates of direct heritabilities for DS2 and DS3 are presented in Figure 4. For both data sets, the RRM estimates agreed closely with those from univariate analysis. However, direct heritability estimates did not decrease after birth, probably because birth weight variances for these two data sets were very small. For all data sets direct heritability estimates tended to be lower when maternal effect estimates were higher. Some of the negative correlation between direct and maternal effects could be due to negative sampling covariance.

Direct heritability estimates for DS4 (same as DS2 excluding birth weight) were almost the same as before. However, differences occurred for animal permanent environmental effects and residual and will be discussed in the next section.

Permanent Environmental Effects

Direct permanent environmental variances as a proportion of the phenotypic variances (c^2) for DS1 using a model with k = 4, 4, 6, 3 (Figure 3) increased rapidly from birth (0.28) to about 50 d of age (0.42) remained almost the same with a slight trend to decrease until 580 d of age and, after that, decreased markedly with age. Meyer (2001a) described a similar pattern for weights from birth to weaning in the Wokalup breed

Table 5. Estimates of coefficients of covariance function for models with order of fit of 4,4,6,3 (above diagonal) and 6,6,6,4 (below diagonal) for additive genetic direct and maternal effects and animal and maternal permanent environmental effects, respectively, and fitting a cubic variance function for measurement errors for data set 1

			1	2	3	4	5	6
			Additive direct effect					
1	108.82		89.95	77.59	–3.91	–2.09		
2	62.16	119.36		146.02	18.14	–53.29		
3	48.38	49.89	59.77		7.83	–13.79		
4	151.94	3.35	32.07	333.97		34.25		
5	–68.25	–32.78	–59.09	–94.62	74.60			
6	–137.84	–47.06	–44.28	–266.19	87.61	233.825		
			Animal permanent environmental effect					
1	166.54		181.33	9.19	–126.28	200.81	16.52	–143.98
2	37.38	230.79		237.42	52.59	–424.67	–23.17	229.62
3	–150.36	19.58	408.18		487.57	–56.95	–350.70	10.57
4	42.82	–378.39	–55.47	1,054.11		1,539.61	–73.23	–1,051.25
5	55.58	–4.71	–275.13	5.82	211.01		294.92	63.92
6	–12.70	203.70	20.88	–680.80	–10.13	470.57		755.74
			Additive maternal effect					
1	77.04		69.63	–23.05	–41.49	50.91		
2	–55.81	41.54		14.27	11.41	–24.97		
3	–49.83	36.64	50.58		25.55	–27.45		
4	161.85	–115.27	–105.80	343.69		47.28		
5	–0.02	–1.40	–16.25	–0.74	15.21			
6	–79.91	54.39	54.99	–174.58	0.13	95.18		
			Maternal permanent environmental effect					
1	42.62		43.34	14.61	–22.99			
2	14.73	5.10		5.39	–6.92			
3	–25.21	–8.88	17.11		13.67			
4	–2.53	–0.98	2.96	1.12				

Table 6. Estimates of coefficients of covariance function for a model with order of fit of 6,0,6,4 for additive genetic direct and maternal effects and animal and maternal permanent environmental effects, respectively, and fitting a cubic variance function for measurement errors for data set 2 (below diagonal) and data set 3 (above diagonal)

			1	2	3	4	5	6
			Additive direct effect					
1	67.06		200.00	16.24	–121.56	232.48	50.20	–126.22
2	7.44	22.22		146.57	83.67	–180.55	–55.95	77.44
3	18.97	30.58	117.86		204.97	–333.79	–140.54	192.67
4	101.86	–11.01	128.82	499.92		601.95	205.30	–320.90
5	–40.70	–19.98	–106.80	–179.70	110.86		109.30	–127.84
6	–65.47	5.16	–132.19	–436.81	165.33	398.04		182.54
			Animal permanent environmental effect					
1	179.87		140.42	84.43	–87.47	–43.78	7.79	18.31
2	42.37	568.51		496.23	–81.93	–1,176.05	118.24	794.69
3	–129.43	–114.56	755.88		592.19	521.97	–484.75	–417.92
4	84.43	–1,460.96	379.23	5,158.22		4,111.34	–651.63	–3,085.80
5	43.62	224.39	–735.13	–825.15	788.88		448.02	502.46
6	–33.97	1,046.62	–373.27	–4,060.34	698.93	3,304.73		2,375.46
			Maternal permanent environmental effect					
1	34.91		41.01	–8.33	–36.93	12.63		
2	–16.39	18.30		38.27	–2.05	–49.10		
3	–17.15	7.53	8.45		36.98	1.71		
4	33.61	–27.63	–15.93	45.61		63.78		

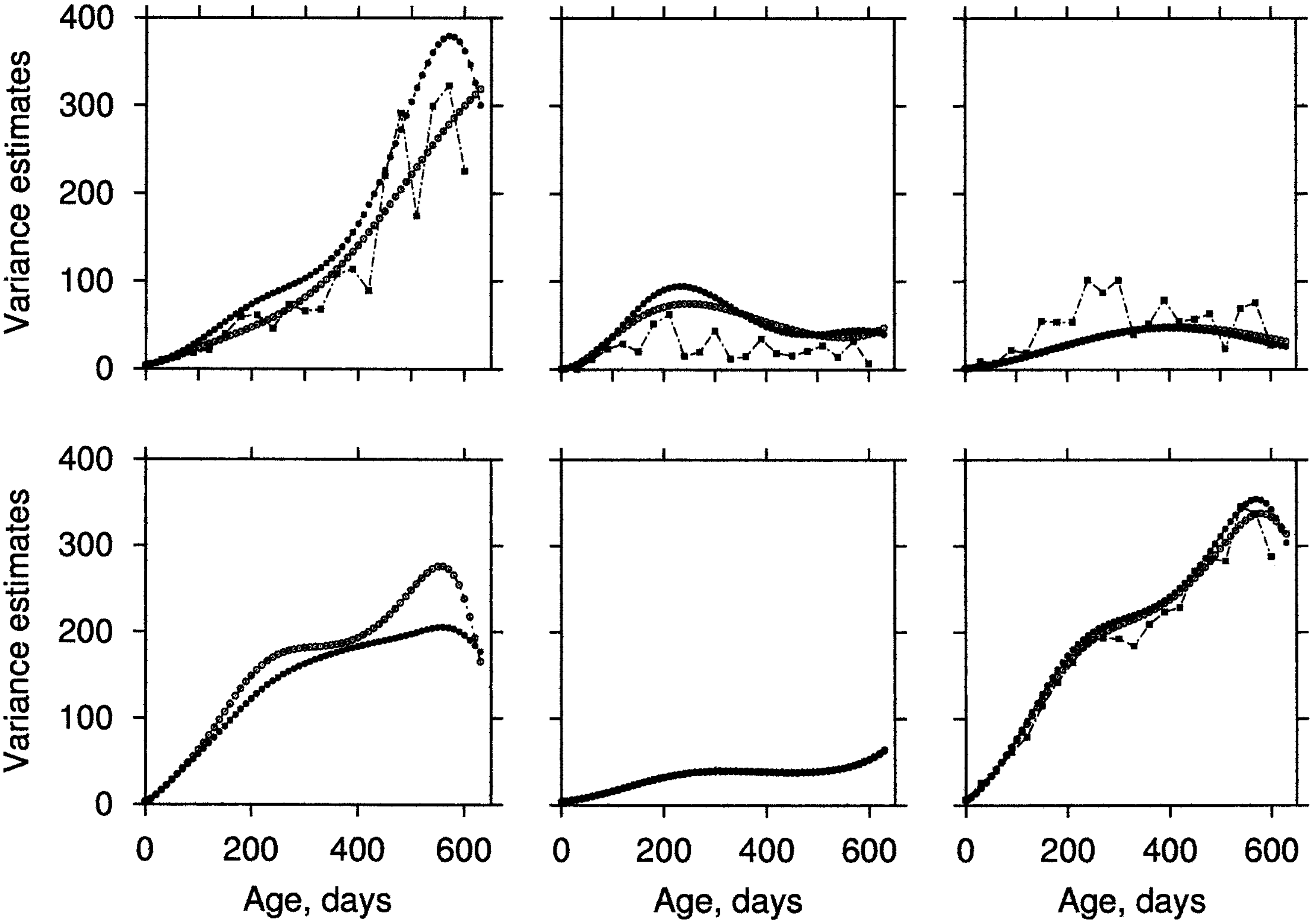

Figure 2. Genetic direct (top left), genetic maternal (top middle), maternal permanent environmental (top right), animal permanent environmental (bottom left), residual (bottom middle), and phenotypic (divided by 2: bottom right) variance component estimates from univariate analysis (■) and random regression analysis with k = 4, 4, 6, 3 (○) and k = 6, 6, 6, 4 (●) for genetic direct and maternal and animal and maternal permanent environmental effects, respectively, and a log linear cubic variance function for measurement error variances for data set 1.

(synthetic breed formed by mating Charolais × Brahman bulls to Friesian × Angus or Hereford cows). However, for Polled Hereford animals c^2 increased with age. The author suggested that the difference between the two could be due to sampling variation in the partition of animal effects.

For DS2 and DS3 (Figure 4), c^2 showed a larger increase after birth than for DS1, followed by a decrease in the residual variance as proportion of phenotypic variance estimates (e^2). After excluding birth weight from the analysis for DS2, c^2 showed a trend similar to that observed for DS1. Because the change in c^2 was accompanied by a proportional change in e^2 there was no difference in the other parameter estimates (i.e., heritabilities and maternal permanent environmental variance, as proportion of phenotypic variance estimates remained the same).

Maternal permanent environmental effect estimates (q^2) for DS1 were almost the same for both models (k = 4, 4, 6, 3 and k = 6, 6, 6, 4), practically did not change with age, and were lower than maternal genetic effects (Figure 3). Estimates of q^2 from univariate analyses were larger than those obtained with RRM. Partition of maternal effects in genetic and permanent environmental effects, mainly using field data, presents some difficulties even for simple, univariate analyses (Willham, 1980; Gerstmayr, 1992; Meyer, 1992a). It is expected that these problems would also arise with RRM. There is evidence that by including only one of the maternal effects (additive genetic or permanent environmental) in the model most of the maternal variation would be accounted for (Meyer, 1992b). For DS2 and DS3, maternal genetic effects were not included in the model and, for both data sets, maternal permanent environmental effects increased from birth (0.04 and 0.02 for DS2 and DS3) to a peak around 100 to 130 d of age (0.13–0.14) and decreased with age thereafter.

Correlation Estimates

Estimates of phenotypic correlations between weights from birth to 630 d of age for DS1 and DS2 are presented in Figure 5. Genetic direct and maternal and animal and maternal permanent environmental correlations for DS1 are shown in Figure 6. In general, correlations tended to decrease with increasing number of days between records.

Phenotypic correlations for DS2 (Figure 5) and DS3 (not shown) were not as smooth as for DS1. This could be due to the high order of polynomial fit for these two data sets. A higher-order polynomial is expected to be more flexible and consequently to be able to follow the changes in (co)variances more closely. However, higher-order polynomials have been known for intensifying sampling problems, producing "wiggly" functions (Kirkpatrick et al., 1994; Meyer, 1998b).

For DS2 and DS3, correlations of all ages with birth weight were low and did not decrease much with increasing lag in ages. These latter results are consistent with the small variance observed for birth weight in DS2 and DS3.

Correlation estimates obtained using k = 4, 4, 6, 3 (Figure 6) and k = 6, 6, 6, 4 (not shown) for DS1 were similar, except for genetic maternal correlation estimates between birth weight and all the other ages, which were larger for k = 6, 6, 6, 4. Estimates obtained for DS2 and DS3 were similar to those found for DS1, although none of them were as smooth as for DS1. Correlations between birth weight and all the other ages for these two data sets were much smaller than for DS1. Maternal permanent environmental correlations between birth weight and some other ages for DS3 were negative. As already pointed out, these differences are probably due to small variances for birth weight in DS2 and DS3 and to the higher-order polynomials applied for these two data sets. Removing birth weights from DS2 did not change correlation estimates. Many authors have reported problems in modeling covariances between early and late records in dairy (Jamrozik et al., 1997; Brotherstone et al., 2000) and beef (Meyer, 1998b, 1999, 2000) cattle. A small number of records for extreme ages, far from the mean, and over-parameterization have been pointed out as possible reasons for these problems (Kirkpatrick et al., 1994; Meyer, 2000). Only results from DS1 are presented in the following.

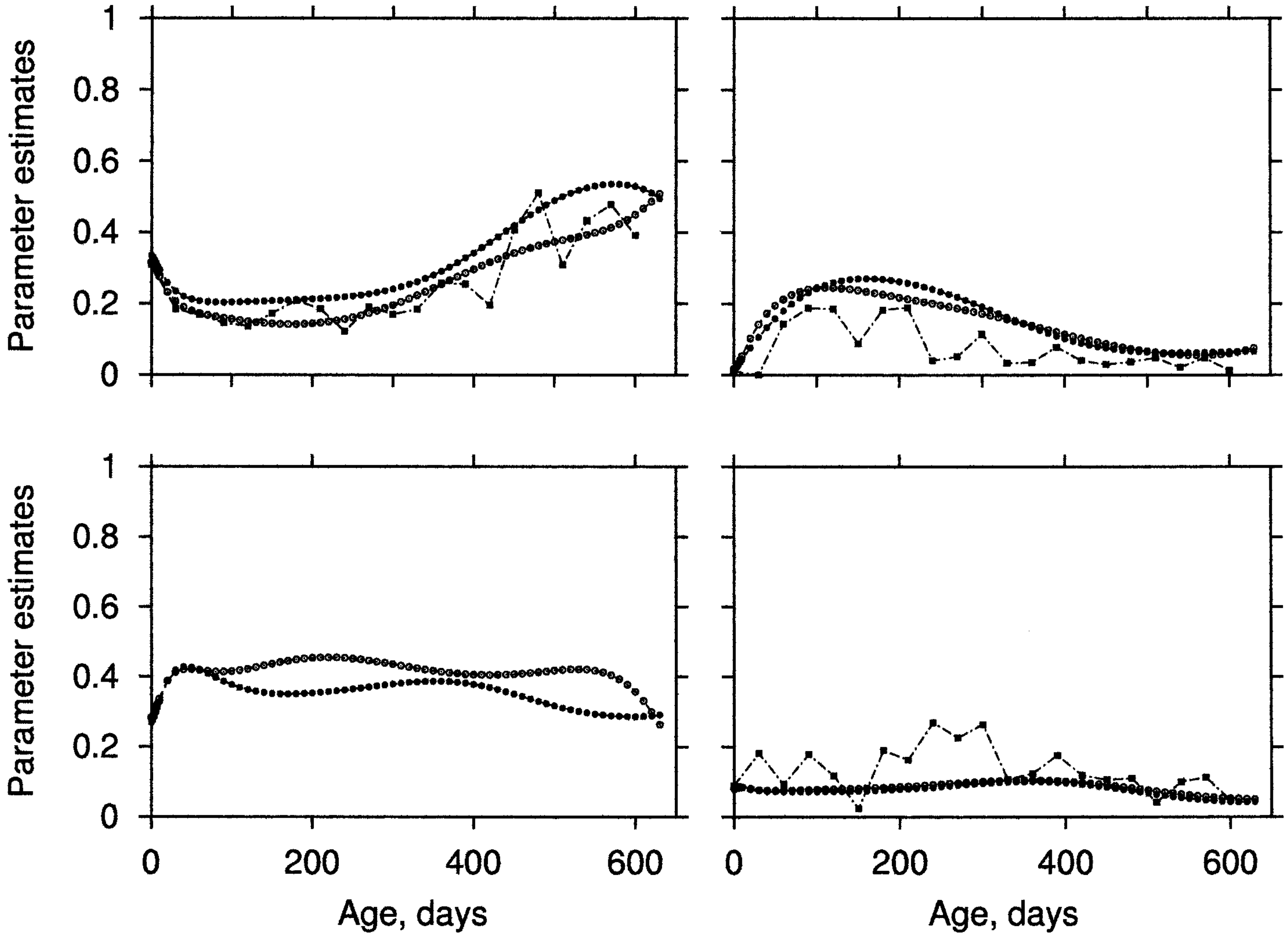

Figure 3. Direct (top left) and maternal (top right) heritability estimates and animal (bottom left) and maternal (bottom right) variance component estimates as proportions of phenotypic variances for data set 1 from univariate analysis (■) and random regression analysis with k = 4 ,4, 6, 3 (○) and k = 6, 6, 6, 4 (●) and a log linear cubic variance function for measurement error variances.

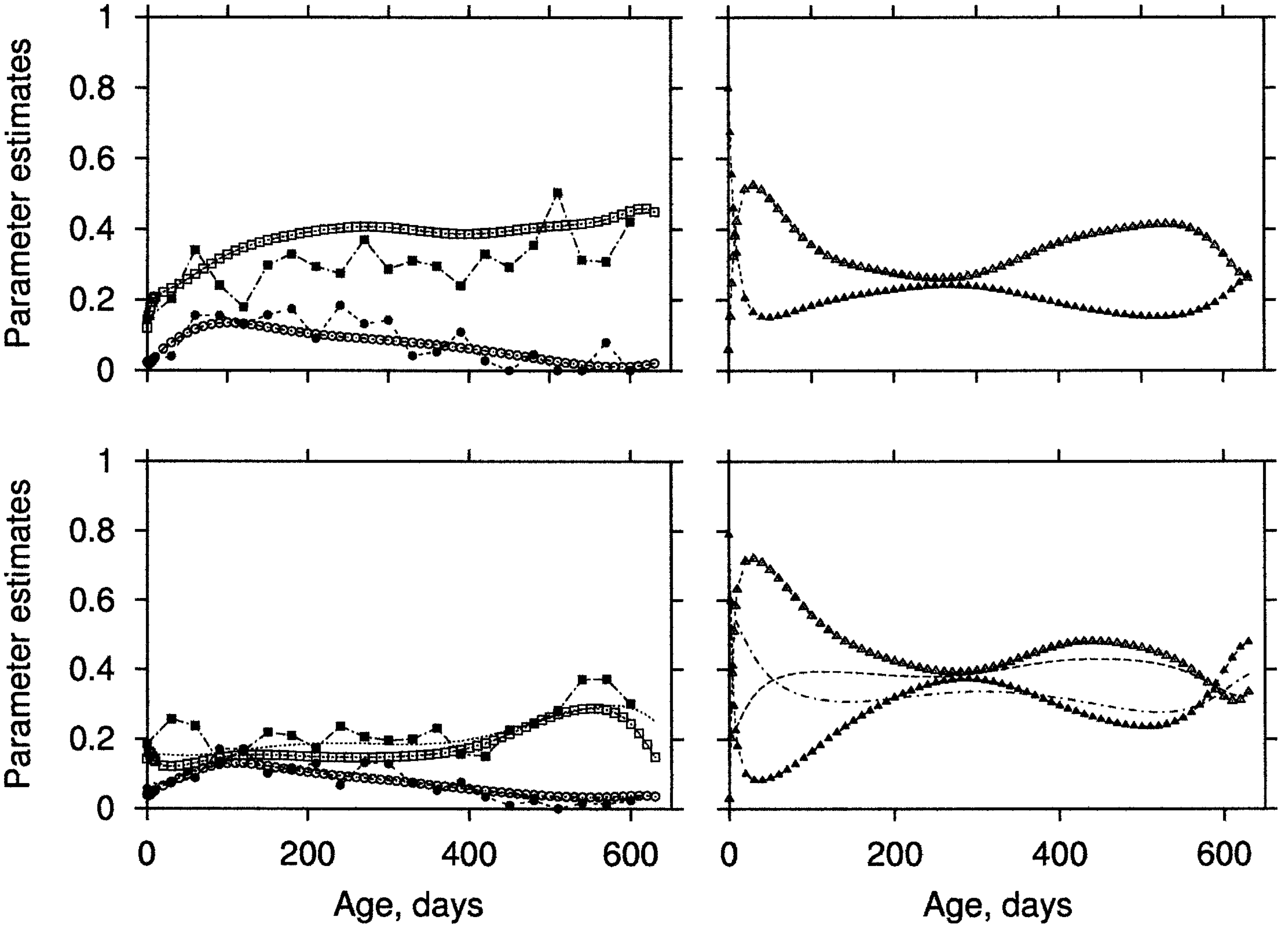

Figure 4. Random regression direct heritability estimates (□), and animal (△) and maternal (○) permanent environmental and residual (▲) variance components as proportion of phenotypic variances. Univariate analysis direct heritability estimates (■) and maternal permanent environmental variances (●) as proportion of phenotypic variances. Data set 2 (bottom) and data set 3 (top). Animal permanent environmental (dash line) and residual (dot dash line) variances as proportion of phenotypic variances for data set 4 (bottom right).

Additive Direct and Maternal Correlations

Genetic direct correlation estimates (Figure 6) decreased with increasing age between weights. However, the estimates showed small peaks at the edges (i.e., between early and late weights), with a minimum value of 0.42 between 30 to 40 d and 540 to 560 d of age.

Estimates of genetic direct correlations were 0.65, 0.53, 0.44, 0.93, 0.82, and 0.97 between birth and 240, birth and 360, birth and 550, 240 and 360, 240 and 550,

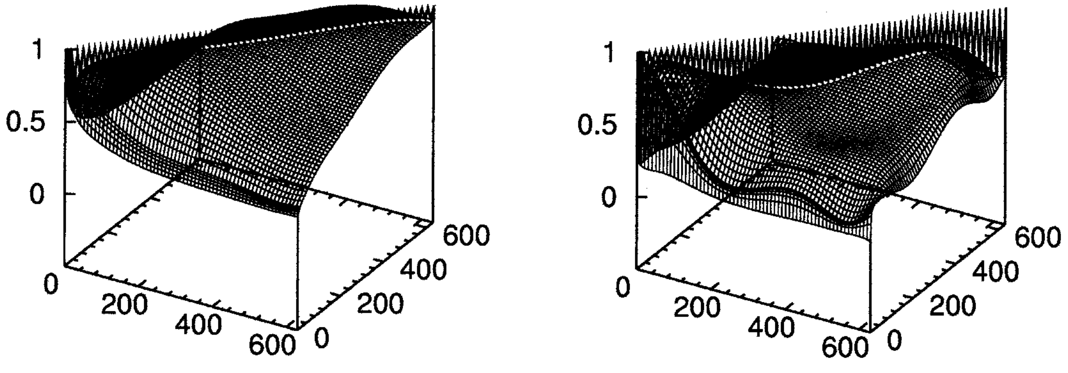

Figure 5. Phenotypic correlation estimates for data set 1 (left) and data set 2 (right), with k = 4, 4, 6, 3 and k = 6, 0, 6, 4, respectively, and measurement error variances modeled as a log linear cubic variance function.

and 360 and 550 d of age, respectively. Mercadante et al. (1995), in a review, reported weighted mean genetic correlations of 0.63, 0.41, 0.40, 0.78, 0.71, and 0.77, respectively, at these same ages for Zebu breeds in the tropics. As pointed out by the authors, most of the estimates were obtained with small data sets and maternal effects were not taken into account. Lôbo et al. (2000), also in a review, found corresponding weighted means for genetic correlation of 0.62, 0.62, 0.60, 0.75, 0.74, and 0.97 for European and Zebu breeds in the tropics. The results we have obtained with RRM are, overall, similar to those reported by these authors.

Additive genetic maternal correlation estimates after 20 d of age were close to unity, forming a flat horizontal plane. Meyer (2001a), using RRM for Polled Herefords in Australia, described a similar pattern. The minimum correlation value occurred between birth and 460 to 480 d of age. Genetic maternal correlations were low between birth and 240 (weaning), 360 (yearling), and 550 (final weight) d of age (0.14, 0.05, and 0.05) and close to unity between the other ages. There are few estimates of genetic maternal correlations for weights of Zebu breeds in Brazil. Eler et al. (1995) found low genetic maternal correlations between birth and weaning and birth and yearling weights for Nelore cattle of 0.21 and 0.18, respectively. Similarly, they found a high genetic maternal correlation between weaning and yearling weights, 0.84.

Permanent Environmental Correlations

Animal permanent environmental correlation estimates decreased with increasing lag between ages reaching a minimum between birth and 630 d of age (0.10). Meyer (2001a), also modeling animal permanent environmental effects using an order of fit of 6 for weights from birth to weaning, found a similar pattern. However, correlations between very early and later ages were higher than would be initially expected.

Estimates of maternal permanent environmental correlations were consistently high, with a minimum value (0.84) occurring between birth and 200 to 240 d of age, forming a horizontal plane after 10 d of age. Maternal permanent environmental correlations between birth and 240, birth and 360, birth and 550, 240 and 360, 240 and 550, and 360 and 550 d of age were 0.84, 0.85, 0.95, 1.00, 0.98, and 0.99, respectively. These values are higher than those reported by Eler et al. (1995) for Nelore cattle in Brazil of 0.27, 0.45, and 0.80 between birth and weaning, birth and yearling and, weaning and yearling weights, respectively. Meyer (2001a) found maternal permanent environmental correlation between birth and weaning weights smaller than in the present study for Polled Hereford (0.66).

General Discussion

Direct heritability estimates decreased after birth and tended to be lowest at ages at which maternal

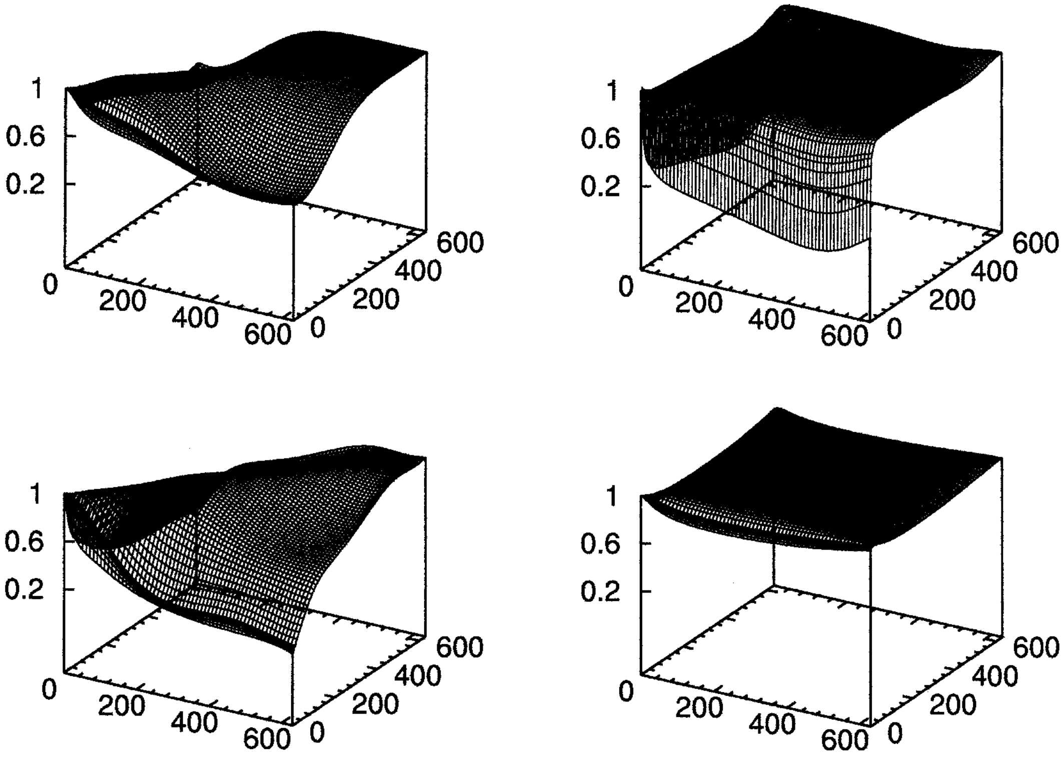

Figure 6. Additive direct (top left), additive maternal (top right), and animal (bottom left) and maternal (bottom right) correlation estimates with k = 4, 4, 6, 3 and measurement error variances modeled as a log linear cubic variance function for data set 1.

effect estimates tended to be highest. Maternal heritability estimates increased after birth to a peak at 110 to 120 d of age and decreased thereafter. Similar results were found by Albuquerque and Meyer (2001) using univariate analyses for Nelore cattle in Brazil and by Meyer (2001a) for two beef cattle breeds in Australia. A higher response to selection for maternal ability would be expected if selection were based on preweaning weights. However, there is evidence that milk production is the main cause of maternal effects (Meyer et al., 1994). Hence, selection for maternal ability is expected to increase milk production and, in the long term, could produce animals with higher nutritional requirements.

A model with RR modeled the pattern of (co)variances in the data adequately, with estimates similar to those obtained with univariate analysis. Increasing the order of polynomial fit increased the flexibility of the curve. However, applying polynomials with a high order of fit increased computational requirements, made convergence difficult to reach, and increased sampling problems (Kirkpatrick et al., 1994; Meyer, 1998b).

A question still to be answered is how much would be gained by applying RRM to genetic evaluations. In general, two approaches have been used to analyze beef cattle data. The most common has been to adjust weights to standard ages and use uni- or multitrait analyses to estimate genetic parameters and to predict breeding values for those ages. Information from relatives is incorporated into the analysis through a relationship matrix. In this case, although multitrait analyses take into account the correlations between traits, covariance matrices are not structured.

Another approach has been to consider weight as a trait that changes with time and to describe the trajectory by a mathematical model. Several nonlinear functions such as Richard's, Brody's, Bertalanffy's, and Gompertz's growth curves (Fitzhugh, 1976) have been used to describe beef cattle growth. Usually, the parameters of the curve are estimated for each animal and, as a second step, environmental effects and variance components are estimated for the parameters. When fitting a curve, all weights available are considered; however, repeated records have correlated errors that have not been taken into account by this method (DeNise and Brinks, 1985). Another aspect is that information on relatives is not considered in the first step, when the growth curve is estimated (i.e., not all information is used and animals with only one or a few records cannot be included in the analysis). This approach has rarely been used for genetic evaluation in a mixed-model context.

With RRM, a fixed regression on age is used to model the population trajectory and each random effect can also be modeled by a trajectory as a function of age. Environmental effects are separated into permanent and temporary effects, and if animal genetic and permanent effects were modeled appropriately, measurement errors would be independent. Covariance functions that give the covariances between any two ages within the range of ages in the data can be estimated by applying a RRM and REML (Meyer, 1998b), and impose a structure on the covariance matrices. Instead of predicting breeding values (**BV**) for each recorded weight, BV are predicted for additive direct and maternal regression coefficients. If the appropriate curve is chosen, the number of traits to be considered is reduced without loss of information (Meyer and Hill, 1997; Meyer, 1998b), (i.e., a RRM with optimal k [order of fit] is equivalent to a multitrait model with less computer requirement).

Using the genetic regression coefficients, BV can be predicted for the growth curve as a whole, for any age (within the range in the data), even those for which the animal had no records and for functions of the growth curve. Animals with only one or even without records can be evaluated using information from relatives. This is particularly important when the selection objective is to select young animals for growth without changing mature weight. However, mature weights of relatives have to be available because predictions can only be done in the range of ages present in the data (Kirkpatrick et al., 1990). Functions of the growth curve, such as rate of maturity, can also be used with this objective. Appropriate functions to find fast-growing and early-maturing animals have to be defined. Another important advantage of RRM is that there is no need for age of animal adjustments because age is in the design matrix, avoiding a source of errors associated with the estimation of adjustment factors. Random regression models are expected to give more accurate estimates of genetic parameters and predictions of breeding values than the conventional multitrait model used nowadays. Future research should concentrate on quantifying how much would be gained in terms of accuracy and response to selection by applying RRM instead of multitrait models, considering a limited number of points such as birth, weaning, yearling, and final weights.

An important issue to consider for genetic evaluations of a large number of animals, as in national evaluation programs, is computational requirements. Applying RRM instead of multitrait models for genetic evaluations of growth traits will increase the number of mixed-model equations, the coefficient matrix of random effects will be denser, and, consequently, computing requirements will increase accordingly. Alternatives to decrease the order of polynomial fit must be investigated. Pool and Meuwissen (2000) found that the order of polynomial fit necessary to model the (co)variance matrix was reduced by using only complete lactation records (from 5 to 4) and by correcting for heterogeneous variances across classes of days in milk (from 4 to 3). Parametric growth curves, generally with a small number of parameters, could be applied with a Bayesian procedure as presented by Varona et al. (1997, 1999). Stationary or nonstationary correlation parametric models could be applied to model within-animal variance, decreasing the number of parameters necessary to describe changes in variance with age (Pletcher and Geyer, 1999; Foulley et al., 2000; Meyer 2001b).

Implications

A model with random regressions modeled the pattern of (co)variances in the data adequately, with estimates similar to those obtained with univariate analysis. Random regression models are expected to give more accurate estimates of genetic parameters and predictions of breeding values than the conventional multitrait model considering a limited number of points, such as birth, weaning, yearling, and final weights, used nowadays.

Literature Cited

Albuquerque, L. G., and K. Meyer. 2001. Estimates of direct and maternal genetic effects for weights from birth to 600 days of age in Nelore cattle. J. Anim. Breed. Genet. 118:83–92.

Brotherstone, S., I. M. S. White, and K. Meyer. 2000. Genetic modeling of daily milk yield using orthogonal polynomials and parametric curves. Anim. Sci. 70:417–416.

DeNise, K. R. S., and J. S. Brinks. 1985. Genetic and environmental aspects of the growth curve parameters in beef cows. J. Anim. Sci. 61:1431–1440.

Eler, J. P., L. D. Van Vleck, J. B. S. Ferraz, and R. B. Lôbo. 1995. Estimation of variances due to direct and maternal effects for growth traits in Nelore cattle. J. Anim. Sci. 73:3253–3258.

Fitzhugh, H. A., Jr. 1976. Analysis of growth curves and strategies for altering their shape. J. Anim. Sci. 42:1036–1051.

Foulley, J.-L., F. Jaffrézic, and C. Robert-Granié. 2000. EM-REML estimation of covariance parameters in Gaussian mixed models for longitudinal data analysis. Genet. Select. Evol. 32:129–141.

Gerstmayr, S. 1992. Impact of the data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. J. Anim. Breed. Genet. 109:321–336.

Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 1999. ASREML Reference Manual. NSW Agric. Biometric Bull. no. 3 NSW Agriculture, Orange, Australia.

Jamrozik, J., and L. R. Schaeffer. 1997. Estimates of genetic parameters for a test day model with random regressions for production of first lactation Holsteins. J. Dairy Sci. 80:762–770.

Jamrozik, J., L. R. Schaeffer., and J. C. M. Dekkers. 1997. Genetic evaluation of dairy cattle using test day yields and random regression model. J. Dairy Sci. 80:1217–1226.

Kirkpatrick, M., and N. Heckman. 1989. A quantitative genetic model for growth, shape and other infinite-dimensional characters. J. Math. Biol. 27:429–450.

Kirkpatrick, M., W. G. Hill, and R. Thompson. 1994. Estimating the covariance structure of traits during growth and aging, illustrated with lactation in dairy cattle. Genet. Res. 64:57–69.

Kirkpatrick, M., D. Lofsvold, and M. Bulmer. 1990. Analysis of the inheritance, selection and evolution of growth trajectory. Genetics 124:979–993.

Lôbo, R. N. B., F. E. Madalena, and A. R. Vieira. 2000. Average estimates of genetic parameters for beef and dairy cattle in tropical regions. Anim. Breed. Abstr. 68:433–462.

Mercadante, M. E. Z., R. B. Lôbo, and A. de los Reyes. 1995. Parámetros genéticos para características de crecimiento en cebuínos de carne: Una revisión. Arch. Latinoam. Prod. Anim. 3:45–89.

Meyer, K. 1992a. Bias and sampling covariances of estimates of variance components due to maternal effects. Genet. Sel. Evol. 24:487–509.

Meyer, K. 1992b. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31:179–204.

Meyer, K. 1998a. "DXMRR"—a program to estimate covariance functions for longitudinal data by restricted maximum likelihood. In: Proc. 6th World Congr. Genet. Appl. Livest. Prod., Armidale, NSW, Australia. 27:465–466.

Meyer, K. 1998b. Estimating covariance functions for longitudinal data using a random regression model. Genet. Sel. Evol. 30:221–240.

Meyer, K. 1999. Estimates of genetic and phenotypic covariance functions for postweaning growth and mature weight of beef cows. J. Anim. Breed. Genet. 116:181–205.

Meyer, K. 2000. Random regressions to model phenotypic variation in monthly weights of Australian beef cows. Livest. Prod. Sci. 65:19–38.

Meyer, K. 2001a. Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. Genet. Sel. Evol. 33:1–28.

Meyer, K. 2001b. Estimating genetic covariance functions assuming a parametric correlation structure for environmental effects. Genet. Sel. Evol. (In press).

Meyer, K., M. J. Carrick, and B. J. P. Donnelly. 1994. Genetic parameters for milk production of Australian beef cows and weaning weight of their calves. J. Anim. Sci. 72:1155–1165.

Meyer, K., and W. G. Hill. 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. Livest. Prod. Sci. 47:185–200.

Olori, V. E., W. G. Hill, B. J. McGuirk, and S. Brotherstone. 1999. Estimating variance components for test day milk records by restricted maximum likelihood with random regression animal model. Livest. Prod. Sci. 61:53–63.

Pletcher, S. D., and C. J. Geyer. 1999. The genetic analysis of age-dependente traits: modeling the character process. Genetics 151:825–835.

Pool, M. H., and T. H. E. Meuwissen. 2000. Reduction of the number of parameters needed for a polynomial random regression test day model. Livest. Prod. Sci. 64:133–145.

Schaeffer, L. R., and J. C. M Dekkers. 1994. Random regressions in animal models for test-day production in dairy cattle. In: Proc. 5th World Congr. Genet. Appl. Livest. Prod., Guelph, Canada. 18:443–446.

Van der Werf, J., M. Goddard, and K. Meyer. 1998. The use of covariance functions and random regressions for genetic evaluation of milk production based on test day records. J. Dairy Sci. 81:3300–3308.

Varona, L., C. Moreno, L. A. Garcia Cortés, and J. Altarriba. 1997. Multiple trait analysis of underlying biological variables of production functions. Livest. Prod. Sci. 47:201–209.

Varona, L., C. Moreno, L. A. Garcia Córtes, G. Yagüe, and J. Altarriba. 1999. Two-step versus joint analysis of Von Bertalanffy function. J. Anim. Breed. Genet. 116:331–338.

Willham, R. L. 1980. Problems in estimating maternal effects. Livest. Prod. Sci. 7:405–418.

Wolfinger, R. D. 1993. Covariance structure in general mixed models. Commun. Statist. 22B:1079–1106.