Estimates of (co)variance function for growth to yearling in Horro sheep of Ethiopia using random regression model

SOLOMON ABEGAZ^{1,2}, JACOB BERNARDUS VAN WYK² and JACOBUS JOHANNES OLIVIER^{2,3}

¹Institute of Biodiversity Conservation, Addis Ababa, Ethiopia, ²Department of Animal, Wildlife and Grassland Sciences, University of the Free State, Bloemfontein, South Africa, ³Irene Animal Improvement Institute, Stellenbosch, South Africa

Abstract

Random regression analyses of weight data from birth to 396 days were done using 22 141 weight records of 1951 Horro lambs. Six different models formed from three different orthogonal polynomial regressions (legendre scale)orders (quadratic, cubic, quartic) of fit for both additive genetic and animals' permanent environmental effects, with assumption of either homogeneous or heterogeneous residual variance, were compared. Fixed effects of year and type of birth, sex and age of dam were fitted along with a fourth order polynomial. Both likelihood ratio test (LRT) and Akaike's Information Criterion (AIC) were used for model comparison. Model fit improved with increased order of polynomial and assumption of heterogeneity of residual variance. Components for additive genetic and permanent environmental (co)variance increased from 0.03 and 0.09 at birth to 23.8 and 37.6 at 396 days of age, respectively. The first three eigenvalues of the coefficient matrix of the additive genetic covariance accounted for about 98% of the sum of all the eigenvalues. Heritability estimates have shown a declining and increasing trend at different parts of the trajectory, the lowest estimate being 0.14 for weight at birth while the highest being 0.36 for weight at about 390 days of age. Higher heritability estimates in previous uni- and bi-variate models and in the current study and also strong correlation with weight at early age makes weight at one year of age the most important trait to consider in improving productivity in Horro sheep.

Keywords: orthogonal polynomial, animal model, heritability estimates, eigenvalues, eigenfunctions, genetic correlations

Zusammenfassung

Schätzung von (Ko)Varianzfunktionen für das Jährlingswachstum von Horroschafen in Äthiopien mittels Random Regressionsmodellen

Für die Random Regressionsanalyse konnten 22141 Gewichtsdaten von 1951 Horroschafen, erfasst von Geburt bis zum Alter von 396 Tagen, genutzt werden. Verglichen wurden sechs unterschiedliche Modelle wobei die fixen Effekte Jahr, Geburtstyp, Geschlecht und Alter der Mutter polynominal angeordnet wurden. Für den Modellvergleich wurde der Likelihoodverhältnistest sowie Akaikes Informationskriterium genutzt. Die Modellanpassung verbesserte sich bei höherer Einordnung im Polynominal und der Annahme von Heterogenität der Restvarianz. Die Komponenten der additiven genetischen Varianz und der permanenten Umwelt Kovarianz verbesserten sich von 0,03 und 0,09 bei Geburt bzw. 23,8 und 37,6 im Alter von 396 Tagen. Die ersten drei Eigenvalues in der Koeffizientenmatrix der additiven genetischen Kovarianz lagen mit über 98 % höher als die Summe aller Eigenvalues. Die Heritabilitätsschätzung zeigt eine Abnahme und Trendanstieg bei einigen Teilen der Kurvenbahn, der geringste Schätzwert lag bei 0,14 für das Geburtsgewicht während der höchste Wert 0,36 für das Gewicht über 390 Tage erreichte. Höhere Heritabilitätsschätzwerte in vorangegangenen ein- und zweidimensionalen Varianzmodellen und der gegenwärtigen Schätzung ebenso wie die Gewichtskorrelationen im frühen Alter machen das Jährlingsalter zum wichtigsten Merkmal für die Erreichung einer besseren Produktivität des Horroschafes.

Schlüsselwörter: orthogonale Polynome, Tiermodell, Heritabilitätsschätzung, Eigenvalues, Eigenfunktion, genetische Korrelation

Introduction

Weights of an animal measured at different stages (longitudinal data) are an extension of the same trait measured along a trajectory of time. Conventionally repeatability or multivariate models are used and occasionally growth curve models were also used. In the repeatability model assumptions are that variances are homogeneous and genetic correlations between measurements at different stages are unity. These assumptions are rarely met for such weights are changing with time. In multivariate analysis in addition to possible over-parameterization when a large number of longitudinal measurements are considered, the use of unstructured covariance matrix for data which are structured is not appropriate. Additionally such analytical models do not provide information about the trend of change of a trait over time. The growth curve approach where a few parameters describing the curve are derived from the data and the components of variation for such parameters are determined, assumes that a certain standard curve equally fits the growth of all animals. However, in practice it is possible that different growth curves could have a different degree of fit for different animals.

Currently random regression models are being applied in the analysis of longitudinal growth in cattle (MEYER 1999, ALBUQUERQUE and MEYER 2001, ROBERT-GRANIÉ *et al.* 2002, KREJČOVÁ *et al.* 2007) sheep (LEWIS and BROTHERSTONE 2002, FARHANGFAR *et al.* 2007, KESBI *et al.* 2008) pig (HUISMAN *et al.* 2002) and test-day lactation (JAMROZIK and SCHAEFFER 1997, OLORI *et al.* 1999, KETTUNEN *et al.* 2000, POOL and MEUWISSEN 2000, TAKIMA and AKBAŞ 2007) data. These models use polynomials in time to describe mean profiles with random coefficients to generate a correlation among the repeated observations on each individual (ROBERT-GRANIÉ *et al.* 2002). This approach has the advantage of studying change and increases statistical power. This is due to units serving as their own control and due to the possibility of estimating (co)variance components at any point on the trajectory of time. Additional advantages include the use of weight measurements without any need to correct for age and the reduction in the number of parameters to be estimated as compared to multivariate analysis. Lower approximate standard error estimates for parameters as compared to estimates from univariate analysis (FISCHER *et al.* 2004) are also additional advantages of the random regression analysis.

In the tropics where large fluctuation in environmental variables, particularly in availability of feed, is common concurrent fluctuations in weight (growth) of animals is likely to occur. Under this condition the use of random regression analyses where the trait is the whole set of measurements along the trajectory may have an advantage in obtaining reliable estimates of parameters.

Previously univariate and bivariate analyses of data on birth, weaning, six-month and yearling weights have been done (ABEGAZ *et al.* 2002). In this study different random regression models were applied in the analysis of weight data taken from birth to 396 days of age with the objective of identifying the appropriate model, obtaining more accurate estimates and identifying the optimal selection age for live weight.

Materials and methods

Data: The data used in this study were collected from a flock of Horro sheep during the period 1978 to 1997 (excluding lambs born in 1984) at Bako research center, Ethiopia. Details on the environment and flock management were decscribed in a companion paper (ABEGAZ *et al.* 2002). Body weight recorded from birth to a maximum of 396 days of age (no weight was available for ages 1 to 9 days) was used. About 8, 7, 6, 6, 12, 16 and 45 % of the animals have 7, 8, 9, 10, 11, 12 and 13 weight measurements, respectively. All animals have a birth weight record. In order to explore the resulting change from fitting polynomials of higher order the edit criteria followed was to keep animals with a minimum of seven weight records. Due to this no record from lambs born in the year 1984 was retained. A total of 22 141 records of 1 951 animals from 158 sires and 679 dams were eventually available. To decrease computer memory requirements observations were categorized to the nearest third day of age (0, 9, 12,...396 d).

Statistical analysis: Fixed effects with a significant (*P*<0.05) effect on weights within the range of age in this study were included in the analytical model. These include year of birth, type of birth, sex and age of dam. To determine the most appropriate polynomial order to be fitted as fixed effect, preliminary analyses with ordinary polynomials of third to seventh order were carried out. Starting from the fourth order, the coefficient of determination and standard error of the regression stabilized (not shown here). Thus in all cases, weight as a function of age in days at weighing was included as a fixed regression of orthogonal polynomial of order four (cubic). This fixed regression describes the average growth curve of all animals with records.

Covariance functions for the random additive genetic and animal's permanent environmental component of variance were modeled with orthogonal polynomial regressions of varying order. Estimations were done by REML using a random regression model with the DXMRR statistical package (MEYER 1998a). The general model in matrix notation is:

$$y = Xb + Za + Wp + e$$

(1)

where **y** is a vector of weights of each animal, **b** is a vector of fixed effects including year, sex, type of birth and age of dam and a polynomial of age in days, **a** is the vector of additive genetic regression, **p** is the vector of permanent environmental random regression coefficients and **e** is the vector of residual effects. **X**, **Z** and **W** are corresponding design matrices. In all cases orthogonal polynomials on the legendre scale were used.

A total of six models (Table 1) formed by concatenation of sub-models varying in the order of polynomial fit (quadratic, cubic and quartic) and in the assumption about the distribution of the residual variance (homogenous or heterogeneous) were compared. Repeated analyses using the AI-REML algorithm were done until no change was observed in log likelihood between consecutive runs. A subsequent analysis using the derivative free Powel's method was also carried out to ensure convergence to a global maximum. Comparison for better order of fit of the different models was done by likelihood ratio test (LRT) and Akaike's Information criteria (AIC) as suggested by BURNHAM and ANDERSON (1998). A model with significantly the highest (*P*<0.05) LRT and with the lowest AIC was considered to be the most appropriate model.

A reduced model of rank four (of Model 6) was used to calculate eigenfunctions for additive genetic and permanent environmental effect. Eigenfunctions were obtained as

$$\Psi_i = \sum_{j=1}^{k=1} v_{ij} \theta_j (t^*)$$
⁽²⁾

where Ψ_i is the *i*-th eigenfunction of the covariance function, v_{ij} is the *ij*-th element of the eigenvector and θ_i (t^*) is the *j*-th order legendre polynomial of the standardized age t^* .

Table 1
Description of models used in random regression analysis
Beschreibung der Modelle bei Nutzung der Random Regressionsanalyse

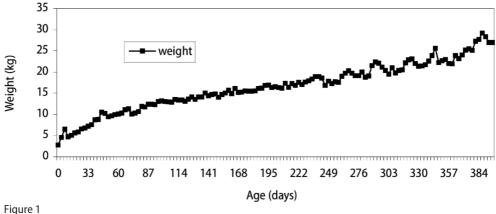
Model	Order of p	No. of error measures ^{b)}	
	Fixed	Random ^{a)}	
1	4	3	1
2	4	3	4
3	4	4	1
4	4	4	4
5	4	5	1
6	4	5	4

^{a)}For both additive genetic and permanent environmental effects, ^{b)}Four error measures (weight at birth, 10 to 90 days, 91 to 180 days and 180 to 408 days)

Results

Weight measurements across the age range are presented in Figure 1. Weight increased from 2.7 kg at birth to 30 kg at about 390 days of age. Fluctuation in mean weight at consecutive ages was observed. This was mainly due to measurements for consecutive ages (days) not being from identical sets of animals.

The log-likelihoods and AIC differences are presented in Table 2. Significantly the highest log liklihood (LRT) (*P*<0.05) and the lowest AIC were observed for Model 6. Both values improved with increase in the order of fit from three (quadratic) to four (cubic) and five (quartic). Assuming heterogeneity of residual variance (four error measures) between weights at different ages has also resulted in significant (*P*<0.05) increases in the log-likelihood estimates under all orders of polynomial fit. For models with the same order of fit for the random effects but with varying assumptions about the distribution of the residual variance the change in log likelihood was 1 134, 1 073 and 1 012 for the quadratic cubic and quartic order of fit, respectively. Under both LRT and AIC, Model 6 was found to be superior to all other models.



Average weights with the range of ages used in the study Altersabhängige Entwicklung der Durchschnittsgewichte

Table 2

Log-likelihood (Log L), likelihood ratio test (LRT) and differences in Akaike's information criteria (AIC) values for different models

Model	No. of parameters ^{a)}	Log L	LRT	AIC differences
1	13	-25 904.7	0.0	5 706.4
2	16	-24771.2	2 267.0	3 4 4 5.4
3	21	-25 226.5	1 356.4	4 366.0
4	24	-24 153.8	3 501.8	2 2 2 6.6
5	31	-24043.0	3723.4	2 019.0
6	34	-23 030.5	5 748.4	0.0

Log-L sowie LRT und Unterschiede der AIC Werte für die 6 Modelle

^{a)}[k(k+1)]+NE, for k=order of fit, NE number of error measures

Estimates of heritability and the ratios of permanent environment to the phenotypic variance obtained from the different models (for points at 30 days interval) are presented in Table 3.

The heritability estimates for the entire period obtained from Model 6 has increased from about 0.14 at birth to about 0.33 around two months of age and then declined to 0.26 at about 200 days of age to increase again to 0.36 at about 390 days of age. As was the case with the variance components, heritability estimates showed a drop at about 90 days of age, but drastic increase towards the end of the period.

Estimates differed between models fitting different polynomial order and error measures for weight at birth and early ages. For most of the growth period afterwards, estimates within the same polynomial order of fit but with different error measures, (Model 1 vs. 2, Model 3 vs. 4, Model 5 vs. 6) were more similar. The animals' permanent environmental effect has accounted for 0.42 to 0.67 % of the total variation. Repeatability values (heritability + ratio of permanent environmental variance) ranged from 0.56 at birth to 0.98 at 390 days of age. The repeatability value obtained in this study for weights at later ages was very high.

Correlation estimates for additive genetic, and phenotypic effects from Model 6 are presented in Table 4. Correlations between weight at birth and at other ages were low in all cases. Genetic correlation estimates showed a more fluctuating trend than phenotypic

correlations. For phenotypic correlations, estimates increased steadily as the difference in age at measurements decreased. The same is true for permanent environmental correlation (not shown here).

Estimates of coefficients of covariance function and eigenvalues for additive genetic and permanent environmental effects from Model 6 are presented in Table 5 and Table 6, respectively. For additive genetic covariance function the first, second and third eigenvalues accounted for 83.2, 9.1 and 5.8%, while for permanent environmental effect they accounted for 87.7, 8.9 and 2.5%, respectively. One of the eigenvalues of the covariance function was close to zero. Eigenfunctions with very small (or zero) eigenvalues represent deformations for which there is little (or no) additive genetic variation (KIRKPATRICK et al. 1990) and a more parsimonious fit of the covariance functions might be obtained by estimating a reduced rank of the coefficient matrix, forcing very low values of the eigenvalue to zero (MEYER 1998b). Hence eigenfunctions of the additive covariance function were estimated from a reduced model of rank four. Corresponding eigenfunctions for the first four eigenvalues of the additive covariance function are presented in Figure 2. The first eigenfunctions were positive throughout the growth period but have shown a decline with age. The second eigenfunction was negative up to about 90 days of age and positive afterwards. The third and fourth eigenvalues were very low in value and their corresponding eigenfunctions are of very little practical significance.

Ta	bl	e	3

Heritability estimates and variance ratios of permanent environmental variance as proportion of total phenotypic variance and residual variance from the different models

Heritabilitätsschätzwerte bei unterschiedlichem Alter und Modell

Age, days	Heritability Model					
	1	2	3	4	5	6
0	0.00	0.13	0.01	0.13	0.03	0.14
30	0.07	0.12	0.18	0.25	0.25	0.31
60	0.16	0.20	0.28	0.31	0.30	0.32
90	0.20	0.23	0.23 0.30 0.31		0.28	0.30
120	0.22	0.25	0.29	0.28	0.28	0.28
150	0.23	0.25	0.27	0.26	0.27	0.27
180	0.24	0.26	0.25	0.25	0.27	0.26
210	0.25	0.25	0.24	0.25	0.25	0.25
240	0.26	0.26	0.25	0.26	0.27	0.27
270	0.28	0.27	0.27	0.28	0.30	0.30
300	0.29	0.28	0.30	0.31	0.34	0.35
330	0.31	0.30	0.34	0.35	0.36	0.35
360	0.34	0.32	0.38	0.40	0.35	0.35
390	0.36	0.34	0.42	0.44	0.35	0.36
Permanent en	vironmental ratio ^{a)}					
0	0.01	0.17	0.01	0.18	0.01	0.42
30	0.24	0.27	0.29	0.37	0.37	0.44
60	0.43	0.46	0.46	0.50	0.51	0.55
90	0.53	0.55	0.53	0.56	0.58	0.61
120	0.58	0.59	0.58	0.58	0.62	0.61
150	0.61	0.62	0.62	0.62	0.64	0.63
180	0.63	0.63	0.65	0.65	0.66	0.66
210	0.64	0.62	0.67	0.65	0.68	0.67
240	0.65	0.63	0.68	0.65	0.68	0.67
270	0.65	0.63	0.67	0.65	0.65	0.64
300	0.64	0.63	0.65	0.63	0.62	0.62
330	0.63	0.63	0.62	0.60	0.61	0.61
360	0.62	0.62	0.59	0.56	0.63	0.62
390	0.61	0.61	0.56	0.53	0.63	0.61
Residual variar	ice ^{b)}					
1	1.99	0.16	1.56	0.15	1.17	0.09
2	-	1.83	-	1.23	-	0.84
3	-	1.92	-	1.76	-	1.42
4	-	2.76	-	2.11	-	1.50

^{a)}Permanent environmental ratio (variance between repeated records of animal/phenotypic variance), ^{b)}One (homogeneous) or four (weight at birth, 10 to 90 days, 91 to 180 days and 180 to 408 days) error measures.

4 3 2 - 0	Table 5 Coefficients <i>Kovarianzfu</i> Effect	Age, days 0 60 90 120 150 150 180 210 2210 2270 3300 330 330 330	Genetic (be <i>Genetische</i> (
4.703 1.855 -1.022 1.897 0.149	Table 5 Coefficients of covariance functions between random regression coefficients for direct genetic effect and amount and percent of Kovarianzfunktionskoeffizient zwischen dem Random Regressionskoeffizienten für den direkten genetischen Effekt und Eigenvalues so Coefficients of covariance function ^a Effect 0 1 2 2 3 4	0 	Genetic (below diagonal) and phenotypic (above diagonal) correlation between weights at different stages estimated from model 6 Genetische (unter Diagonale) und phänotypische (über Diagonale) Korrelationen zwischen Gewichten und Alter bei Modell 6
	nce functior fizient zwise	30 - 0.23 0.97 0.87 0.87 0.74 0.63 0.63 0.64 0.65 0.65 0.65 0.65 0.65 0.65 0.65	al) and phei nale) und pi
1.855 11.539 14.414 –9.875 –14.723	is between <i>hen dem Ra</i> 1	60 0.21 0.79 0.96 0.96 0.79 0.74 0.72 0.71 0.68 0.65 0.63 0.59 0.45	hotypic (abc hänotypisch
	random reg <i>indom Regr</i> i Coeffic	90 0.21 0.75 0.87 0.97 0.97 0.97 0.92 0.87 0.83 0.83 0.76 0.61 0.61 0.55	ove diagona e (über Diag
-1.022 14.414 35.160 -15.757 -35.555	ression coe essionskoeff ients of cov	120 0.20 0.67 0.81 0.88 0.99 0.99 0.99 0.99 0.99 0.99 0.89 0.79 0.79 0.56 0.58 0.56	al) correlatic Jonale) Korre
22 14 57 57	lom regression coefficients for dire m Regressionskoeffizienten für den d Coefficients of covariance function 2	150 0.19 0.76 0.85 0.85 0.88 - 0.99 0.99 0.93 0.93 0.93 0.93 0.57 0.57 0.62 0.68	on between elationen zu
	' direct gen <i>den direkter</i> ction ^ª	180 0.18 0.71 0.82 0.86 0.90 - 0.90 0.77 0.68 0.77 0.65 0.70	weights at <i>vischen Gew</i>
1.897 9.875 15.757 14.038 18.255	etic effect <i>a</i> 1 <i>genetische</i> 3	210 0.17 0.54 0.67 0.77 0.82 0.87 0.91 - 0.91 0.97 0.88 0.81 0.79 0.88	different st vichten und .
	nd amount n Effekt und	240 0.16 0.53 0.64 0.72 0.76 0.76 0.87 0.87 0.91 0.97 0.93 0.93 0.93 0.74	ages estima Alter bei Mo
0.149 14.723 35.555 18.255 39.078	: and percer <i>1 Eigenvalue</i> 4	270 0.14 0.52 0.66 0.66 0.68 0.74 0.80 0.80 0.87 0.93 - 0.93 0.99 0.97 0.92	ated from m dell 6
	nt of eigenv s sowie % b	300 0.13 0.50 0.57 0.60 0.62 0.67 0.74 0.83 0.90 0.94 0.99 0.94	iodel 6
11.982 1.313 0.002 0.838 0.263	Table 5 Coefficients of covariance functions between random regression coefficients for direct genetic effect and amount and percent of eigenvalues under Model 6 Kovarianzfunktionskoeffizient zwischen dem Random Regressionskoeffizienten für den direkten genetischen Effekt und Eigenvalues sowie % bei Modell 6 Coefficients of covariance function ^a Effect 0 1 2 2 3 4 Eigenvalues	330 0.12 0.49 0.55 0.58 0.59 0.64 0.71 0.79 0.67 0.87 0.93 0.95 - 0.95 0.97 0.75	
	· Model 6	360 0.12 0.52 0.55 0.55 0.59 0.59 0.63 0.70 0.77 0.84 0.89 0.92 0.95 - 0.89	
83.2 9.1 5.8 1.8	%	390 0.13 0.24 0.52 0.57 0.57 0.57 0.57 0.63 0.67 0.71 0.71 0.74 0.75 0.75 0.77 0.82 0.91	

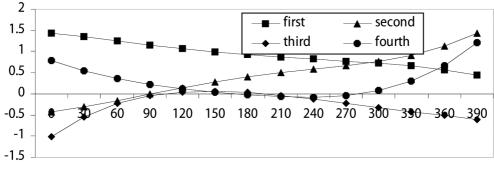
Table 6

Coefficients of covariance functions between random regression coefficients for animals' permanent effect and the eigenvalues under Model 6

Kovarianzfunktionskoeffizient zwischen Random Regressionskoeffizienten des ständigen Tiereffektes und Eigenvalues sowie % bei Modell 6

Coefficients of covariance function ^a							
Effect	0	1	2	3	4	Eigenvalues	%
0	12.239	6.463	-4.005	1.119	-0.382	24.902	87.7
1	6.463	15.644	5.796	-8.924	-5.433	2.535	8.9
2	-4.005	5.796	19.501	-4.593	-14.329	0.006	0.0
3	1.119	-8.924	-4.593	11.521	6.020	0.703	2.5
4	-0.382	-5.433	-14.329	6.020	15.206	0.260	0.9

^a0 intercept, 1 linear, 2 quadratic, 3 cubic, 4 quartic



Age (days)

Figure 2

Eigenfunctions of additive covariance function corresponding to the eigenvalues of a reduced model of rank 4 Eigenfunktion der additiven Kovarianzfunktion entsprechend Eigenvalues des reduzierten Modells 4

Discussion

Model fit improved with increasing polynomial regression order. Improved fit was also realized for models with the same order of fit for the random effects but with varying assumptions about the distribution of the residual variance. For assumption of heterogeneity of the residual variance log likelihood increased by 1 134, 1 073 and 1 012 over assuming uniform variance for the quadratic, cubic and quartic order of fit, respectively. This implies that part of the residual variance would be taken up by the increase in the order of polynomial fit. For most of the growth periods (after the early ages) estimates of heritability and ratio of permanent environmental effect within the same polynomial order of fit but with different error measures, (Model 1 vs. 2, Model 3 vs. 4, Model 5 vs. 6) were more similar. Similarly OLORI *et al.* (1999), found little difference in estimates of additive genetic and environmental variances of test day records in dairy cows when fitting different numbers of measurement error variances. MEYER (2000) also reported little difference in estimates of between-animal standard deviations for higher (\geq 12) orders offit with widely varying number of error measures

(1 to 66). Therefore, for sufficient order of fit, different regression curves to model betweenanimal variations can be examined under the assumption of homogeneous measurement error variances (MEYER 2000). In this study, high orders of fit (six and seven) failed to converge to a global maximum and assuming heterogeneity was therefore necessary.

The heritability estimate for birth weight from Model 6 in the current study was lower than previous estimates from bivariate analyses (ABEGAZ *et al.* 2002) while estimates for weaning and yearling weight were slightly higher. Change in the trend of heritability estimates were observed which is similar to trends reported by AZIZ *et al.* (2005) for Japanese Black cattle and MOLINA *et al.* (2007) for Spanish Merino sheep.

For weight at six month the estimates from both studies were similar. Due to different edit criteria used (animals with number of weight records of less than seven were not included in the current study) the data set for birth and weaning weight in the previous study were much higher than (3 664 and 2 752 Vs 1 951) used in the current study and comparison would be difficult. More similar data sets (2 152 Vs 1 951) were used for six-month weight and this may account for the similarity in the estimate from both previous and current analyses. However total heritability estimates from univariate analysis in the previous study (ABEGAZ *et al.* 2002), with the exception of birth weight, were lower than estimates in this study. In addition to differences in the data set, this may be due to the exclusion of maternal effects in this study. For traits that are likely to be influenced by the maternal effect the exclusion of this effect in the model of analyses would result in overestimation of heritability. Similarly, LEWIS and BROTHERSTONE (2002) reported higher heritability estimates from random regression models ignoring maternal effects than models which included them, with a decline in the difference with increasing age.

In the present study the animals' permanent environmental effect has accounted for 42 to 67 % of the total variation and repeatability values ranged from 0.56 at birth to 0.98 at 390 days of age. In addition to the possibility of improved partitioning of the total variance into environmental and genetic origin, the permanent environmental effect (and the repeatability) indicates how reliable estimates at a specified age could be. The repeatability value increased with an increase in age. Similarly, in pigs, HUISMAN *et al.* (2002) reported increasing values of repeatability which reached a maximum of 0.96 (h^2 =0.18; ratio of permanent environment=0.79) for weight at about 190 days of age. In contrast MEYER (2001) reported relatively lower and stable estimates of repeatability with change in age for weights from birth to weaning in beef cattle.

Genetic and phenotypic correlation estimates for additive genetic and phenotypic effects have shown an increase with decrease in time between the ages considered. Correlations between weight at birth and at other ages were low in all cases. Previous bivariate analyses (ABEGAZ *et al.* 2002) have also resulted in low direct additive and phenotypic correlations between birth weight and weight at weaning (about three months of age), 6 and 12 months of age. Genetic correlation estimates showed a more fluctuating trend than phenotypic correlations. Inappropriate modelling of the genetic effects as a result of ignoring the maternal effect might have caused this. Since the maternal genetic effect varies with age, corresponding (co)variances and resulting correlations are also likely to vary. Fluctuations of correlations of a much higher magnitude for monthly weights of beef cows related with sampling variation in the genetic covariances were reported by MEYER (1998b). For phenotypic correlations, estimates increased steadily as the difference in age at measurements decreased. The same is true for permanent environmental correlation (not shown here). Genetic correlation estimates between weaning (about 90 days of age), six months and yearling weight from previous work (ABEGAZ *et al.* 2002) were in the range of 0.84 to 0.98. Estimates in the current study were lower (0.60 to 0.87) while phenotypic correlation estimates were slightly higher. Inclusion of the permanent environmental effect in the current random regression analysis makes straightforward comparison impossible.

The contribution of the first eigenvalue of the additive genetic covariance function (83.2%) to the total in this study is lower than the value of 95% reported by LEWIS and BROTHERSTONE (2002) for a similar order of fit. This indicates the existence of a sizeable variation (about 17%) that needs to be explained by functions higher than the first order. From a different order of fit on cattle Albuquerque and MEYER (2001) also reported first eigenvalues accounting more than 93% of the total. FARHANGFAR *et al.* (2007) however reported a 80% contribution of the first eigenvalue for daily gain of Lori-Bakhtiari sheep with.

Eigenfunctions corresponding to the first eigenvalue of the additive covariance function have a positive value throughout the growth stage studied. This implies positive genetic correlations across all stages and that selection for weight at any age would result in an increase at all other ages (positive correlation). The second eigenfunction have changed from negative values to about 90 days of age to positive value afterwards. This suggests that genetic effects acting differently (probably different genes) before and after about 90 days of age and selection on this variable decreases weight at early ages, but increases weight at later ages. The eigenvalue represented by this value may be used to select for change in growth curve (e.g. select for lower birth and very early age weight and for higher weight at later ages [marketable age]). This may have an implication on finishing practices and on lambing ease in ewes.

In the current study however, limitations in not including maternal genetic and environmental effects may prohibit firm conclusions to be made with regard to the implication of the random regression analysis in selection. The study has shown the importance of appropriate polynomial regression order and modeling the residual variance. Consistent estimates in a previous and in the current study indicate that weight at about one year of age is the most important trait to consider in improving productivity in Horro sheep.

References

- Abegaz S, Negussie E, Duguma G, Rege JEO (2002) Genetic parameter estimates for growth traits in Horro sheep. J Anim Breed Genet 119, 35-45
- Albuquerque LG, Meyer K (2001) Estimates of covariance functions for growth from birth to 630 days of age in Nelore cattle. J Anim Sci 79, 2776-89
- Aziz MA, Nishida S, Suzuki K, Nishida A (2005) Estimation of direct and maternal genetic and permanent environmental effects for weights from birth to 356 days of age in a herd of Japanese Black cattle using random regression. J Anim Sci 83, 519-30
- Burnham PK, Anderson RD (1998) Model selection and Inference: A practical Information Theoretic approach. Springer, New York, USA, 353
- Farhangfar H, Naeemipour H, Zinvand B (2007) Application of Random Regression Model to Estimate Genetic Parameters for Average Daily Gains in Lori-Bakhtiari Sheep Breed of Iran. Pak. J Biol Sci 10, 2407-12

- Fischer TM, Gilmour AR, Werf van der Werf JHJ (2004) Computing approximate standard errors for genetic parameters derived from random regression models fitted by average information REML. Genet Sel Evol 36, 363-9
- Huisman AE, Veerkamp RF, van Arendonk JAM (2002) Genetic parameters for various random regression models to describe the weight data of pigs. J Anim Sci 80, 575-82
- Jamrozik J, Schaeffer LR (1997) Estimates of genetic parameters for test day model with random regressions for yield traits of first lactation Holsteins. J Dairy Sci 80, 762-70
- Kesbi FG, Inasab ME, Shahir MH (2008) Estimation of direct and maternal effects on body weight in Mehraban sheep using random regression models. Arch Tierz 51, 235-46
- Kettunen A, Mäntysaari EA, Jukka P (2000) Estimation of genetic parameters for daily milk yield of primiparous Ayrshire cows by random regression test day models. Livest Prod Sci 66, 251-61
- Kirkpatrick M, Lofsvold D, Bulmer M (1990) Analysis of the inheritance, selection and evolution of growth trajectories. Genetics 124, 979-93
- Krejčová H, Mielenz N, Přibyl J, Schüler I (2007) Estimation of Genetic Parameters for Daily Gains of Bulls with Multi-Trait and Random Regression Models. Arch Tierz 50, 37-46
- Lewis RM, Brotherstone S (2002) A genetic evaluation of growth in sheep using random regression techniques. Anim Sci 74, 63-70
- Meyer K (1998a) »DXMRR« A program to estimate covariance functions for longitudinal data by Restricted Maximum Likelihood. Proc. 6th World Congr. Genet. Appl Livest Prod 27, 465-6
- Meyer K (1998b) Estimating covariance functions for longitudinal data using a random regression model. Genet Sel Evol 30, 221-40
- Meyer K (1999) Estimates of genetic and phenotypic covariance functions for post-weaning 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 (2001) Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. Genet Sel Evol 33, 487-514
- Molina A, Menéndez-Boxadera A, Valera M, Serradilla JM (2007) Random regression model of growth during the first three months of age in Spanish Merino sheep. J Anim Sci 85, 2830-9
- Olori VE, Hill WG, McGuirk BJ, Brotherstone S (1999) Estimating variance components for test days milk records by restricted maximum likelihood with a random regression animal model. Livest Prod Sci 61, 53-63
- Pool MH, Meuwissen THE (2000) Reduction of the number of parameters needed for a polynomial random regression test day model. Livest Prod Sci 64, 133-45
- Robert-Granié C, Heude B, Foulley JL (2002) Modeling the growth curve of Maine-Anjou beef cattle using heteroskedastic random coefficients models. Genet Sel Evol 34, 423-45
- Takma Ç, Akbaş Y (2007) Estimates of genetic parameters for test day milk yields of a Holstein Friesian herd in Turkey with random regression models. Arch Tierz 50, 327-36

Received 20 November 2008, accepted 15 July 2010.

Corresponding author:

SOLOMON ABEGAZ email: solo_abegaz@yahoo.co.uk

Institute of Biodiversity Conservation, P.O.Box 30726, Addis Ababa, Ethiopia