ESTIMATES OF GENETIC COVARIANCE FUNCTIONS FOR GROWTH OF NELORE CATTLE ASSUMING A PARAMETRIC CORRELATION STRUCTURE FOR ANIMAL PERMANENT ENVIRONMENTAL EFFECTS

Lucia Galvão de Albuquerque[1] and **Karin Meyer**

Animal Genetics and Breeding Unit[2], University of New England, Armidale,
NSW 2351, Australia

INTRODUCTION

Random regressions (RR) on Legendre polynomial (LP) of age have been used to model longitudinal data such as milk production and weights at different ages. Usually such models involve high degree polynomials, especially for direct permanent environmental effects and, consequently, a large number of parameters to be estimated. High order polynomials are associated with sampling problems (Kirkpatrick *et al.*, 1994) and high computational requirements. Parametric correlation functions combined with variance functions provide a more parsimonious alternative, and have been suggested to model within animal (co)variances (Foulley *et al.*, 2000). This paper presents estimates of genetic covariance functions for growth of Nelore cattle, fitting a parametric correlation function to describe the covariance structure between animal, permanent environmental effects.

MATERIAL AND METHODS

Data. A total of 20,065 weights from 3,016 Nelore animals, offspring of 87 sires and 1903 dams, distributed in 523 contemporary groups (CG) in a single herd were analysed. CG were defined as year-month of birth, sex, weaning status (suckling or weaned) and year-month of weighing subclasses. Numbers of animals and mean weights are shown in figure 1. Animals were weighed every three months from birth to 630 days of age. All animals had birth weight, and 79% of animals had six or more records. To increase the number of animals for each age, animals weighed within four days intervals were considered the same age, creating 156 age classes, including birth weight. Data have been analysed previously, see Albuquerque and Meyer (2001) for further details.

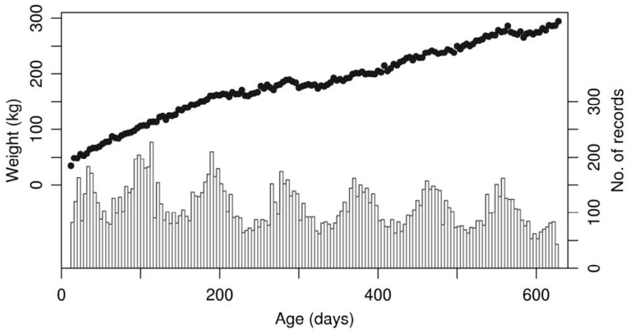

Figure 1. Number of animals (▌) and mean weights (●).

Analysis. Direct (A) and maternal (M) genetic effects and maternal

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[1] on leave from : Depto. de Zootecnia, FCAV – UNESP, 14994-900 Jaboticabal, SP, Brazil. Supported by FAPESP and CNPq.

[2] AGBU is a joint institute of NSW Agriculture and The University of New England

Table 1. Correlation functions

RF	P	r_{ij}
EXP	θ	$e^{-\theta(t_j-t_i)}$
DEX	θ, κ	$e^{-\theta(t_j-t_i)^{\kappa}}$
SAD	ρ, κ	$\rho^{f(t_j,\kappa)-f(t_i,\kappa)}$ for j=i+1
		$\prod_{k=i+1}^{j-1} r_{k(k+1)}$ for j>i+1

r_{ij}: correlation between records taken at times t_i and t_j, i <j, ρ : auto-correlation, θ: corresponding exponential parameter, and κ : scale parameter.

permanent environmental (C) effects were modelled through RR on LP of age. Orders of fit for A, M and C were 4, 4 and 3 respectively. Changes in variances due to direct permanent environmental (PE) effects were modelled through a polynomial variance function (VF), considering orders of fit up to 5. A parametric correlation function (RF) was used to model the PE correlation between ages. Two stationary RF (EXP : exponential and DEX : `damped´ exponential) and a non-stationary function (SAD : first- order structured ante-dependence model) were considered. Formulae for RF are shown in table 1. EXP has a single parameter, the exponential equivalent to an auto-correlation. DEX has a second parameter to scale - attenuate or accelerate - the exponential decay of the auto correlation. SAD applies a deformation. $f(t_i, \kappa) = (t^{\kappa}_i - 1)/\kappa$ for $\kappa \neq 0$ and $\log(t_i)$ for $\kappa=0$, of the time scale to accommodate non-stationarity (Nuñez-Anton and Zimmerman, 2000). Temporary environmental effects were considered independently distributed with homogeneous (e=1) or heterogeneous variances (σ^2). The latter were modelled as a step function with e=6 (0-103, 104-159, 160-255, 256-527, 528-591, 592-630 days) or e=7 classes (as e=6 except for a separate class for birth weight), or through a VF involving a cubic polynomial of $\log(\sigma^2)$. Analyses were carried out by restricted maximum likelihood (REML) as described by Meyer (2001). Model fit was compared using the REML forms of Akaike's (AIC) and Schwarz' Bayesian (BIC) information criterion, and by examining variance and correlation estimates for ages in the data. Results were contrasted with estimates from previous analyses fitting LP on age to model direct PE effects (Albuquerque and Meyer, 2001). In the following, "LP*k*" denotes a model fitting a LP of order *k* for PE, and "X.VF*v*" is a model fitting a parametric RF together with a VF of order *v* with X= EXP, DEX or SAD.

RESULTS

Table 2 presents likelihoods, information criteria and estimated parameters of the RF, showing ρ= EXP{-θ} instead of θ. Estimates of the lag-1 correlation, ρ, were high for all models. A cubic polynomial sufficed to model PE variances adequately. All analyses resulted in smaller BIC values than the LP model, even for homogeneous σ^2. This was due to the stringent penalty for the number of parameters inherent in BIC. Modelling PE through a RF instead of LP reduced the number of parameters by at least 12. For models fitting a VF for residual variances, κ were all close to unity reducing SAD to an auto-correlation function. There were small differences in log L, and BIC was smaller for EXP than for DEX and SAD. However, for e=6 or e=7, estimates of κ were around 0.5, i.e. correlations between records equidistant in time increased with age. Models assuming SAD VF3 with e=6 or e=7 had higher log L and smaller AIC and BIC than SAD VF3 with a cubic VF for residuals. Presumably this was due to the higher number of parameters available to model environmental variances not explained

Table 2. Likelihood criteria and RF parameters

Model	p[a]	log L[b]	AIC[c]	BIC[d]	ρ[e]	κ[f]
Residuals modelled by a cubic VF						
LP6	51	-61	224	625		
EXP VF3	35	-125	320	597	0.981	1.00
DEX VF3	36	-124	319	603	0.983	1.02
DEX VF4	37	-123	319	611	0.985	1.02
DEX VF5	38	-121	318	617	0.983	1.00
SAD VF3	36	-122	317	600	0.980	0.95
Classes of residuals						
SAD VF3 e1	33	-145	356	616	0.982	1.04
SAD VF3 e6	38	-55	226	526	0.945	0.59
SAD VF3 e7	39	-63	**206**	**513**	0.926	0.47

[a]number of parameters, [b]log likelihood (+51,500), [c]Akaikes´s and [d]Schwarz´ Bayesian information criterion (both –103,000), [e]auto-correlation and [f]scale factor.

by animal permanent environmental effects. Based on both criteria (AIC and BIC) model SAD VF3 with 7 classes for σ^2 and 39 parameters to be estimated fitted best.

Estimates of variances for the best model, and the corresponding LP model for PE (from Albuquerque and Meyer (2001)) are shown in figure 2. Phenotypic variance estimates agreed well. Differences, albeit small, occurred mainly in the partitioning of animal and residual variances, while estimates of maternal variances (not shown) were not affected by the model for PE. Modelling residual variances as a cubic variance function (SAD VF3, 36 parameters) or a step function with *e*=6 classes (38 parameters) instead of *e*=7 produced large changes not only in residual variance estimates, but also in the estimates of direct effect variances. In contrast, Olori *et al*. (1999) found that fitting different models for residual variances resulted in changes in log L and in estimates of residual variances, without affecting estimates of animal effect variances notably. Analyses fitting SAD for PE and a quintic LP for A (Albuquerque and Meyer, unpublished), however, showed a behaviour similar to Olori's *et al.* (1999) results, i.e. estimates of genetic direct variance components were robust to differences in modelling the residual variances. Heritabilities estimated (not shown) by the best RF model were similar to those obtained by the LP model.

Average correlations, plotted against lags in age at recording, for models fitting LP, EXP or SAD for PE are shown in figure 3. Residual variances were modelled trough a cubic variance

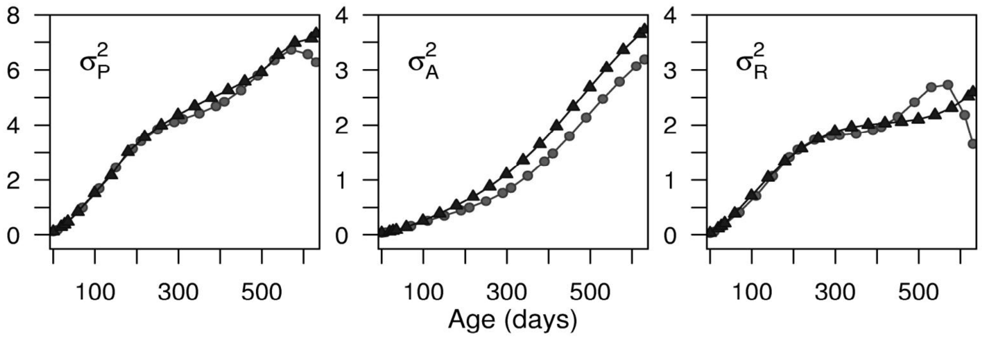

Figure 2. Phenotypic (σ_P^2), direct genetic (σ_A^2) and permanent environmental (σ_R^2) variance estimates (kg^2/100), fitting LP6 (●) and SAD VF3 with *e*=7 (▲) for PE

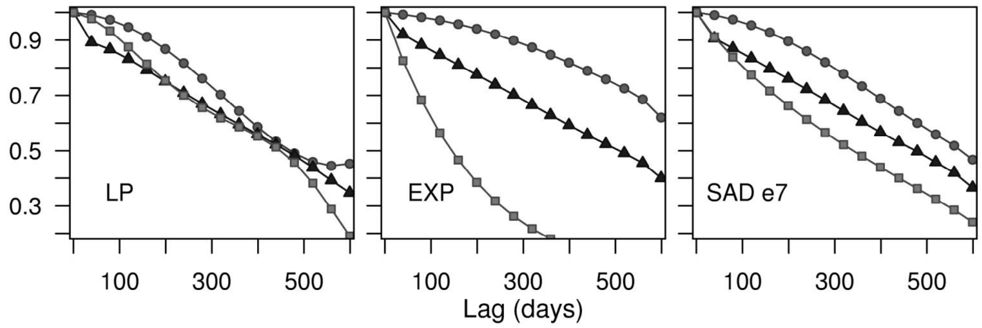

Figure 3. Average estimates of phenotypic (▲), direct genetic (●) and permanent environmental (■) correlations.

function for LP and EXP models and a step function (e=7) for SAD. Average correlation estimates for SAD fitting a cubic variance function for residual variances (not shown) were very similar to those obtained using EXP. This was to be expected, as SAD corresponds to a stationary model (autocorrelation function) for κ close to unity. The model for PE did not affect phenotypic correlation estimates markedly, though estimates for a lag of one day were smaller for LP than for the RF models. However, correlation estimates for direct effect differed between models. EXP is a stationary function i.e. correlations depend only on the lag between ages. PE correlation estimates thus showed a steady decline with increase in lag. For LP and SAD, the decrease in estimates with lag in age at recording was smaller than for EXP. Estimates of direct genetic correlations for the LP model levelled of for lags larger than 560 day, indicating a slight increase in estimates of correlations between early and late weights.

CONCLUSIONS

Results suggest that correlation functions, combined with a variance function to account for heterogeneous variances, can model covariances between direct permanent environmental effects adequately. Moreover, they can reduce the number of parameters needed substantially compared to a model fitting a RR on LP of age. A non-stationary function appears most appropriate. There are indications that the robustness of variance component estimates to changes in the model for residual variances depends on the order of polynomial fit for direct genetic effect variances. Further research is necessary to verify this result. Furthermore, consequences of different partition of direct effect variances on predictions of breeding values and response to selection have to be investigated.

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