ESTIMATES OF COVARIANCE FUNCTIONS FOR MATURE WEIGHT OF BEEF COWS IN THE WOKALUP SELECTION EXPERIMENT

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SUMMARY

Genetic and residual covariance functions and temporary environmental variances were estimated for January weights of cows in the Wokalup selection experiment, recorded at ages from 2 to 10 years. Various subsets of the data and orders of fit (k) from 2 to 4 were considered. For Wokalups, a quadratic function ($k=3$) described the data adequately while a cubic coefficient ($k=4$) was required for Herefords. Results indicate that a minimum of 3 'traits' is necessary to model the growth curve of beef cattle.

Keywords : Beef cattle, genetic parameters, mature weight, covariance function

INTRODUCTION

There has been interest in including mature weight in genetic evaluation of beef cattle. Previous work assumed cow weights to represent the same genetic trait. However, cows tend to grow up to 5 or 6 years of age and early cow weights may be more closely related to 400- or 600-day weight than late mature weights. Covariance functions (CF) provide a way to model growth over the period of an animal's life with the appropriate number of 'traits'. CF are, in essence, the 'infinite dimensional' equivalents to covariance matrices for traits recorded at (potentially infinitely) many times (Kirkpatrick *et al.*, 1990). Meyer and Hill (1996) reviewed their application to longitudinal data in animal breeding and showed that CFs can readily be estimated by Restricted Maximum Likelihood (REML) fitting an animal model. This paper presents a covariance function analysis of mature weight records of beef cows which have previously been analysed fitting a repeatability model or fitting a Gompertz curve for each animal and analysing its parameters as new traits (Meyer, 1995).

MATERIAL AND METHODS

Data. Data consisted of January weights of cows in the Wokalup selection experiment. This comprised two herds of about 300 cows each, one herd consisting of straightbred Polled Herefords, the other of a synthetic breed formed by mating Charolais × Brahman bulls with Friesian × Angus or Hereford cows, 'Wokalups' for short. Animals were selected for increased preweaning growth rate; see Meyer *et al.* (1993) for further details. With weaning in November/December and seasonal pasture growth in winter and spring, cows tended to be at their top weight in the year in January. Data were extracted for cows from 2 to 10 years of age, with n years referring to cows in their $n-$th year of life. 3-year olds, for example, were on average 33 months old in January. Characteristics of the data structure are given in Table 1.

Analyses. Estimates of genetic ($\mathcal{A}$) and permanent environmental ($\mathcal{R}$) CFs and measurement errors (σ^2_ε) were obtained by REML as described by Meyer and Hill (1996), fitting a simple animal model with year-paddock subclasses as fixed effects and utilising all pedigree information available. Analyses were carried out fitting both CFs to the same order k for $k=2,3$ and 4, and considering increasingly

Table 1. Characteristics of the data structure

Age (years)	2	3	4	5	6	7	8	9	10
					Hereford				
No. records	753	666	514	443	321	243	180	121	75
Mean (kg)	403.0	488.3	551.9	586.7	597.1	603.2	611.3	604.1	609.0
SD[a] (kg)	52.2	64.2	60.9	65.7	64.1	59.2	59.0	58.5	60.6
CV (%)[b]	12.9	13.1	11.0	11.2	10.7	9.8	9.7	9.7	10.0
No. CG[c]	38	35	31	30	26	24	22	19	18
					Wokalup				
No. records	808	662	513	440	372	289	201	145	94
Mean (kg)	447.5	522.2	584.0	611.9	625.7	640.9	637.8	632.1	633.9
SD (kg)	57.3	70.7	71.8	72.5	74.0	68.8	63.6	64.9	65.6
CV (%)	12.8	13.5	12.3	11.9	11.8	10.7	10.0	10.3	10.4
No. CG	41	35	32	30	27	25	23	21	17

[a]Standard deviation
[b]Coefficient of variation
[c]No. of year-paddock subclasses

larger subsets of the data, i.e. records from 2 to 5 years only, 2 to 6 years only, and so forth. 'Reconstructed' estimates of the covariance matrices for the 9 ages were calculated from the estimated CFs and measurement errors. In addition, variance components for individual ages were estimated (univariate analyses).

RESULTS AND DISCUSSION

Order of fit. Log Likelihoods ($\mathcal{L}$), expressed as deviation from $\mathcal{L}$ for $k=4$, are given in Table 2 for analyses considering an increasing number of ages. For Herefords, $k=2$ did not describe the data adequately in any case, i.e. an increase in variation over time could not be attributted to increasing size (scale effect). Fitting a cubic polynomial ($k=4$) gave a significant increase in $\mathcal{L}$ over $k=3$ when weights from cows older than 9 years were considered. For Wokalups, $k=3$ was sufficient and for records up to 6 years $\mathcal{L}$ did not increase significantly over $k=2$. Previous analyses (Meyer *et al.*, 1993) showed growth in Herefords to be subject to substantial maternal effects, with a carry-over to adult weight. This analysis ignored maternal effects, i.e. the extra term required for Herefords might, in part at least, reflect their influence.

Table 2. Log likelihoods

	2–5	2–6	2–7	2–8	2–9	2–10
			Hereford			
$k=2$	-15.28	-30.77	-43.13	-60.08	-56.65	-70.14
$k=3$	-5.37	-0.87	-1.05	-6.19	-11.72	-21.66
			Wokalup			
$k=2$	-9.02	-8.96	-23.92	-23.58	-30.97	-28.54
$k=3$	-3.92	-3.74	-7.13	-2.65	-2.48	-2.09

Covariance functions. Estimates of the coefficients of CF (considering ages 2–10) are given in Table 3. From these, estimates of ($\mathcal{A}$) and ($\mathcal{R}$) can be calculated as :

$$\mathcal{A}(a_i,a_j) = 533.2 - 207.4(a_i+a_i) + 2.6(a_i^2+a_j^2) + 400.7(a_i^3+a_j^3) + 123.8a_ia_j - 52.2(a_ia_j^2$$
$$= + a_i^2a_j) - 261.3(a_ia_j^3+a_i^3a_j) + 164.1a_i^2a_j^2 + 100.9(a_i^2a_j^3+a_i^3a_j^2) + 563.7a_i^3a_j^3$$
$$\mathcal{R}(a_i,a_j) = 2111.4 - 249.0(a_i+a_i) - 1091.1(a_i^2+a_j^2) - 185.4(a_i^3+a_j^3) + 2091.6a_ia_j + 459.2$$
$$= (a_ia_j^2+a_i^2a_j) - 1653.4(a_ia_j^3+a_i^3a_j) + 812.4a_i^2a_j^2 - 442.6(a_i^2a_j^3+a_i^3a_j^2) + 1588.9a_i^3a_j^3$$

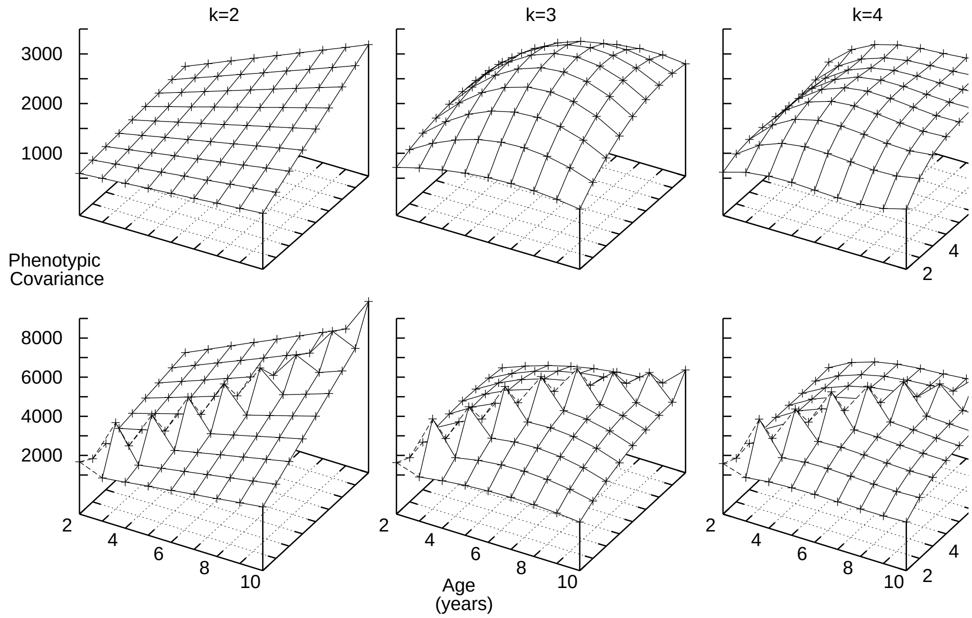

Figure1.

'Reconstructed' covariance matrices for Wokalups.

for Herefords ($k = 4$), and

$$\mathcal{A}(a_i, a_j) = 2326.3 + 416.1(a_i + a_i) - 860.4(a_i^2 + a_j^2) + 201.5 a_i a_j - 92.7(a_i a_j^2 + a_i^2 a_j) + 555.7 a_i^2 a_j^2$$

$$\mathcal{R}(a_i, a_j) = 1188.0 + 214.0(a_i + a_i) - 401.3(a_i^2 + a_j^2) + 124.3 a_i a_j + 4.4(a_i a_j^2 + a_i^2 a_j) + 255.3 a_i^2 a_j^2$$

for Wokalups ($k = 3$), with a_i denoting the $i-$th age standardised to the interval -1 to 1. Note that for an age of 6 years, $a_i = 0$, i.e. the estimated variance at this age is equal to the scalar term in $\mathcal{A}$ or $\mathcal{R}$.

Covariance matrices. The CFs given above can be used to 'reconstruct' genetic and permanent environmental covariance matrices for the ages in the data. These are shown in Figure 1 for Wokalups. For $k = 2$, all covariance estimates lie on a plane, the linear coefficient determining its tilt. For $k = 3$ the surface is quadratic, and the cubic term in the CF makes it less regular for $k = 4$. Estimates of the measurement error variances (σ_ε^2) are given in Table 4. For Wokalups, all σ_ε^2 are of similar magnitude, i.e. a model fitting the same temporary environmental variance (single parameter) for all 9 ages might have been appropriate. Table 4 also contrasts estimates of phenotypic variances (σ_P^2), calculated from the diagonals of the reconstructed covariance matrices and the estimates of σ_ε^2 (for $k = 4$), with estimates of σ_P^2 from univariate analyses. Estimates from CF and univariate analyses agree closely for up to 6 years, i.e. the ages with comparatively many observations. These dominate the estimates of the CF. Animals are still growing to this age with correspondingly increasing variances (see Table 1), i.e. the estimated CFs reflect this 'upward trend' which leads to overestimates of variances for later ages with few records. Figure 1 shows how the estimates of phenotypic (co)variances for later ages are 'pulled down' as k increases, and how σ_P^2 are inflated due to the variance of measurement errors.

Table 3. Estimates of coefficients (K_{ij}) of covariance functions

		P. Hereford						Wokalup					
		Genetic			Residual			Genetic			Residual		
i	j	$k=2$	$k=3$	$k=4$	$k=2$	$k=3$	$k=4$	$k=2$	$k=3$	$k=4$	$k=2$	$k=3$	$k=4$
1	1	3669	1537	1146	1416	2715	2948	2369	3629	3051	3675	1898	1959
1	2	1011	-282	41	50	574	491	519	445	344	1058	249	249
1	3		-421	34		-435	-489		-403	-248		-189	-136
1	4			131			11			116			24
2	2	348	95	9	176	495	453	207	134	123	305	83	99
2	3		127	3		141	67		-32	-29		2	1
2	4			13			-122			-3			5
3	3		188	29		215	144		99	79		45	23
3	4			9			-4			-6			4
4	4			26			73			11			12

Table 4. Estimates of variance components

Age	2	3	4	5	6	7	8	9	10
					Hereford				
σ_ε^{2a}	413	1022	783	820	906	886	827	1153	732
σ_P^{2b}	1030	2450	3044	3425	3571	3593	3625	4058	4121
	1117	2455	3074	3324	3309	3120	3011	3382	–[c]
					Wokalup				
σ_ε^2	1220	1204	1166	1246	1250	1237	1292	1341	1502
σ_P^2	1586	3590	3841	4455	4482	4451	4073	4124	4679
	1598	3651	4111	4064	4339	3614	3362	3371	3566

[a] temporary environmental variance
[b] phenotypic variance; 1*st* line : 're-constructed values' from CF analysis, 2*nd* line : from univariate analyses
[c] Analysis failed

CONCLUSIONS

Results clearly show that a minimum of 3 'traits' is needed to model growth in beef cows, the last factor being required when records past maturity (5–6 years) are considered. CFs can also be modelled by fitting k random regression coefficients (both for $\mathcal{A}$ and $\mathcal{R}$). This yields estimates of the genetic and phenotypic growth curves for each animal. In contrast to previous analyses fitting a Gompertz curve, it does not require any *a priori* assumptions about the shape of the curve.

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