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**GENETIC EVALUATION OF PRODUCTION, REPRODUCTION AND
SURVIVAL IN A FLOCK OF ETHIOPIAN HORRO SHEEP**

by

Solomon Abegaz Kebede

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PHILOSOPHIAE DOCTOR

**Promoter : Professor J.B. van Wyk
Co-promoter : Dr J.J. Olivier**

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**Dedicated to my mother, Ayalnesh Mesfin, without whose selfless
sacrifice my educational career would have terminated at the beginning**

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Table of contents

ACKNOWLEDGMENT	I
TABLE OF CONTENTS	II
LIST OF TABLES	IV
LIST OF FIGURES	VII
PREFACE	VIII
Chapter 1	
GENERAL INTRODUCTION	1
1.1 Background	1
1.2 Objectives of the study	4
Chapter 2	
ESTIMATION OF GENETIC AND ENVIRONMENTAL PARAMETERS OF PRE- AND POST-WEANING GROWTH AND KLEIBER RATIO	5
2.1 Introduction	5
2.2 Material and Methods	7
2.3 Results and Discussion	11
2.4 Conclusions	25
Chapter 3	
GENETIC AND MATERNAL ENVIRONMENTAL EFFECTS ON PERINATAL, PRE- AND POST-WEANING SURVIVAL OF LAMBS	26
3.1 Introduction	26
3.2 Material and Methods	27
3.3 Results and discussion	29
3.4 Conclusions	36

Chapter 4**GENETIC PARAMETER ESTIMATES OF EWE PRODUCTIVE AND REPRODUCTIVE TRAITS 37**

4.1 Introduction 37

4.2 Material and Methods 38

4.3 Results and Discussion 40

4.4 Conclusions 48

Chapter 5**GENETIC AND PHENOTYPIC PARAMETERS OF GROWTH CURVE AND THE RELATIONSHIP WITH EARLY GROWTH 49**

5.1 Introduction 49

5.2 Material and Methods 50

5.3 Results and Discussion 52

5.4 Conclusions 62

Chapter 6**GENETIC EVALUATION OF EARLY GROWTH USING A RANDOM REGRESSION MODEL 63**

6.1 Introduction 63

6.2 Material and methods 64

6.3 Results and Discussion 68

6.4 Conclusions 81

Chapter 7**GENERAL CONCLUSIONS AND RECOMMENDATIONS 82****ABSTRACT 85****OPSOMMING 89****REFERENCES 94**

List of tables

Table 2.1 Description of data used for the analysis of pre- and post-weaning average daily gain and Kleiber ratio, and for body weight at different ages.....	9
Table 2.2 Models used in the analysis of pre- and post-weaning average daily gain Kleiber ratio and weights at different ages.....	10
Table 2.3 Log-likelihood values for pre- and post-weaning average daily gain and Kleiber ratio, and for body weight at different ages, with values from the most appropriate model in bold	13
Table 2.4 (Co)variance components and parameter estimates for pre-weaning average daily gain and Kleiber ratio under twelve different models (best model in bold).....	15
Table 2.5 Co(variance) components and parameter estimates for post-weaning average daily gain and Kleiber ratio under twelve different models (best model in bold).....	16
Table 2.6 Estimates of (co) variance components and genetic parameters for birth weight (BWT), weaning weight (WWT) and weights at two (WT2), four (WT4), six (WT6), eight (WT8), 10 (WT10) 12 (WT12) and 18 (WT18) months of age from univariate analyses under the 'best' model.....	19
Table 2.7 Estimates of phenotypic (r_{p12}) direct genetic (r_{a12}) maternal genetic (r_{m12}) temporary environmental (r_{t12}) and residual (r_{e12}) correlations and direct-maternal (r_{a1m2}) maternal direct (r_{a2m1}) genetic cross-correlations among pre- and post- weaning gain and Kleiber ratio and with weight at birth, weaning, six-month, yearling and 18-month age.....	21
Table 2.8 Estimates of phenotypic (r_{p12}) direct genetic (r_{a12}) maternal genetic (r_{m12}) temporary environmental (r_{t12}) and residual (r_{e12}) correlations and direct-maternal (r_{a1m2}) maternal direct (r_{a2m1}) genetic cross-correlations between birth, weaning, six-month, yearling and 18-month weight.	22

Table 3.1 Fixed effects included in the final model for perinatal (3DS), pre-weaning (3MS), post-weaning (3-6MS) and pre-and post-weaning (6MS) survival.....	28
Table 3.2 (Co)variance estimates and log-likelihood values from univariate analyses under different models for perinatal survival (3DS), pre-weaning survival (3MS), post-weaning survival (3-6MS) and pre- and post-weaning survival (6MS).....	30
Table 3.3 Total phenotypic variance (σ_p^2), heritability estimates (h^2) and proportion of temporary (litter) effect (t^2) from univariate analyses of survival using logit and probit analyses.....	32
Table 3.4 Estimates of heritability (h^2) and proportion of temporary environment (t^2) and genetic (r_g) phenotypic (r_p) temporary environmental (r_t) and residual correlation (r_e) from bivariate analysis of survival with birth weight	35
Table 4.1 Description of data used in the analysis of production and derived efficiency traits.....	40
Table 4.2 Log-likelihood values and estimates of genetic and environmental parameters (\pm S.E.) for total birth and weaning weight and reproductive traits.....	43
Table 4.3 Genetic (above diagonal), phenotypic (below diagonal), and residual (below diagonal in parenthesis) correlation and pooled heritability estimates (bold, on diagonal) from a two trait analysis of productivity traits.....	48
Table 5.1 Descriptive statistics for birth, weaning, six-month and yearling weight and growth curve parameters.....	54
Table 5.2 Mean observed and predicted weights for the different age intervals and correlation between observed and predicted weights	56
Table 5.3 Heritability estimates (diagonal) of growth curve parameters and genetic (above diagonal) and phenotypic correlations (below diagonal) between the growth curve parameters and with immature body weights.....	58
Table 5.4 Pearson correlations (r) between growth curve parameters and ewe productivity traits.....	59
Table 6.1 Description of data used for random regression analysis.....	65
Table 6.2 Description of models used in random regression analysis.....	67

Table 6.3 Log-likelihood values for different models and likelihood ratio (LRT) and Akaike's information criteria (AIC) values.....	69
Table 6.4 Heritability and ratio of permanent environmental variance from models with different orders of polynomial and error measures.....	70
Table 6.5 Coefficients of covariance functions between random regression coefficients (0: intercept, 1:linear, 2:quadratic, 3:cubic and 4:quartic) for additive genetic effect and the eigenvalues under Model 6.....	77
Table 6.6 Coefficients of covariance functions between random regression coefficients (0: intercept, 1:linear, 2:quadratic, 3:cubic and 4:quartic) for animals' permanent effect and the eigenvalues under Model 6.....	77

List of figures

Figure 1.1. An adult Horro ewe (left) a flock of Horro ewes (centre) and an adult Horro ram (right) from a flock at Bako Research Center	3
Figure 6.1. Average of the recorded weights within the range of ages used in this study	68
Figure 6.2. Additive genetic (Gene), permanent environmental (Perm), phenotypic (Phen) and residual (Res) variance estimates from Model 6 over the entire period....	73
Figure 6.3. Trend in heritability estimates along the range of the trajectory	74
Figure 6.4. Additive genetic (left), permanent environmental (centre) and phenotypic (right) correlations between weights at different ages.	75
Figure 6.5. Eigenfunctions of the additive covariance function corresponding to the first to fifth eigenvalues from Model 6	79
Figure 6.6. Eigenfunctions of the permanent environmental covariance corresponding to the first to fifth eigenfunctions from Model 6.....	80
Figure 6.7. Estimated breeding values (EBVs) of four sires (sire 1,2,3,4 with 35, 31, 36 and 32 progeny) along the trajectory of age.....	80

Preface

This document contains results from a genetic analysis of data on a flock of Ethiopian Horro sheep. A number of traits which contribute to productivity have been analyzed. Depending on the trait and method of analysis the result was partitioned into five chapters (chapter two to six) which are self contained. The second chapter contains results of analysis for body weight, daily gain and Kleiber ratio at early growth. The third chapter contains results of analysis for lamb survival to different ages, while the fourth chapter presents the results of ewe reproduction and productivity. The fifth chapter contains results of analysis of growth curve. The sixth chapter has results of analysis of early growth data using a random regression model. A general introduction (chapter one) and conclusion (chapter seven) have been included. Additionally an abstract of the whole report (including Afrikaans translation) and a list of references used are presented at the end. The results and discussion section of each chapter are independent of one another. There are, however, some overlaps among chapters in terms of the background information and in the conclusions made. Care has been taken to minimize such repetitions.

General introduction

1.1 Background

Ethiopia is a largely agrarian country where agriculture is a source of livelihood for about 82% of a human population of 62.9 million (FAO, 2002). Livestock is an important part of the agricultural production and broadly, there are two livestock production systems. In the mid-altitude and highland areas smallholder crop-livestock mixed farming is dominant, while in the lowland arid and semi-arid areas pastoral systems are common. In the mixed farming system livestock play, among others, the role of providing traction power and security against crop failure and serve as a source of income, food (meat and milk) and manure. In the pastoral system, in most cases, livestock production is the only way of life and provides food and income. In both systems small ruminants are common, with sheep and goats being dominant in the highland and lowland areas respectively. Due to their requirement for small investment, shorter production cycles, faster rates of growth and greater environmental adaptability, small ruminants have a special niche in Ethiopian smallholder agriculture. Apart from their on-farm role, small ruminants have national importance as they provide for about 46% of the national meat consumption and 58% of the value of hide and skin production, which is one of the few items for export earnings (Kassahun *et al.*, 1991). Current sheep population estimates vary from 20 to 25.4 million (Beyene, 1998; Kassahun, 2000; FAO, 2002).

Though there are breeds which provide coarse fibre and milk, meat is the primary product from sheep in Ethiopia and current levels of on-farm production are low (Tembley, 1998). Estimates of annual production of live animals (off-take rate) are about 37% of the total sheep population, with a carcass yield of about 10 kg per animal (FAO, 2002). The indigenous sheep are year round breeders and no control of mating is practised. Under such conditions the present off-take rate is below the potential which can be realized. On

top of that the yield of carcass per animal is also low. Increasing the current level of productivity is required to improve meat consumption for the existing and increasing human population, to increase export earnings and to improve the standard of living of a large number of smallholders.

All the sheep under production are indigenous breeds, though few on-station trials and on farm extension activities which involve crossing the coarse-wool Menz sheep with a number of exotic breeds (mainly Awassi breed) have been made (Hassen *et al.*, 2002). The indigenous breeds are well adapted to the existing environmental conditions and can be used in pure or in crossing systems with improved breeds (Olivier *et al.*, 2002). One step in improving the indigenous breeds is their proper characterization. For this purpose on-station data collection on a few sheep breeds has been under way since 1977. One of the indigenous sheep populations under study was a breed known as Horro. The breed (and its ecotypes) is the most dominant sheep in the Southwestern areas of the country. It is named after one of the localities it inhabits and is distributed in the area which lies within 35°-38°E and 6°-19°N. Though the current population size of the breed is not known, from the area it inhabits and from statistical reports of sheep populations for these areas, a guesstimate of over two million can be made. Features that identify the Horro sheep have been described by Galal (1983). Briefly: they have a solid tan to dark brown colour, short smooth hair, a triangular fat tail with relatively narrow base and with the pointed end hanging downward or with a slight twist. Often the rams have a mane between the head and the brisket and above the neck (Figure 1.1.).

With the availability of data collected over a period of 20 years (1978 to 1997) there was a need to analyze these data so that estimates of productivity and other important phenotypic and genetic parameters could be made. These could be useful in designing breeding programs to increase productivity in the future. An initial study to this effect has been done in co-operation with the International Livestock Research Institute (ILRI) and the current study was designed to refine the previous work with the use of advanced analytical models and methodologies and also to estimate phenotypic and genetic parameters of other economically important traits.



Figure 1.1 An adult Horro ewe (left) a flock of Horro ewes (centre) and an adult Horro ram (right) from a flock at Bako Research Center

1.2 Objectives of the study

Overall meat productivity of sheep is an aggregate trait and constitutes growth and survival of lambs and reproduction and productivity of ewes. In this study variation in growth and survival during early age of lambs, weight change from birth through maturity and reproduction (fertility and litter size) and lifetime productivity were considered. The overall objective of the study was

1. to evaluate data through genetic analyses (estimation of genetic parameters) of
 - a. lamb growth and efficiency (Kleiber ratio)
 - b. survival of lambs to different ages
 - c. reproduction of ewes in terms of fertility (conception) and litter size
 - d. total weight of lamb weaned per ewe
 - e. growth curve parameters from birth to maturity
2. to suggest directions for future improvement of the breed.

Estimation of genetic and environmental parameters of pre- and post-weaning growth and Kleiber ratio

2.1 Introduction

Sheep production in Ethiopia is characterized by smallholder farming. The productivity under this system is low due to inadequate management and possibly low genetic potential of the animals. Genetic improvement of farm animals is one of the means to raise production. Crossbreeding with exotic animals is an option, but such programs for sheep and goats are often difficult to manage in low input production systems and selection within local populations are generally recommended (Olivier *et al.*, 2002). Development of breeding plans requires accurate estimates of heritability, repeatability and genetic and phenotypic correlations of economically important traits. Under the smallholder system these estimates are hard to come by and estimates should be made from on-station data where management is kept similar to that at a typical farm. Cognizant of this fact, genetic parameters of birth weight, weaning weight, six-month and yearling weight have been estimated for Horro sheep from data collected at Bako research centre, Ethiopia (Abegaz *et al.*, 2002a). Genetic models used in that study included (co)variance components of direct and maternal genetic effects. Studies elsewhere (Tosh & Kemp, 1994; Saatci *et al.*, 1999; Roden *et al.*, 2001; Maniatis & Pollott, 2002) indicate that maternal environmental effects have sizeable contributions to the overall variance, and incorporation of this component in the analytical models will contribute to the accuracy of estimates of parameters while exclusion may lead to biased estimates (Van Wyk *et al.*, 1993; Saatci *et al.*, 1999). The maternal environmental effect in litter bearing animals has two components: those which emanate from repeated records of the same dam (permanent environmental effect); and those specific to one litter (temporary environmental effects).

Traits can be either component or contributing. The former are traits (e.g. weaning weight) which can be partitioned into contributing traits (e.g. birth weight and pre-weaning gain) (Hohenboken, 1985). Depending on the relationship between the contributing traits there are situations where selection for contributing traits are more advantageous than selection on the component trait (e.g. selection for pre-weaning gain to improve weaning weight without a change in birth weight). Therefore, in sheep, besides weights at different growth stages, the gain achieved per unit time is of value to make important decisions. Kleiber ratio (ratio of average daily gain to metabolic weight at the end, $ADG/W^{0.75}$) has been suggested to be a useful indicator of efficiency (without the need to have feed intake data) of the growing lamb and was also suggested to be an important selection criterion for efficiency of growth (Bergh, 1990; Köster *et al.*, 1994). In a recent work Arthur *et al.* (2001) showed that the Kleiber ratio is highly correlated ($r=-0.81$) with feed conversion efficiency in beef cattle.

Under the existing marketing conditions in Ethiopia, sheep are sold at milk tooth stage, usually between the ages of six months to one year. Previous work (Abegaz *et al.*, 2002a) has shown that heritability increased from weaning (three months of age) to six months and to yearling, indicating that selection for growth will be more accurate some time around one year of age. Due to the need to have an earlier option for selection and due to marketing of lambs as early as six months of age, genetic parameters for bi-monthly weights between six and 12 months were considered. Though the sheep breeds of the tropics are year round breeders, in a situation where feed availability is seasonal there may be a need to have a controlled once-in-a-year breeding season. Under this condition many maiden ewes will not achieve the required size (weight) for breeding in their first season and should be mated in the second breeding season. Due to this, in addition to weights at earlier ages, genetic parameters of 18-month weight were considered. Genetic and environmental relationships between the different traits are also required to make appropriate decisions related to selection and to estimate the response to selection. Estimates of cross-correlations between direct additive genetic effect for one trait and maternal additive genetic effect for another trait are also necessary for multi-trait calculation of estimated breeding value, using the most appropriate model, as they

provide guidance in relation to expected correlated response to selection (Vaez Torshizi *et al.*, 1996).

The objectives of this study were to select appropriate models for genetic and environmental parameter estimates of pre- and post-weaning daily gain, Kleiber ratio and to refine earlier parameter estimates of body weights and suggest future improvement directions.

2.2 Material and Methods

Study area: The data for this study were generated at Bako Agricultural Research Centre located about 250 km West of Addis Ababa at an altitude of 1650 m above sea level. The centre lies at about 09°6'N and 37°09'E. The area has a hot and humid climate and receives a mean annual rainfall of about 1220 mm, of which more than 80% falls in the months of May to September. Mean monthly minimum and maximum temperatures are about 14° C and 28° C respectively, with an average monthly temperature of 21°C. The daily mean minimum and maximum temperatures are 9.4°C and 31.3°C respectively.

Flock management: A semi-intensive management system was followed with the flock grazing outdoors during the day (8:00 – 17:00) and being housed in pens (made up of bamboo walls and corrugated metal sheet roofs) at night. During mating and for the first few weeks after lambing the flock was kept indoors and fed on grass hay and concentrate supplements.

With the exception of the mating period, which usually lasted for about 42 days, ewe and ram flocks were herded separately. Ewes were allowed to breed for the first time at 17 to 19 months of age (a few lambs were joined at about seven months of age). Controlled once-a-year mating was practised except for three (1982-1985) and two years (1989-1991) when accelerated lambing at eight and nine monthly intervals respectively, was applied on part of the flock. About 20 (occasionally 10-25) ewes were assigned to each ram, using a stratified (ear tag order) random procedure. Rams were selected on general

health and absence of observable defects (small testes, hocked joint, over and under shot jaw). The pedigree of each ram and ewe was checked to avoid mating of animals that are closely related. The flock was closed until the last four years of the study, when rams and some ewe replacements were brought from outside. Soon after birth (within the first 12 hrs), each lamb was identified with a permanent plastic ear tag, and its birth weight was recorded. Lambs were weaned at about three months of age.

Data: Data used in this study were collected on a flock of Horro sheep in the years 1978-1997. The flock was initially established with 100 ewes and 10 rams. After preliminary editing 4031 lamb records (3014 lambings) of the progeny of 904 ewes and 184 sires were used. Traits considered were pre- and post-weaning average daily gain (ADG1 and ADG2 respectively) and Kleiber ratio (KR1 and KR2 respectively). Bi-monthly weights from birth to one year of age (BWT, WT2 to WT12) and weaning weight (WWT) at about three months of age and eighteen-month weight (WT18) were also considered. ADG1 and ADG2 were calculated as total gain divided by number of days in the period, while KR1 and KR2 were calculated as a ratio of ADG1 and ADG2 to metabolic weight at weaning and six months of age respectively. Description of data for the traits used in this study is presented in Table 2.1.

Statistical analysis: Important fixed effects and interactions for all traits were identified from preliminary analyses, using the GLM procedure of SAS (SAS, 1994). Year of birth, sex, type of rearing (type of birth for BWT and WT2) and age at measurement were found to be significant ($P < 0.05$) in all cases. Age of dam was also found to have a significant effect ($P < 0.05$) on pre-weaning gain and KR1 and weights to the age of 12 months. Interaction of sex and year was found to be important for 12 and 18-month weights.

(Co)variance components were estimated for each trait, using an animal model in a univariate analysis with ASREML (Gilmour *et al.*, 1999). Twelve different models were employed. The simplest model has terms of the direct additive genetic and residual variance, while the most complete model has additional terms of maternal additive

genetic, permanent and temporary (litter) environmental variance, and covariance between direct and maternal additive genetic components. A complete list of models used is presented in Table 2.2. Log-likelihood ratio tests were conducted to determine the most appropriate model for each trait in a univariate analyses.

Table 2.1 Description of data used for the analysis of pre- and post-weaning average daily gain and Kleiber ratio, and for body weight at different ages

Trait	N	\bar{x}	SD	CV(%)	Range	Age (range)
ADG1(g)	2865	100.4	35.7	35.6	21-230	-
KR1	2864	15.3	2.49	16.3	6.8-22.8	-
ADG2(g)	2245	36.3	27.3	75.1	-42-131	-
KR2	2257	4.4	3.15	71.6	-7.7-13.3	-
BWT(kg)	3958	2.6	0.61	23.8	1.0-4.5	-
WT2(kg)	2567	9.7	2.83	29.1	4.0-19.0	60(38-93)
WWT(kg)	2859	12.0	3.47	28.9	5.0-23.0	93(70-110)
WT4(kg)	2422	13.1	3.72	28.3	5.0-27.0	120(90-152)
WT6(kg)	2269	15.8	4.25	26.9	6.0-35.0	183(140-220)
WT8(kg)	1915	17.8	4.85	27.3	6.0-37.0	238(202-308)
WT10(kg)	1627	20.1	5.80	28.7	8.0-45.0	294(258-366)
WT12(kg)	1469	23.8	6.36	26.8	11.0-45.0	366(322-408)
WT18(kg)	1013	27.3	7.08	25.9	12.5-51.0	528(481-597)

N=number of records \bar{x} =mean SD=standard deviation CV=coefficient of variation

ADG1 and ADG2=pre- and post-weaning average daily gain respectively

KR1 and KR2= pre- and post-weaning Kleiber ratio respectively

BWT and WWT=birth weight and weaning weight respectively

WT2, WT4, WT6, WT8, WT10, WT12, WT18=body weight at two, four, six, eight, 10, 12 and 18 month of age respectively

Table 2.2 Models used in the analysis of pre- and post-weaning average daily gain Kleiber ratio and weights at different ages

Model	(Co) Variance Component
1	$\sigma_a^2 + \sigma_e^2$
2	$\sigma_a^2 + \sigma_t^2 + \sigma_e^2$
3	$\sigma_a^2 + \sigma_c^2 + \sigma_e^2$
4	$\sigma_a^2 + \sigma_c^2 + \sigma_t^2 + \sigma_e^2$
5	$\sigma_a^2 + \sigma_m^2 + \sigma_e^2$
6	$\sigma_a^2 + \sigma_m^2 + \sigma_t^2 + \sigma_e^2$
7	$\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_e^2$
8	$\sigma_a^2 + \sigma_m^2 + \sigma_t^2 + \sigma_{am} + \sigma_e^2$
9	$\sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_e^2$
10	$\sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_t^2 + \sigma_e^2$
11	$\sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_{am} + \sigma_e^2$
12	$\sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_t^2 + \sigma_{am} + \sigma_e^2$

The representation of the complete animal model (Model 12) is as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_a \mathbf{a}_a + \mathbf{Z}_m \mathbf{a}_m + \mathbf{Z}_c \mathbf{c} + \mathbf{Z}_t \mathbf{t} + \mathbf{e} \quad (\text{Cov}_{\mathbf{a}_a \mathbf{a}_m} \neq 0)$$

Where \mathbf{y} is the vector of records, \mathbf{b} is a vector of an overall mean and fixed effects with incidence matrix \mathbf{X} ; \mathbf{a}_a , \mathbf{a}_m , \mathbf{c} and \mathbf{t} are vectors of random additive direct genetic, additive maternal genetic, permanent environmental, and temporary (litter) environmental effects with incidence matrices \mathbf{Z}_a , \mathbf{Z}_m , \mathbf{Z}_c , and \mathbf{Z}_t respectively, and \mathbf{e} is a vector of random errors.

The (co)variance structure of the model was,

$$\mathbf{V} \begin{bmatrix} \mathbf{a}_a \\ \mathbf{a}_m \\ \mathbf{c} \\ \mathbf{t} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_c^2 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_t^2 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

Where A is the additive relationship matrix, I_c is an identity matrix of order equal to the number of dams, I_l is an identity matrix of order equal to the number of litters and I_n is an identity matrix of order equal to the number of records.

Correlations and cross-correlations among the different components of the different traits were estimated from bivariate analyses using the model chosen as the most appropriate from the univariate analyses for each of the traits. In some cases the analysis failed to converge, thus a 'reduced' model, where only the direct model was included for both traits was used. Genetic and environmental parameters were calculated using the variances estimated at convergence. Direct (h_a^2) and maternal (h_m^2) heritability, ratios of permanent and temporary environmental variances, and the direct and maternal additive covariance and associated sampling error were calculated as (where σ_p^2 is total phenotypic variance) σ_a^2/σ_p^2 , σ_m^2/σ_p^2 , σ_d^2/σ_p^2 , σ_t^2/σ_p^2 , and σ_{am}/σ_p^2 respectively. Total heritability was calculated as $(\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$, while direct and maternal additive correlation and cross-correlations were expressed as a ratio of the covariance to the square root of the product of the two variances. All calculations were done using the options available in ASREML (Gilmour *et al.*, 1999) for parameter and sampling error estimation.

2.3 Results and Discussion

Log-likelihood values for the different models on all traits are presented in Table 2.3. Maternal genetic components were important for ADG1 and KR1 and for weights to eight months of age. In the presence of the other components, with the exception of WT2 and WWT, the permanent environmental component was found to have no significant ($P>0.05$) contribution to pre- and post-weaning gain, Kleiber ratio and weights at the different ages. The temporary environmental effect was found to be important in all pre- and post-weaning gains and Kleiber ratio and weights to the age of six months. The importance of the maternal temporary environmental effect was highest for BWT and it declined with age. For weights after eight months of age, the only important component (apart from the residual variance) is the direct additive variance (Model 1). The

covariance between direct and maternal genetic effects was found to be important for ADG1 and weights to weaning (BWT, WT2, WWT).

In a previous study (Abegaz *et al.*, 2002a) models considered did not include the maternal environmental components. For BWT, WWT, and WT6 the inclusion of maternal environmental components (permanent and/or temporary) were found to improve model fit significantly ($P < 0.05$) (Table 2.3).

Numerous reports have been published on the contribution and importance of the maternal genetic variance, permanent environmental variance and direct-maternal genetic covariance in improving the fit of models in growth performance of sheep (e.g. Van Wyk *et al.*, 1993; Maria *et al.*, 1993; Snyman *et al.*, 1996; Okut *et al.*, 1999; Cloete *et al.*, 2001; Maniatis & Pollott, 2002) beef cattle (e.g. Meyer, 1993; Swalve, 1993; Gutierrez *et al.*, 1997) and goats (e.g. Van Niekerk *et al.*, 1996). Due to the low incidence of multiple births in cattle and in some sheep breeds and also to the analytical problem which might arise when maternal genetic, permanent environmental and temporary environmental variances are fitted simultaneously, reports which considered the importance of temporary (litter) variance in model choice are limited. Improved fit of analytical models by including a temporary (litter) environmental component (but with different other components which were fitted simultaneously) was reported for weaning and hogget body weight of New Zealand Coopworth sheep (Lewis & Beatson, 1999), for weaning (about 65 days), 90 and 120 days of weight of crosses involving three breeds (Al-Shorepy & Notter, 1996) and for 12-week weight of Welsh mountain lambs (Saatci *et al.*, 1999) and for birth and weaning weight, ADG and Kleiber ratio of the Boer goats (Schoeman *et al.*, 1997). Hagger (1998) also reported that in two breeds of sheep the litter effect had a significant ($P < 0.05$) contribution to the total variance of ADG for the first 30 days. Most of the studies involved sheep with a higher average litter size than in this study. However, the twinning rate (35%) of sheep reported in the study of Saatci *et al.* (1999) is similar to the rate in the current study (34%). This implies the temporary environmental effect can be significant in situations where the incidence of twinning is as low as 30%.

Table 2.3 Log-likelihood values for pre- and post-weaning average daily gain and Kleiber ratio, and for body weight at different ages, with values from the most appropriate model^{a)} in bold

Model	Trait												
	ADG1	KR1	ADG2	KR2	BWT	WT2	WWT	WT4	WT6	WT8	WT10	WT12	WT18
1	-10832.2	-3543.1	-8234.3	-3531.6	571.5	-3190.7	-4213.0	-3668.6	-3470.9	-3323.8	-2972.8	-2778.2	-1895.1
2	-10823.9	-3530.0	-8230.0	-3526.8	749.7	-3180.0	-4204.8	-3658.8	-3731.6	-3322.6	-2972.5	-2778.0	-1895.1
3	-10808.7	-3529.3	-8234.3	-3531.4	603.5	-3171.3	-4183.9	-3661.2	-3738.6	-3322.3	-2972.9	-2777.2	-1894.9
4	-10806.8	-3521.4	-8230.0	-3526.8	757.4	-3166.0	-4181.0	-3654.7	-3730.7	-3321.7	-2972.5	-2777.2	-1894.9
5	-10806.5	-3528.3	-8233.9	-3531.4	598.6	-3172.3	-4182.6	-3656.1	-3733.6	-3319.8	-2972.8	-2776.8	-1895.1
6	-10802.2	-3518.8	-8228.8	-3526.7	758.1	-3166.1	-4178.9	-3649.4	-3726.5	-3319.3	-2972.5	-2776.7	-1895.1
7	-10804.8	-3527.7	-8233.6	-3531.1	604.2	-3170.1	-4180.2	-3655.8	-3733.6	-3319.7	-2971.7	-2774.9	-1894.9
8	-10800.3	-3518.1	-8229.7	-3526.7	761.7	-3163.9	-4176.5	-3649.0	-3726.5	-3319.1	-2971.5	-2774.9	-1894.9
9	-10804.4	-3526.3	-8234.1	-3531.3	606.5	-3168.9	-4179.5	-3656.1	-3734.4	-3319.8	-2972.8	-2776.9	-1894.9
10	-10800.8	-3518.0	-8229.8	-3526.7	759.6	-3163.6	-4176.5	-3649.4	-3727.6	-3319.3	-2972.5	-2776.7	-1894.9
11	-10802.9	-3525.9	-8233.6	-3531.0	612.0	-3166.9	-4177.6	-3655.8	-3733.6	-3319.7	-2971.7	-2774.8	-1894.7 [†]
12	-10799.2	-3517.4	-8229.7	-3526.7	763.3	-3161.6	-4174.4	-3649.0	-3726.5	-3319.1	-2971.5	-2774.8	-1894.7 [†]

^{a)}P<0.05 was used to identify the best model

ADG1 and ADG2=pre- and post-weaning average daily gain respectively

KR1 and KR2= pre- and post-weaning Kleiber ratio respectively

BWT and WWT=birth weight and weaning weight respectively

WT2, WT4, WT6, WT8, WT10, WT12, WT18=body weight at two, four, six, eight, 10, 12 and 18 month of age

Unlike the result in this study, Matika *et al.* (2003) reported that for ADG1 in Sabi sheep the direct and maternal genetic covariance was not significant ($P < 0.05$) while the permanent environmental effect was significant ($P < 0.05$) for weights to the age of one year. Similarly Cloete *et al.* (2001) reported, for Australian Merino sheep the covariance between the direct and maternal genetic effect not to be important for birth and weaning weight. The magnitude and the importance of this component is highly variable among reports in the literature.

Genetic and environmental parameter estimates from all models for ADG1, KR1, ADG2, and KR2 are presented in Tables 2.4 and 2.5. For ADG1 and KR1 models which ignore the maternal genetic and environmental components (Model 1) gave inflated estimates of the direct heritability. The exclusion of temporary environmental variance had a relatively small effect on the other components, but affected the error variance markedly (reduced the error variance by about 20%). Quantifying the temporary environmental variance is helpful in disentangling the variance component which is amenable to management intervention. The inclusion of the permanent rather than the temporary environmental effect showed more influence on the direct and maternal genetic parameter estimates. The permanent environmental variance, which is related to variation between repeated records of the ewe, are more likely to be confounded with the genetic variance. The temporary environmental effect is an effect restricted to within-litter variability of the ewe and is more related to the residual variance. Hence the inclusion of the permanent environmental variance showed more pronounced effect on direct and maternal genetic variance while the temporary environmental variance reduced the residual variance.

Table 2.4 (Co)variance components and parameter estimates for pre-weaning average daily gain and Kleiber ratio under twelve different models (best model in bold)

Model	Pre-weaning average daily gain							
	σ_p^2	h_a^2	h_m^2	r_{am}	t^2	c^2	h_t^2	σ_e^2
1	768.2	0.26±0.04					0.26±0.04	571.77
2	769.8	0.24±0.04			0.19±0.04		0.24±0.04	441.52
3	760.9	0.15±0.04				0.13±0.02	0.15±0.04	547.07
4	762.7	0.14±0.04			0.11±0.04	0.12±0.02	0.14±0.04	471.52
5	774.1	0.11±0.04	0.15±0.03				0.19±0.03	569.44
6	773.8	0.11±0.04	0.14±0.03		0.13±0.04		0.18±0.03	482.67
7	770.6	0.15±0.05	0.21±0.04	-0.43±0.16			0.14±0.04	550.20
8	771.1	0.15±0.05	0.20±0.04	-0.45±0.16	0.13±0.04		0.13±0.04	461.89
9	765.2	0.12±0.04	0.09±0.03			0.06±0.03	0.16±0.04	559.50
10	767.1	0.11±0.04	0.10±0.03		0.12±0.04	0.05±0.03	0.16±0.04	481.66
11	763.2	0.15±0.05	0.14±0.05	-0.44±0.18		0.06±0.03	0.13±0.04	542.66
12	765.5	0.15±0.05	0.15±0.05	-0.46±0.17	0.12±0.04	0.04±0.03	0.12±0.17	462.03

Model	Pre-weaning Kleiber ratio							
	σ_p^2	h_a^2	h_m^2	r_{am}	t^2	c^2	h_t^2	σ_e^2
1	4.30	0.21±0.04					0.21±0.04	3.39
2	4.29	0.18±0.04			0.22±0.04		0.18±0.04	2.56
3	4.26	0.13±0.04				0.09±0.02	0.13±0.04	3.31
4	4.26	0.12±0.04			0.17±0.04	0.08±0.02	0.12±0.04	2.69
5	4.29	0.10±0.04	0.10±0.02				0.15±0.03	3.45
6	4.28	0.09±0.04	0.08±0.02		0.19±0.04		0.13±0.03	2.74
7	4.29	0.12±0.05	0.13±0.04	-0.33±0.22			0.13±0.04	3.38
8	4.28	0.12±0.05	0.12±0.04	-0.40±0.22	0.19±0.04		0.11±0.04	2.65
9	4.26	0.11±0.04	0.05±0.03			0.06±0.03	0.13±0.04	3.38
10	4.26	0.09±0.04	0.06±0.03		0.18±0.04	0.04±0.03	0.12±0.04	2.74
11	4.26	0.13±0.05	0.07±0.04	-0.36±0.25		0.06±0.03	0.11±0.04	3.31
12	4.27	0.12±0.05	0.09±0.04	-0.43±0.24	0.18±0.04	0.04±0.03	0.10±0.04	2.65

Phenotypic variance (σ_p^2) direct heritability (h_a^2) maternal heritability (h_m^2) direct-maternal correlation (r_{am}) ratio of temporary (t^2) and permanent (c^2) environmental variance total heritability (h_t^2) and residual variance (σ_e^2)

Table 2.5 Co(variance) components and parameter estimates for post-weaning average daily gain and Kleiber ratio under twelve different models (best model in bold)

Model	Post-weaning average daily gain							
	σ_p^2	h_a^2	h_m^2	r_{m}	t^2	c^2	h_i^2	σ_e^2
1	595.0	0.06±0.03					0.06±0.03	560.62
2	596.8	0.04±0.03			0.22±0.05		0.04±0.03	440.10
3	594.8	0.05±0.03				0.01±0.02	0.05±0.03	559.13
4	596.5	0.04±0.03			0.22±0.05	0.00	0.04±0.03	436.93
5	594.8	0.05±0.03	0.01±0.02				0.05±0.03	559.16
6	596.7	0.04±0.03	0.01±0.02		0.22±0.05		0.04±0.03	441.34
7	595.1	0.06±0.04	0.03±0.03	-0.45±0.44			0.05±0.03	553.33
8	596.8	0.04±0.04	0.01±0.03	-0.25±0.93	0.21±0.05		0.04±0.03	440.47
9	595.7	0.05±0.03	0.02±0.02			0.00	0.06±0.03	555.81
10	596.5	0.04±0.03	0.01±0.02		0.22±0.05	0.00	0.04±0.03	441.14
11	595.1	0.06±0.04	0.03±0.03	-0.45±0.44		0.00	0.05±0.03	553.34
12	596.5	0.04±0.04	0.01±0.03	-0.25±0.93	0.21±0.05	0.00	0.04±0.03	440.28

Model	Post-weaning Kleiber ratio							
	σ_p^2	h_a^2	h_m^2	r_{m}	t^2	c^2	h_i^2	σ_e^2
1	7.83	0.02±0.02					0.02±0.02	7.67
2	7.86	0.01±0.02			0.20±0.05		0.01±0.02	6.22
3	7.83	0.02±0.02				0.01±0.02	0.02±0.02	7.61
4	7.86	0.01±0.02			0.20±0.05	0.00	0.01±0.02	6.22
5	7.83	0.01±0.02	0.01±0.02				0.02±0.02	7.64
6	7.86	0.01±0.02	0.01±0.02		0.19±0.05		0.01±0.02	6.23
7	7.84	0.03±0.04	0.03±0.03	-0.73±0.42			0.01±0.02	7.53
8	7.86	0.01±0.03	0.01±0.03	-0.46±0.43	0.19±0.06		0.01±0.02	6.22
9	7.83	0.01±0.02	0.01±0.02			0.01±0.02	0.02±0.02	7.62
10	7.84	0.01±0.02	0.01±0.02		0.19±0.05	0.00	0.01±0.02	6.23
11	7.84	0.03±0.04	0.03±0.03	-0.74±0.45		0.00±0.02	0.01±0.02	7.51
12	7.86	0.01±0.03	0.01±0.03	-0.46±1.43	0.19±0.05	0.00	0.01±0.02	6.22

Phenotypic variance (σ_p^2) direct heritability (h_a^2) maternal heritability (h_m^2) direct-maternal correlation (r_m) ratio of temporary (t^2) and permanent (c^2) environmental variance total heritability (h_i^2) and residual variance (σ_e^2)

Estimates of total heritability for ADG1 and KR1 from the most appropriate models were 0.13 and 0.13 respectively. Total heritability estimates are useful in estimating response to selection based on phenotypic value. By means of comparison total h^2 was calculated from studies in the literature which reported direct and maternal variance and covariance. Heritability estimates of ADG1 from the different animal models ranging from 0.08 to 0.27 in sheep (Van Wyk *et al.*, 1993; Analla *et al.*, 1995; Yazdi *et al.*, 1997; Hagger, 1998; Larsgard & Olesen, 1998; Matika *et al.*, 2003), in goats (Van Niekerk *et al.*, 1996; Schoeman *et al.*, 1997) and in beef cattle (Gutierrez *et al.*, 1997) were reported. The current estimate falls in the lower end of this range. Very high estimates (0.44) from sire models were reported for Muzffarnagri sheep (Sinha & Singh, 1997), while Maria *et al.* (1993) estimated direct and maternal (co)variance values (from an animal model) which when calculated into total heritability (Willham, 1972), would yield values out of the parameter space. Though breed differences are apparent, the difference in data size and structure (particularly pedigree depth) and type of models used are likely to contribute to the discrepancy in the results from different studies. With regard to this, Okut *et al.* (1999) reported total heritability estimates (calculated from the contributing values in the report) of ADG to weaning varying from 0.00 to 0.86 for a range of breeds and age groups. For KR to weaning, literature estimates of total heritability range from 0.10 for Sabi sheep (Matika *et al.*, 2003) to 0.15 for Dormer sheep (Van Wyk *et al.*, 1993) and to 0.16 in the Boer Goat (Van Niekerk *et al.*, 1996; Schoeman *et al.*, 1997). These values are in agreement with an estimate of 0.13 in this study.

Estimates of total heritability for ADG2 and KR2 were 0.04 and 0.01 and both are lower than estimates for ADG1 and KR1. Similarly on a small data set Greeff *et al.* (1993) reported lower heritabilities for ADG and KR after about three months (78 to 94 days) of age than estimates prior to that age. Analla *et al.* (1995) estimated heritability for pre- and post-weaning ADG of 0.27 and 0.12 respectively. Overall estimates of heritability of post-weaning daily gain in the literature for sheep (Badenhorst *et al.*, 1991; Notter & Hough, 1997; Yazdi *et al.*, 1997; Notter, 1998; Mousa *et al.*, 1999) and for beef cattle (Schoeman & Jordaan, 1999) were higher than the estimates in this study. Post-weaning Kleiber ratio estimates from the literature are also high for sheep (Badenhorst *et al.*,

1991; Greeff *et al.*, 1993) and (from a sire model) for beef cattle (Köster *et al.*, 1994). It appears that the environmental component during this phase of growth is very high, probably due to the presence of post-weaning compensatory growth caused by environmental contribution and full dependence of lambs on themselves. For post-weaning gain from a sire model, Sinha & Singh (1997) reported a heritability of 0.34, while Cameron (1988) reported a value of 0.30 for average daily gain between eight and 16 weeks of age. These values are higher than the current estimates.

The temporary environment is the most important component accounting for 22 and 20 per cent of the total variation in ADG2 and KR2 respectively. As a component accounting for a within full-sib similarity against the between-litter variability it would be reasonable for this effect to remain for sometime after weaning when the maternal genetic effect is waning.

Total phenotypic variances and ratios of different components from the most appropriate model for weights are presented in Table 2.6. For weights from birth to six months of age, temporary environment accounted for 11 to 51 per cent of the total variation, while the maternal additive component accounted for 5 to 17 per cent for weight until about eight months of age. Permanent environmental variance accounted for 7 and 6 per cent of the variation in WT2 and WWT respectively. The fact that in most cases the permanent environmental effect was not significant ($P > 0.05$) implies that the maternal contribution differs at each parity and it can be considered as separate traits where heterogeneity of variance within parity exists. From analyses using different models and breeds it was reported that the temporary environmental variance accounted for four to 44 per cent of the total variance in birth and weaning weight (Al-Shorepy & Notter, 1996; Larsgrad & Olesen, 1998; Lewis & Beatson, 1999; Nagy *et al.*, 1999; Saatci *et al.*, 1999). Tosh & Kemp (1994) also found that litter effect accounted for about 12 to 37 per cent of the variance on weight at birth, 50 days and 100 days of age. The estimate of 0.51 in the current study for BWT is higher than the literature estimates, while the estimate for WWT falls within the range. The higher contribution of a temporary environmental component to BWT may be the result of rounding of birth weights to the nearest quarter

kilogram, a procedure followed in the recording of the birth weight data. Usually twin born lambs have birth weights close to each other and when rounded during recording to the nearest figure thus become identical. The within-litter variation will therefore become less while the between-litter variation might remain unchanged, leading to a higher portion of the phenotypic variance to come from the temporary environmental variance.

Estimates of total heritability for BWT, WWT and WT6 were 0.14, 0.12 and 0.21 respectively. For BWT and WWT, these values are slightly lower than estimates reported from the same data set under Model 4 (Model 7 in this study) by Abegaz *et al.* (2002a). Exclusion of important components obviously has the effect of inflating the remaining parameter estimates. For bi-monthly weights from two to 12 months and for WT18 heritability estimates were 0.06, 0.21, 0.21, 0.21, 0.29, 0.33 and 0.33 respectively. With the importance of maternal environmental and genetic effects waning after about eight months, the direct heritability has shown a sizeable increase. It appears that the direct heritability stabilizes from about the age of ten months.

Table 2.6 Estimates of (co) variance components and genetic parameters for birth weight (BWT), weaning weight (WWT) and weights at two (WT2), four (WT4), six (WT6), eight (WT8), 10 (WT10), 12 (WT12) and 18 (WT18) months of age from univariate analyses under the 'best' model

Trait	σ_p^2	h^2_a	h^2_m	r_{am}	t^2	c^2	h^2_t
BWT	0.27	0.20±0.05	0.10±0.03	-0.53±0.13	0.51±0.02	-	0.14±0.03
WT2	4.28	0.10±0.05	0.11±0.04	-0.53±0.20	0.17±0.04	0.07±0.03	0.06±0.04
WWT	6.81	0.16±0.05	0.15±0.05	-0.47±0.17	0.11±0.04	0.06±0.03	0.12±0.04
WT4	7.50	0.16±0.05	0.09±0.03	-	0.16±0.04	-	0.21±0.04
WT6	9.78	0.18±0.05	0.07±0.02	-	0.17±0.04	-	0.21±0.04
WT8	11.55	0.18±0.05	0.06±0.03	-	-	-	0.21±0.04
WT10	13.98	0.29±0.05	-	-	-	-	0.29±0.05
WT12	18.49	0.33±0.06 (0.28±0.05)	-	-	-	-	0.33±0.06 (0.28±0.05)
WT18	20.41	0.33±0.07	-	-	-	-	0.33±0.07

Estimates from a previous study of Abegaz *et al.* (2002a) in parenthesis.

Phenotypic variance (σ_p^2) direct heritability (h^2_a) maternal heritability (h^2_m) direct-maternal correlation (r_{am}) ratio of temporary (t^2) and permanent (c^2) environmental variance, total heritability (h^2_t)

Unlike what has evinced from the present study, carry-over effects of the maternal genetic effect has been shown to persist to the age of 18 months (Snyman *et al.*, 1996) and 22 months (Vaez Torshizi *et al.*, 1996) and the permanent environmental effect to the age of 12 months (Matika *et al.*, 2003). The latter, however, reported an absence of maternal genetic effect at the age of 12 months. Lewis & Beatson (1999) observed an important temporary environmental effect for hogget weight taken between eight and 12 months of age. In the current study, however, the importance of temporary environmental effect was limited up to the age of six months. From a model comparable to Model 11 Snyman *et al.* (1996) estimated total heritability of 0.30, 0.40 and 0.63 for WWT, WT6 and WT18. All of these values are higher than the present estimates. For weight at 18 months of age Lee *et al.* (2000; direct animal model) reported a direct heritability of 0.43 while Groenewald *et al.* (1999; sire model) estimated a heritability of 0.34 for weight of Merino sheep taken between 15 and 18 months of age. The latter value is close to current estimate.

Genetic and phenotypic correlations and cross-correlations among ADG1, KR1, ADG2, KR2, BWT, WWT, WT6, WT12 and WT18 are presented in Tables 2.7 and 2.8. Phenotypic correlations of ADG1 with KR1, ADG2 and KR2 were 0.98, -0.11 and -0.27, while genetic correlations were 0.96, 0.63 and 0.89 in the respective order. It appears that lambs with higher gain in the pre-weaning period gain less during the post-weaning period and vice versa. Since genetic correlations are all positive, it is likely that compensatory growth, mediated through environmental effect may occur in lambs which were gaining at a lower rate during the pre-weaning period. Hence better gain and efficiency were realized during the post-weaning than in the pre-weaning period. Similar negative phenotypic correlations between pre- and post-weaning ADG have been reported for Muzaffarnagri sheep (Sinha & Singh, 1997) and for Baluchi sheep (Yazdi *et al.*; 1997), while Maria *et al.* (1993) reported high positive phenotypic correlations for Romanov sheep. The age at weaning and the level of post- weaning management may account for the discrepancy in the results. Both Maria *et al.* (1993) and Yazdi *et al.* (1997) reported negative genetic correlations between pre- and post-weaning ADG.

Table 2.7 Estimates of phenotypic (r_{p12}) direct genetic (r_{a12}) maternal genetic (r_{m12}) temporary environmental (r_{t12}) and residual (r_{e12}) correlations and direct-maternal (r_{a1m2}) maternal direct (r_{a2m1}) genetic cross-correlations among pre- and post- weaning gain and Kleiber ratio and with weight at birth, weaning, six-month, yearling and 18-month age

Trait ^{a)}		KR1	ADG2	KR2	BWT	WWT	WT6	WT12	WT18
ADG1	r_{p12}	0.98±0.00	-0.11±0.02	-0.27±0.02	0.09±0.03	0.72±0.07	0.61±0.03	0.53±0.03	0.51±0.031
	r_{a12}	0.96±0.02	0.63±0.33	0.89±0.47	0.04±0.21	0.96±0.02	0.92±0.09	0.79±0.12	0.53±0.154
	r_{e12}	0.95±0.00	-0.18±0.05	-0.39±0.05	0.06±0.06	1.00±0.00	0.64±0.02	0.42±0.04	0.42±0.049
	r_{m12}	0.99±0.01			0.68±0.15	1.00±0.00	0.92±0.07	-	-
	r_{a1m2}	-0.40±0.19			-	-0.39±0.16	0.16±0.10	0.39±0.14	0.47±0.133
	r_{a2m1}	-0.41±0.22	0.46±0.25		-	-0.36±0.17	-0.03±0.15	-	-
	r_{t12}	0.86±0.04	-0.26±0.19	-0.31±0.18	-	0.88±0.05	-	-	-
KR1	r_{p12}	-	-0.11±0.02	-0.28±0.02	-	0.75±0.03	0.48±0.05	0.44±0.03	0.47±0.031
	r_{a12}	-	0.59±0.36	0.33±0.54	-	0.74±0.10	0.66±0.16	0.56±0.17	0.57±0.174
	r_{e12}	-	-0.18±0.05	-0.37±0.05	-	0.87±0.01	0.52±0.03	0.40±0.05	0.40±0.051
	r_{m12}	-	-	-	0.56±0.24	0.89±0.06	0.81±0.11	-	-
	r_{a1m2}	-	-	-	-	-0.19±0.15	-0.10±0.20	0.40±0.18	0.60±0.141
	r_{a2m1}	-	0.44±0.27	0.69±0.45	0.10±0.25	0.032±0.13	0.05±0.30	-	-
	r_{t12}	-	-0.15±0.16	-0.20±0.15	-	-	-	-	-
ADG2	r_{p12}	-	-	0.96±0.01 ^{b)}	0.02±0.02	-0.12±0.02	0.61±0.02	0.26±0.02	0.23±0.031 ^{b)}
	r_{a12}	-	-	0.99±0.01 ^{b)}	-	0.54±0.37	0.90±0.16	0.99±0.00	1.00±0.233 ^{b)}
	r_{e12}	-	-	0.96±0.00 ^{b)}	0.04±0.06	-0.20±0.05	0.58±0.04	0.20±0.03	0.17±0.050 ^{b)}
	r_{a2m1}	-	-	-	0.09±0.31	0.51±0.28	0.41±0.23	-	-
	r_{t12}	-	-	-	0.01±0.09	-0.12±0.24	0.77±0.10	-	-
	r_{p12}	-	-	-	-	-0.25±0.02	0.43±0.02	0.16±0.03 ^{b)}	0.15±0.033 ^{b)}
	r_{a12}	-	-	-	-	0.47±0.52	0.91±0.51	0.99±0.00 ^{b)}	1.00±0.430 ^{b)}
KR2	r_{e12}	-	-	-	-	-	0.44±0.03	0.11±0.03 ^{b)}	0.08±0.047 ^{b)}
	r_{a2m1}	-	-	-	-	0.60±0.40	-	-	-
	r_{t12}	-	-	-	-	-	-	-	-
	r_{p12}	-	-	-	-	-	-	-	-

^{a)} row=trait1 column=trait 2; ADG1=pre-weaning daily gain, KR1=pre-weaning Kleiber ratio, ADG2=post-weaning gain, KR2=post-weaning Kleiber ratio, BWT=birth weight, WWT=weaning weight, WT6=six-month weight, WT12=12-month weight, WT18=18-month weight

^{b)}=A 'reduced' model for either one or both of the traits was used due to lack of convergence to fit the best model.

Table 2.8 Estimates of phenotypic (r_{p12}) direct genetic (r_{a12}) maternal genetic (r_{m12}) temporary environmental (r_{t12}) and residual (r_{e12}) correlations and direct-maternal (r_{a1m2}) maternal direct (r_{a2m1}) genetic cross-correlations between birth, weaning, six-month, yearling and 18-month weight

Trait1	BWT	BWT	BWT	BWT	WWT	WWT	WWT	WT6	WT6	WT12
Trait2	WWT	WT6	WT12	WT18	WT6	WT12	WT18	WT12	WT18	WT18
$r_{p12}^{a)}$	0.27±0.04	0.23±0.03	0.16±0.03	0.14±0.03	0.60±0.03	0.54±0.03	0.50±0.03	0.61±0.02	0.55±0.03	0.69±0.02
	0.25±0.02	0.21±0.02	0.12±0.03	-	0.73±0.01	0.51±0.02	-	0.57±0.02	-	-
$r_{a12}^{a)}$	0.29±0.20	0.27±0.20	0.28±0.15	0.05±0.19	0.92±0.10	0.76±0.12	0.48±0.14	0.83±0.09	0.77±0.12	0.99±0.04
	0.45±0.09	0.33±0.11	0.31±0.11	-	0.98±0.02	0.84±0.07	-	0.87±0.06	-	-
r_{e12}	0.18±0.06	0.22±0.07	0.13±0.07	0.16±0.08	0.69±0.02	0.43±0.04	0.41±0.05	0.54±0.04	0.43±0.05	0.56±0.04
r_{m12}	0.77±0.14	0.73±0.02	-	-	0.96±0.06	-	-	-	-	-
r_{a1m2}	-0.29±0.19	-0.31±0.28	-	-	-0.39±0.20	-	-	-	-	-
r_{a2m1}	-0.11±0.21	0.01±0.21	0.16±0.16	0.35±0.17	0.04±0.12	0.37±0.14	0.53±0.14	0.44±0.16	0.55±0.14	-
r_{t12}	0.18±0.09	0.12±0.08	-	-	-	-	-	-	-	-

BWT=birth weight, WWT=weaning weight, WT6=six-month weight, WT12=12-month weight WT18=18-month weight

^{a)} = Estimates in the second line of the row are from a previous study (Abegaz *et al.*, 2002a) on a direct additive model for both traits.

The temporary environmental correlation between ADG1 and ADG2 was -0.26 . This is lower than (absolute value) estimates of -0.78 and -0.79 for two flocks of Baluchi sheep (Yazdi *et al.*, 1997). For phenotypic and genetic correlations between ADG1 and KR1, Van Wyk *et al.* (1993) reported a value of 0.93 and 0.94 in Dormer sheep while Van Niekerk *et al.* (1996) from a sire model on Boer goats, estimated a genetic correlation of 0.97. These estimates are close to the value obtained in the current study (0.98 phenotypic and 0.96 genetic). The maternal genetic correlation is close to unity. The KR1 as a measure of pre-weaning lamb efficiency shows that higher gain is related to high efficiency.

Except for the maternal additive correlations with ADG1 and KR1, all correlations and cross-correlations among BWT and ADG1, KR1, ADG2, and KR2 were low and in some cases negative. The absence of hefty direct additive correlation between ADG1 and BWT (and medium and positive maternal additive correlations) indicates that these traits are not antagonistic to each other. Bromley *et al.* (2000) reported direct correlations ranging from 0.18 to 0.57, maternal correlations ranging from -0.03 to 0.40, and cross-correlations of -0.12 to 0.21 between BWT and ADG in four breeds of sheep. The maternal genetic correlation estimate of 0.68 between BWT and ADG1 in this study, though slightly higher, agrees with the estimate of Bromley *et al.* (2000). Medium and negative direct genetic correlation was estimated between KR1 and BWT, but the estimate had a high standard error.

Cross-correlations between the direct and maternal additive effects of ADG1 with WWT, and WT6 were negative, while the phenotypic, direct additive, maternal additive and residual correlations were positive and high. Similarly Analla *et al.* (1995) reported negative cross-correlations for all direct and maternal effects of WWT, ADG, and weight at 90 days of age. High correlations between ADG1 and weaning and subsequent weights are expected as these are governed by a part-whole relationship. Phenotypic and residual correlations between WWT and ADG2 were negative and low while there was a medium genetic correlation between them. In Targhee sheep, Notter & Hough (1997) reported additive direct and residual correlations of 0.71 and 0.15 between weaning weight and

post-weaning ADG respectively. Both values are higher than estimates of 0.54 and -0.21 for additive direct and residual correlations respectively, between WWT and ADG2 in this study. For cross-correlations between the direct and maternal effects of weaning weight and pre-weaning Kleiber ratio in a multi-breed beef cattle Schoeman & Jordaan (1999) reported values of -0.18 and -0.30. In the current study values which are similar (-0.21) and lower (0.01, absolute value) were obtained. ADG2 and KR2 had negative phenotypic and residual but medium and positive genetic correlations with WWT. Correlations between temporary environmental effects of ADG1 and the other traits, with the exception of WWT, were negative and low. The temporary environmental correlation between ADG1 and WWT was 0.88.

Phenotypic, direct, maternal additive and residual correlations among BWT, WWT, WT6, WT12, and WT18 were positive. All direct genetic correlations among the weights were lower than values reported from the same data set using only direct animal models for both traits (Abegaz *et al.*, 2002a). Similar overestimation of the direct genetic covariance when models did not include maternal effects have been reported by Analla *et al.* (1995) for sheep and by Meyer (1994) for beef cattle. Cross-correlations between direct and maternal effects of the weight traits were low to medium and in some cases negative. Similar negative cross-correlations between direct and maternal additive effects and positive and high correlations between direct additive and maternal additive, and residual effects have been reported for birth weight and weaning weight of Australian Merino sheep (Vaez Torshizi *et al.*, 1996), for 30 and 60 day weights of Suffolk and Polypay sheep (Notter, 1998), for birth and weaning weights of Australian Simmental beef cattle (Swalve, 1993), and for WWT, WT12 and final weight (average age of 574 or 596 days) of Angus and Zebu crosses (Meyer, 1994).

Correlation of temporary environmental effects between BWT and WWT and between BWT and WT6 were 0.18 and 0.12. Similar correlation estimates could not be detected in the literature. For permanent environmental effects between 60-day and 120-day weights of Targhee sheep, Notter & Hough (1997) reported a correlation of 0.97. For WWT and WT12 in Australian Simmentals a correlation close to unity has been reported by Swalve

(1993) for permanent environmental effects of the two traits. Notter (1998) also reported values ranging from 0.69 to 0.99 for permanent environmental correlations between weights during the pre-weaning period and at weaning.

2.4 Conclusions

It appears that for accurate parameter estimation of growth performance and efficiency during early life in Horro sheep, operational models should consider the maternal genetic and temporary and permanent environmental components. Weight traits from weaning to 18 months of age have higher heritability than ADG and KR. Strong genetic correlations exist between ADG1 and KR1 and the weight traits. Therefore it would be appropriate to make use of performance for weight traits in selection programs so that both growth and efficiency traits can be improved. The efficiency trait doesn't need to be considered separately since the presence of a strong correlation with ADG can address the efficiency of growth. Cross-correlation estimates were low to moderate in value and in some cases negative. In most cases these estimates have high standard errors. Thus, unless verified from a large data set, the practical importance of these cross-correlations in estimating breeding values should be viewed with caution. Correlations of gain and Kleiber ratio and weight traits with BWT in most cases were low implying it has no strong relationship with the other traits. BWT would therefore not be adversely affected by selection for the other traits. Since BWT has been found to have a moderate genetic correlation with pre-weaning survival (Chapter 3), it can be manipulated by genetic means for optimum weight to improve survival, without having a negative effect on the other traits.

Genetic and maternal environmental effects on perinatal, pre- and post-weaning survival of lambs

3.1 Introduction

In a smallholder sheep production system, which is common in Ethiopia, an increase in productivity is more likely to be achieved through an increase in the number of lamb output (marketable lambs) than production (size) per individual animal. Production is solely based on grazing on natural pasture and finishing of lambs before marketing is not practised. Lambs are usually sold at lighter weights between the age of six months and one year. Under these conditions increasing the number of lamb output is more practical than increasing the size (weight) of each animal. The Horro and its ecotypes are the dominant sheep breed in South-Western Ethiopia and its characteristics has been described by Galal (1983). It has a 34% twinning rate (average of all age groups) and under controlled single sire mating has about 77% fertility (number of ewes lambled to number of ewes exposed) (Abegaz *et al.*, 2002b). Lamb mortality amounts to 4% in the perinatal period (3 days of age) and 20% and 14% in each of the pre- and post-weaning three months respectively. Significant increases in productivity could be made through a reduction of the existing level of lamb mortality.

Genetic means could be one of the avenues to be considered in improving survival. In most cases reports on heritability of survival were low and genetic improvement in survival is believed to be difficult. Equivocally, existence of breed variation when mortality is considered as a trait of the lamb (Wiener *et al.*, 1983; Gama *et al.*, 1991b; Fogarty *et al.*, 2000; Matos *et al.*, 2000) and response to selection in rearing ability of ewes (Donnelly, 1982; Haughey, 1983; Cloete & Scholtz, 1998) have also been reported. There are also indications that survival of lambs varies among sires (Gama *et al.*, 1991b;

Mukasa-Mugerwa *et al.*, 2000). In addition to direct effects, maternal genetic and/or environmental contributions are important in influencing lamb survival (Gama *et al.*, 1991a; Burfening, 1993; Matos *et al.*, 2000). Genetic differences in survival to different ages have been indicated between flocks selectively bred for high and low lifetime rearing ability (Haughey, 1983) and between sheep with different inbreeding levels (Galal *et al.*, 1981).

As a means of avoiding problems related with low heritability, selection can be applied for traits which have a higher heritability and at the same time have a high correlation with the traits of interest. One such trait for indirect selection of survival is birth weight. Birth weight was found to have a strong relationship with survival, though both the low and the high end of birth weight reduce survival (Wiener *et al.*, 1983; Knight *et al.*, 1988). In Horro sheep it appears that birth weights on the higher end of the range are not detrimental to survival (Abegaz *et al.*, 2000; Mukasa-Mugerwa *et al.*, 2000).

The objectives of the current study were to identify appropriate genetic models and to estimate genetic parameters of survival to the different ages along with its relationship with birth weight in Horro sheep.

3.2 Material and Methods

Data: Records from 3894 individual lambs representing progeny of 890 dams and 184 sires were used. Twinning was about 34%, thus slightly more than 50% of the lambs were born as twins. Survival of lambs was scored 1 for lambs surviving and 0 for those which died earlier than a specified age. All stillbirths were excluded from the study.

Statistical analysis: Survival in all cases was considered as a lamb trait. Effects of year of birth (1978 to 1997), birth status (single and twin), sex of the lamb (male and female), and age of the dam (1 through 6 and above) along with covariates of weight of dam at mating and lamb birth weight were fitted in a preliminary fixed model analysis. Second degree polynomial was fitted for lamb birth weight, but it was found to be significant

($P < 0.05$) only for survival to weaning and six-month age. For post-weaning survival, age at weaning was also included. Effects found to be significant ($P < 0.05$) (Table 3.1) were included in the final mixed model for model comparison and variance component estimation. Though they were found to be significant in some cases interactions between main effects contributed for only a small portion of the total variability. Therefore all interactions were not included in the final analysis to avoid overparametrization.

Univariate analyses were done using the ASREML program (Gilmour *et al.*, 1999) fitting animal models. Logit and probit link functions were used to analyze perinatal survival (first three days after birth, 3DS), pre-weaning (birth to three months of age, 3MS), post-weaning (from three to six months of age, 3-6MS) and both pre- and post-weaning survival (birth to six month of age, 6MS). Additionally observed scores were analyzed using linear methods so that the result from these analyses could be used as an additional measure in choice of the most appropriate model. Twelve models were compared (see Table 2.2. in chapter 2). Log-likelihood ratio tests were conducted to determine the most appropriate model. The model which was found to be consistent across ages and in both non-linear and linear methods of analyses was considered to be the most appropriate.

Table 3.1 Fixed effects included in the final model for perinatal (3DS), pre-weaning (3MS), post-weaning (3-6MS) and pre- and post-weaning (6MS) survival

Effect	Trait			
	3DS	3MS	3-6MS	6MS
Year of birth	X	X	X	X
Birth status	X	X	X	X
Birth weight	X	X	-	X
Weaning age	-	-	X	X
Dam age	-	X	-	-
Sex	-	-	-	-
Dam weight at mating	-	X	-	-

X= $P < 0.05$

Genetic and environmental parameters were estimated based on the most appropriate model from both logit and probit analyses. Bivariate analyses between survival at each age and birth weight were done on the untransformed survival score using the most appropriate model chosen for each trait. Model choice for birth weight is reported in chapter 2.

3.3 Results and discussion

Importance of year of birth, birth status, dam age and birth weight in affecting perinatal pre- and post-weaning survival was similar to reports from studies which involved the Horro breed (Kassahun, 2000; Mukasa-Mugerwa *et al.*, 2000). In addition weaning age has an effect on post-weaning survival. Post-weaning survival has improved by 0.3% for each day increase in weaning age over the average of 92 days.

Log-likelihood values from the different models under different modes of analysis for survival at the different ages and birth weights are shown in Table 3.2. Analysis on the observed scale shows that for 3MS and 3-6MS a model with the direct additive and the temporary (litter) environmental effect (Model 2) is the most appropriate, while for 3DS a model with the direct additive effect, maternal additive and permanent environmental effect, along with the covariance between the direct and maternal additive effects (Model 11) was found to be the most appropriate. For 6MS a model with direct and maternal additive and temporary environmental effect, along with the direct-maternal covariance (Model 8) was the most appropriate. In the logit and probit analysis the log-likelihood has shown an inexplicable pattern (in most cases log-likelihood values decreased with inclusion of additional components) and in some models convergence was not possible.

Table 3.2 (Co)variance estimates and log-likelihood values from univariate analyses under different models for perinatal survival (3DS), pre-weaning survival (3MS), post-weaning survival (3-6MS) and pre- and post-weaning survival (6MS)

Model	Trait											
	3DS			3MS			3-6MS			6MS		
	Obs.	Logit	probit	Obs.	Logit	Probit	Obs.	Logit	Probit	Obs.	Logit	Probit
1	3635.9	-13913.5	NC	1681.3	-9937.9	-5834.2	1003.2	-6881.0	-3610.3	1240.7	-8439.2	-4451.8
2	3656.5	-13638.2	NC	1694.8	-9842.5	-5778.0	1018.3	-6857.2	-3603.1	1250.1	-8410.0	-4440.0
3	3642.7	-13872.3	-7929.8	1682.3	-9928.0	-5834.9	1003.7	-6880.6	-3621.9	1243.1	-8450.1	-4466.8
4	3658.9	-13690.1	NC	1694.8	-9848.8	-5791.2	1018.3	-6857.2	-3615.6	1250.6	-8429.8	-4464.1
5	3637.9	-13991.4	-8017.3	1682.0	-9947.2	-5852.3	1003.2	-6881.0	-3629.6	1241.8	-8462.2	-4480.7
6	3657.3	-13660.0	NC	1694.9	-9857.5	-5800.4	1018.3	-6857.2	-3623.0	1250.4	-8434.6	-4471.3
7	3657.9	NC	NC	1684.7	-9921.9	-5832.4	1005.1	NC	NC	1245.8	-8447.2	-4465.9
8	3658.7	-13742.8	NC	1696.8	-9846.8	-5759.8	NC	NC	NC	1254.0	-8430.2	-4464.5
9	3642.7	-13881.9	-7929.8	1682.4	-9944.7	-5856.6	1003.1	-6880.6	-3640.6	1243.1	-8467.9	-4491.2
10	3658.9	-13700.4	NC	1694.9	-9865.4	-5812.0	1018.3	-6857.2	-3633.9	1250.6	-8447.9	-4487.4
11	3660.9	NC	NC	1685.0	-9922.8	-5839.7	NC	NC	NC	1246.9	-8453.6	-4477.7
12	NC	NC	NC	1696.8	-9846.8	-5759.8	NC	NC	NC	1254.2	-9227.5	-5072.5

Obs.=observed scale Logit=logit analyses Probit= probit analyses NC=not converged

The lack of convergence and the unusual pattern of the log-likelihood could be the result of inability of the data to support higher models. The model with temporary environmental effect as the only additional component on the basic direct model (Model 2) was found to be consistently superior in analysis under both logit and probit analyses. The only exception was for 3MS under probit analysis, where Model 8 was found to be superior. For the linear analysis on observed scale the inclusion of the temporary environmental component was responsible for a large increase in the log-likelihood values. Thus, Model 2 was considered to be consistent and the most appropriate model for survival at the different ages. There are only a few reports of model comparisons for survival in the literature. Cloete *et al.* (2001) compared models where direct and maternal additive genetic and permanent environmental components were considered and found significant ($P < 0.05$) maternal permanent effects, but with no evidence of maternal genetic variation in Australian Merino sheep. Morris *et al.* (2000) reported that for perinatal survival in Romney sheep, permanent environmental effects contributed more to the total variance than the direct and maternal additive genetic effects in all of three flocks studied (Morris *et al.*, 2000). The same was found for survival to weaning in two of the flocks studied. In the present study the permanent environmental term was found to be consistently significant ($P < 0.05$) for perinatal survival (Model 1 vs Model 3), but not for survival to weaning.

Heritability estimates of survival to the different ages, along with the proportion of total variance contributed by the temporary environmental (litter) components obtained from Model 2 are presented in Table 3.3. Except for the presence of non-estimable parameters for 3DS in the probit analyses, estimates from logit and probit analyses were found to be similar thus only estimates from the logit analysis were discussed. In all cases heritability estimates were low with a slight increase with age. Estimates of heritability on a logit-transformed scale under animal model are rare in the literature. Lopez-Villalobos & Garrick (1999), Morris *et al.* (2000) and Cloete *et al.* (2001) reported values ranging from 0.03 to 0.1 for lamb survival to weaning, while Morris *et al.* (2000) reported heritability estimates of perinatal survival ranging from 0.04 to 0.11. From paternal half- and full-sib

linear sire models Gama *et al.* (1991a) estimated average heritability of perinatal mortality on the binomial and normal scale to be 0.04 and 0.12 respectively.

For mortality to 60 days of age, values of 0.05 in the binomial and 0.1 in the normal scale were estimated. From a linear animal model on the observed scale of pre-weaning survival, Brash *et al.* (1994) and Fogarty *et al.* (1994) estimated values of zero and 0.07, respectively. In these latter reports however, survival was considered a ewe trait and was expressed as lambs weaned per lambs born. Linear sire model estimates ranging from 0.00 to 0.14 were also reported by Abdulkhaliq *et al.* (1989), Burfening & Carpio (1993) and Matos *et al.* (2000). Bunge *et al.* (1990), using a linear paternal half-sib analysis, reported a heritability of 0.15 for survival to weaning at about two months of age. In general, estimates in the present study are in agreement with literature values though the estimates for 3DS and 3MS were lower.

Table 3.3 Total phenotypic variance (σ_p^2), heritability estimates (h^2) and proportion of temporary (litter) effect (t^2) from univariate analysis of survival using logit and probit analyses

Trait		σ_p^2	h^2	t^2
Perinatal survival (3DS)	Logit	4.11	0.00±0.00	0.20±0.05
	Probit	Ne	Ne	Ne
Pre-weaning survival (3MS)	Logit	3.70	0.02±0.03	0.09±0.04
	Probit	1.12	0.02±0.03	0.08±0.04
Post- weaning Survival (3-6MS)	Logit	3.62	0.07±0.03	0.04±0.04
	Probit	1.14	0.09±0.03	0.03±0.04
Pre- and post-weaning survival (6MS)	Logit	3.65	0.05±0.03	0.05±0.03
	Probit	1.11	0.06±0.03	0.04±0.04

Ne=non-estimable

Threshold sire model estimates for heritability of survival to weaning (Konstantinov *et al.*, 1994; Olivier *et al.*, 1998; Snyman *et al.*, 1998) are in most cases similar to the current animal model estimates from logit analysis. Matos *et al.* (2000) reported higher total heritabilities from threshold models than linear models for Rambouillet and Finnsheep. However, there was little advantage of threshold model over linear models in terms of goodness of fit and predictive ability. Similar results have also been reported from a number of studies (Weller & Ron, 1992; Olesen *et al.*, 1994; Matos *et al.*, 1997b) in cattle or sheep. In a recent simulation study, however, Abdel-Azim & Berger (1999) found the threshold model to be more efficient than linear models. Besides the equivocation, at present, threshold models do not have the flexibility of linear models in terms of fitting different fixed (particularly covariates) and random effects. Additionally there is a lack of knowledge about the genetic mechanism of the underlying difference in survival to support the assumption of underlying continuous liability. Etiologically the resistance of the lamb to factors causing ill health and death, and the strength of these factors interact in a peculiar way to result in a specific outcome (survival or death). Under these conditions it is not clear if the threshold model would be a model of choice in the analysis of survival. Elston (1977) suggested, under the condition where there is no adequate knowledge about the underlying mechanism, it would seem preferable to estimate heritability of the trait itself instead of the underlying scale. The use of logit and probit link function to approximate normal distribution could be an alternative solution. The ability to fit different components in the analysis would be an added advantage of analyses using link functions.

The temporary effect for 3MS was estimated to be 0.09. The proportion of the phenotypic variance accounted for by the temporary environmental component was higher (Table 3.3) than heritability estimates. Morris *et al.* (2000), from a model which also included the maternal genetic component, estimated proportions ranging from 0.06 to 0.10 for litter effects of pre-weaning survival and from 0.10 to 0.14 for perinatal survival. The latter values are lower than estimates of 0.2 for 3DS in this study. The death of both mates occurs in more than 70% of all the mortalities in twin born lambs. This implies that there is lower within-litter variation (either both the twins die or survive) and higher

between-litter variation. This supports the relatively high level of litter effect observed in this study. Analyses to determine if this has a genetic basis in rearing ability of ewes (not reported here) have failed to show any genetic variation. Heritability of survival shows a slight increase from 3DS to 3MS and to 6MS and is less affected by the litter effect after the perinatal period. Thus the importance of the maternal component, part of which is mediated through litter effect, diminishes in the post-weaning period, while the direct additive effect shows an increase in importance.

Results from bivariate analyses between survival to the different ages and birth weight are shown in Table 3.4. With the exception of 3DS heritability estimates were similar to univariate estimates under logit transformation, while the ratio of litter effects were higher than the univariate estimates. Because it was fitted as a correlated trait to survival, birth weight was not included as covariate in the model for survival in the bivariate analysis. Part of the effect of birth weight on survival is expected to be expressed as a litter effect, which in turn emanates from similarity of birth weight within litters (twins) and dissimilarity between litters. This could explain the increased temporary (litter) effect estimate in the bivariate model as compared to the univariate model. Similarity of the heritability estimates between the univariate logit analyses and the bivariate analysis done on the observed binary scale for survival could be the result of the contribution of birth weight. Abdel-Azim & Berger (1999) in a simulation study showed that estimates from linear models were similar to estimates from logarithmic transformation and transformation to Snell scores. Parameter estimates from two-trait survival and birth weight analyses are rare in the literature, probably due to the lack of software to handle a continuous and a binomial trait simultaneously. Notwithstanding the analytical problem, the analysis of survival with birth weight is likely to benefit in terms of improved accuracy, even when both were analyzed using linear method for observed data. Ramirez-Valverde *et al.* (2001) showed that a higher increase in accuracy of prediction can be obtained in multiple trait models with respect to single trait models than with threshold over linear models. Additionally Varona *et al.* (1999) suggested that predictive ability for a categorical trait could be improved by a bivariate analysis with a continuous trait.

Table 3.4 Estimates of heritability (h^2) and proportion of temporary environment (t^2) and genetic (r_g) phenotypic (r_p) temporary environmental (r_t) and residual correlation (r_e) from bivariate analysis of survival with birth weight

Parameters	Survival			
	3DS	3MS	3-6MS	6MS
h^2	0.03±0.02	0.02±0.02	0.03±0.02	0.06±0.02
t^2	0.18±0.03	0.16±0.03	0.23±0.04	0.15±0.03
r_g	0.20±0.23	0.68±0.34	0.45±0.26	0.26±0.17
r_p	0.17±0.02	0.15±0.02	0.12±0.02	0.15±0.02
r_t	0.29±0.06	0.37±0.07	0.27±0.07	0.34±0.08
r_e	0.14±0.04	0.08±0.04	0.04±0.05	0.07±0.05

3DS=Perinatal survival, 3MS=Pre-weaning survival, 3-6MS=Post- weaning Survival 3-6MS= Pre- and post-weaning survival

Matika *et al.* (2001) from a bivariate analysis with birth weight estimated a heritability of 0.01 for pre-weaning survival in Sabi sheep. Genetic correlation estimates in this study were relatively higher for 3MS and 6MS, but standard errors were higher. Burfening & Carpio (1993) reported genetic and residual correlations of 0.34 and 0.13 between survival to weaning at 120 days of age and birth weight in Junin sheep, while Matika *et al.* (2001) reported a genetic correlation of 0.18 for Sabi sheep. Reported values from both sources are lower than current estimates for survival to weaning at 90 days, but comparable to survival to 180 days of age. In the Junin sheep twinning is rare (1%) unlike in the Horro sheep (34%) while there is also a lower level of twinning in the Sabi sheep (20%), hence lower genetic correlations may be the result of the difference in twinning rate. Phenotypic correlations were low for all survival traits. Abdulkhaliq *et al.* (1989) reported phenotypic correlations ranging from 0.51 to 0.58 for litter weight at birth and litter size at weaning. Significant influences of birth weight on survival have been widely reported (Wiener *et al.*, 1983; Knight *et al.*, 1988; Burfening & Carpio, 1993; Fogarty *et*

al., 2000; Morris *et al.*, 2000). Correlation between temporary effects of birth weight and survival was sizeable. The litter effect was found to be important in univariate analysis for both traits and the sizeable correlation observed in this study is the reflection of that relationship.

3.4 Conclusions

In the literature the evidence on the merit of a threshold model over other models of analysis is equivocal. Subsequent comparative work could show if the threshold model has advantage over the models used in the current study. The temporary environmental (litter) effect was found to be more important in affecting survival than the maternal genetic and permanent environmental component. This implies that more attention to differential management of lambs from different birth types is necessary. Additionally it could also be a reflection of variation in rearing ability of ewes: i.e. twin lambing dams either have the ability to rear both lambs or rear none. Analysis in this regard has shown no genetic variation for lifetime rearing ability (not reported) and the actual cause is worth investigation. Heritability estimates of survival are low. This causes improvement through direct selection based on predicted breeding values to be very slow. The genetic correlation between survival to weaning and birth weight was found to be moderately high. This may give an opportunity for indirect selection for survival through birth weight. Birth weight has been reported to have moderate heritability (Abegaz *et al.*, 2002a; chapter 2).

Genetic parameter estimates of ewe productive and reproductive traits

4.1 Introduction

Sheep production in parts of Ethiopia, where smallholder farming is common, is characterized by small flock sizes. Productivity is low due to the fact that animals are largely naturally selected for survival under sub-optimal environments. Genetic improvement could contribute to raise productivity from this system. Due to small flock sizes, genetic parameters which are required for genetic improvement have to be generated from on-station data where management is kept as close as possible to that existing under farm conditions.

Productivity in any sheep enterprise where meat is the main product, can be measured in terms of total weight of lambs weaned per ewe. This trait depends on fertility, litter size, weight (growth) of individual lambs, mothering ability and survival. Under the smallholder system, measuring each component trait is difficult in practice. Additionally being an aggregate trait, total weight of lamb weaned may eliminate the shortcomings of improvement based on individual traits with resulting unfavourable consequences in situations where there are antagonistic relationships between component traits (e.g. Lasslo *et al.*, 1985).

Although total weight of lamb weaned per lambing (mating) is a good indicator of productivity, statistical analysis of this trait is hampered by abnormal distributions due to zero values from non-lambing or non-weaning ewes. Thus estimates of this trait are usually obtained with a breach of the required statistical assumption. As an alternative cumulative or lifetime production could be used, since this has a better distribution and is much more amenable to statistical analysis than individual observations during the

different parities of the ewe (e.g. Snyman *et al.*, 1997). In this study the objective was to estimate genetic parameters of ewe productivity and the component traits for use in designing genetic improvement strategies to raise productivity.

4.2 Material and Methods

Data: Fertility of ewes was coded as 1 for ewes having given birth (or lost foetus due to abortion) and 0 for those that had not. Twinning was coded as 0 for lambing single and 1 for lambing twins (triplets were less than 1 % and considered as twins). Litter size at weaning was coded as 0, 1 and 2 for ewes which had no, one or two lambs at weaning. Total weight of lamb at birth (TBW) was calculated as the sum of individual birth weights after weight of each lamb had been adjusted to the average sex (overall mean). Similarly total weaning weight (TWW) per lambing was calculated as weight of lambs at weaning after adjustments had been made for sex and weaning age. Cumulative TWW for the first four parities (TWW4) was summed up as an estimate of lifetime productivity. TWW was set to zero for ewes which had given birth but failed to wean a lamb. Adjustment of birth and weaning weights to the average sex was done by using multiplicative factors derived as least squares mean of each sex as a ratio of the overall mean. Thus a factor of 0.98 and 1.03 was applied to male and female birth weights respectively, while a factor of 0.96 and 1.05 was applied for weight at weaning. Weaning weight was linearly adjusted to 90 days of weaning age.

Statistical analysis: Important fixed effects and interactions were identified using the generalized linear model (GLM) of SAS (SAS, 1994). The age of dam, year of lambing and the interaction between the two effects were found to be highly significant ($P < 0.01$) for TBW and TWW and were included in the genetic analysis model. Year of birth of the ewe and her weight as a yearling were found to have significant ($P < 0.05$) effects on TWW4. Due to the small number of records and lest over-parameterization might occur in the mixed model analysis, interactions with less than a 2% contribution to the total variation were excluded from the final model, even if found significant. Ewe weight at mating was fitted as a linear covariate in the analysis of fertility, twinning and litter size

at weaning. Year of lambing and ewe age were also included for twinning, while only year was included for litter size at weaning. (Co)variance components for litter size at weaning, TBW and TWW were estimated by using the ASREML program (Gilmour *et al.*, 1999). Two models were used, viz. the direct additive genetic and the repeatability models. Since all traits were analyzed as ewe traits, maternal genetic and litter effects, which are more prominent at an earlier age, were assumed to have no sizeable effect. The same program was used in the analysis of fertility and twinning with logit transformation. Service sire was included either as random or fixed in the analysis of fertility. (Co)variance estimates for TWW4 were also obtained by using the direct animal model.

Bivariate analyses between all the traits at birth and at weaning were performed. In all bivariate analyses observed (non-transformed) values were used. The model used in the bivariate analysis was,

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} x_1 & 0 \\ 0 & x_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} z_1 & 0 \\ 0 & z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_1 and y_2 are values of the first and second trait in a two trait analysis, b_1 and b_2 are fixed effects affecting the first and the second trait, u_1 and u_2 are vectors of breeding values for the first and the second trait, e_1 and e_2 are vectors of residual effects of the first and the second trait and x_1, x_2, z_1, z_2 are known incidence matrices.

The covariance matrices are

$$\text{Cov}(u_1, u_2) = G_{12} = A\sigma_{u_1 u_2}$$

$$\text{Cov}(e_1, e_2) = R_{12} = I\sigma_{e_1 e_2}$$

$\sigma_{u_1 u_2}$ is the covariance due to breeding values of the first and the second trait,

$\sigma_{e_1 e_2}$ is the covariance due to residual effects,

A is the numerator relationship matrix and I is an identity matrix.

The phenotypic covariance matrix was,

$$\text{Cov}(y_1, y_2) = ZG_{12}Z' + R_{12}$$

Heritability estimates of a trait from different bivariate analyses were pooled (h^2_{pooled}) and standard errors (SE) were calculated using the following formula as used by Koots *et al.* (1994).

$$h^2_{\text{pooled}} = \frac{\sum_{i=1}^n h_i^2 / (SE_{h_i^2})^2}{\sum_{i=1}^n 1 / (SE_{h_i^2})^2}$$

$$SE(h^2_{\text{pooled}}) = \sqrt{\frac{1}{\sum \left(\frac{1}{SE_{h_i^2}}\right)}}$$

Table 4.1 Description of data used in the analysis of production and derived efficiency traits

Trait	N	Mean (SD)
Fertility	3223	0.73 (0.44)
Twinning	2409	0.34 (0.05)
Number of lambs weaned	2409	1.02 (0.66)
Total birth weight per parity (TBW, kg)	2403	3.53 (1.20)
Total weaning weight per parity (TWW, kg)	2409	11.71 (7.78)
Cumulative TWW to the 4 th parity (TWW4, kg)	252	55.0(21.00)
Service sire	179	
Number of ewes	901	
Number of sires of ewes	151	
Number of dams of ewes	393	

4.3 Results and Discussion

The data used in the study and means (SD) are presented in Table 4.1. The mean values for TBW and TWW are 3.53 and 11.71 kg respectively. Values of TBW for other breeds reported elsewhere (Boujenane *et al.*, 1991; Rosati *et al.*, 2002) were higher than the value of TBW in this study. Due to large differences in mean litter size of the breeds, meaningful comparison is not possible. For comparable and a slightly higher litter size (1.30 to 1.65) Abdulkhaliq *et al.* (1989) reported higher values (5.8 to 8.1 kg) of TBW for Columbia, Suffolk and Targhee. The most likely reason for this high TBW could be the

difference in genetic size between the breeds. It is, however, also possible that the birth weight realized in Horro sheep is below the potential for the breed, implying that birth weight can be improved. As corroborative evidence, unlike in most breeds where survival declines at high birth weights, previous studies on Horro sheep have shown that survival invariably increased with an increase in birth weight (Mukasa-Mugerwa *et al.*, 2000; Abegaz *et al.*, 2000).

The mean value for TWW in this study is higher than the value reported by Bedier *et al.* (1992) for weight of lamb weaned per ewe joined (9.45 kg) of Barki sheep. However, Armbruster *et al.* (1991) for Côte d'Ivoire sheep and Awemu *et al.* (1998) for Yankasa sheep reported higher values of TWW. Mukasa-Mugerwa & Lahlou-Kassi (1995) reported comparable values of TWW for Menz sheep in the Ethiopian highlands. Values for TWW from reports elsewhere (e.g. Abdulkhaliq *et al.*, 1989; Long *et al.*, 1989; Boujenane *et al.*, 1991; Ligda *et al.*, 2000; Bromley *et al.*, 2001; Carson *et al.*, 2001; Matika *et al.*, 2001) were also higher than in this study. Apart from the fact that in some of the studies the sheep were large breeds (hence heavier weight than the smaller breeds at same age during growth), for some of the breeds the means reported were based only on lambs surviving to weaning (excluding ewes which lost their lambs). In other cases means were from weights taken at later weaning ages than in this study (e.g. Bromley *et al.*, 2001) or from production under shorter lambing intervals, which provide more than one lambing chance per year (e.g. Armbruster *et al.*, 1991; Mukasa-Mugerwa & Lahlou-Kassi, 1995). In the current study a value of zero has been included for those ewes which lost all lambs before weaning and most of the data set is from a once-a-year controlled lambing system. The TWW4 value is comparable to values reported for one of two Merino flocks studied by Snyman *et al.* (1997), while it is by far lower than values for the Afrino flock and the second Merino flock.

Average litter size at weaning in this study is lower than values reported by Boujenane *et al.* (1991) for D'man and by Bromley *et al.* (2001) for Colombia, Polypay, Rambouillet and Targhee sheep breeds, but is higher than for Barki sheep (Bedier *et al.*, 1992). Most of the difference is a result of difference in litter size at birth, though differences in

proportion of lambs surviving to weaning can also be the cause. At comparable litter size at birth (1.31 vs. 1.34) Brash *et al.* (1994) reported a higher proportion (0.85 vs. 0.76) of lambs surviving to weaning than in the current study.

Estimates of genetic and environmental parameters from univariate analyses are presented in Table 4.2. Except for fertility where service sire was considered as random, in all cases the repeatability model was found to be significantly ($P < 0.05$) different from the direct model. Direct heritability estimates for all the traits were low and fall within the range of zero for number and weight of lambs weaned under the repeatability model, to 0.15 for twinning under the direct model. For four sheep breeds, Bromley *et al.* (2001) reported direct heritability estimates of litter weight at weaning, ranging from 0.02 to 0.11, while Snyman *et al.* (1997) obtained values ranging from 0.05 to 0.26 for Afrino and Merino sheep. Albeit on the lower side, the current estimate falls in the range of values from the former report, but below that of the latter. Estimates from other studies (Abdulkhaliq *et al.*, 1989; Long *et al.*, 1989; Boujenane *et al.*, 1991; Ligda *et al.*, 2000; Rosati *et al.*, 2002) are higher than the estimate in this study. The distribution of data for TWW in the current study is highly skewed due to the inclusion of a large number of zero values for those ewes which had not weaned a lamb. This might have contributed to the low estimates of heritability.

Heritability of twinning was estimated to be 0.15 and 0.07 for the direct additive and repeatability models. This is slightly higher than previous estimates of 0.11 to 0.06 on the observed scale (Abegaz *et al.*, 2002b). Similarly, from a simulated comparison between linear model on observed scale and Snell scores transformation, Abdel-Azim & Berger (1999) found an improvement (up to 13%) in estimated heritability, while higher estimates were obtained from threshold models. However the flexibility with respect to fixed effects (e.g. ability to fit covariates) and random components that can be fitted in the analysis, and availability of modern software packages are advantages of transformation (logit link functions) over the threshold analysis. For number of lambs born alive from linear animal models on observed scale, Rosati *et al.* (2002) estimated a

Table 4.2 Log-likelihood values and estimates of genetic and environmental parameters (\pm S.E.) for total birth and weaning weight and reproductive traits

Trait ¹⁾	Model ¹⁾	Log-likelihood	h^2_a	c^2	s^2	r	σ^2_p
TBW	1	-1369.19	0.08 \pm 0.02				1.09
	2	-1366.47	0.03 \pm 0.02	0.06 \pm 0.03		0.10 \pm 0.02	1.09
TWW	1	-5427.54	0.04 \pm 0.02				37.11
	2	-5424.12	0.00 \pm 0.02	0.06 \pm 0.03		0.07 \pm 0.02	37.03
Twinning	1	-5502.88	0.15 \pm 0.03				3.88
	2	-5451.91	0.07 \pm 0.04	0.09 \pm 0.04		0.16 \pm 0.03	3.92
Litter size weaned	1	11.40	0.03 \pm 0.02				0.35
	2	14.71	0.00 \pm 0.00	0.06 \pm 0.02		0.06 \pm 0.02	0.35
Fertility	1	-7355.05	0.02 \pm 0.02		0.16 \pm 0.02		4.03
	1a	-7355.05	0.02 \pm 0.02	0.00 \pm 0.00	0.16 \pm 0.02	0.02 \pm 0.02	4.03
	2	-8312.15	0.06 \pm 0.02				3.50
	2a	-8280.28	0.02 \pm 0.02	0.06 \pm 0.04		0.08 \pm 0.03	3.58
TWW4	1		0.05 \pm 0.16				251.10

h^2_a -Direct heritability, c^2 -proportion of permanent environmental variance, s^2 -proportion of service sire variance, r-repeatability, σ^2_p -total phenotypic variance

TBW-total birth weight, TWW-total weaning weight, and TWW4-TWW in the first four parities

¹⁾ 1=Direct animal model; 1a= Model 1 with service sire considered as random; 2 =repeatability model; 2a=Model 2 with service sire considered as fixed

direct and maternal heritability of 0.05 and 0.01 respectively, while from sire models for three sheep breeds Hansen & Shrestha (1997) estimated heritabilities ranging from 0.15 to 0.20. Rao & Notter (2000), for three sheep breeds, estimated heritabilities of 0.09 to 0.11 for litter size. From an animal model for Rambouillet sheep, Burfening & Davis (1996) reported a direct heritability of 0.16. Except for the estimate of Rosati *et al.* (2002) which is very low, all estimates are close to estimates in this study. The estimate of repeatability of twinning (0.16) in this study is higher than an estimate of 0.12 in a previous study based on linear models on observed scale (Abegaz *et al.*, 2002b). Similar estimates of repeatability were made by Hansen & Shrestha (1997), but their estimates were in most cases lower than heritability estimates. Matos *et al.* (1997a) also reported

higher heritabilities than repeatabilities in threshold models and vice versa for linear animal models. These results are obviously caused by lack of constraints (non-negativity of variance) in the analytical method used and have no meaningful interpretation.

Heritability of total number of lambs at weaning in this study is 0.03 ± 0.011 . Studies elsewhere show similar low heritability estimates for both animal (Hall *et al.*, 1994; Brash *et al.*, 1994; Bromley *et al.*, 2000; Rosati *et al.*, 2002) and sire models (Fogarty *et al.*, 1985; Boujenane *et al.*, 1991). Higher estimates from sire models have been reported by More O'Ferrall (1976) and Abdulkhaliq *et al.* (1989). From a large number of reports Fogarty (1995) reported a weighted mean value of 0.05, which is in close agreement with the estimate in this study.

The direct heritability estimate of total litter weight at birth in this study was 0.08. This is at the lower end of a range of sire model estimates of 0.08 to 0.31 reported by Abdulkhaliq *et al.* (1989) for three sheep breeds. Other studies (Boujenane *et al.*, 1991; Rosati *et al.*, 2002; Hansen & Shrestha, 1997) also reported higher estimates than that obtained in this study. Yearly least square means for individual birth weight in the period studied, varied from 2.2 to 3.4 kg implying a very high environmental variation which did affect birth weight. This is clearly one of the main reasons for the low estimate of heritability of TBW in this study.

The estimate of direct heritability of fertility was 0.02 ± 0.01 and 0.06 ± 0.02 when service sire was considered as random and fixed respectively. These estimates are in accordance with estimates obtained by linear sire and animal models, but are lower than estimates from threshold sire and animal models by Matos *et al.* (1997a). Similar low estimates were reported by Brash *et al.* (1994). From linear animal models, where service sire was not included as random, Rosati *et al.* (2002) reported a heritability of 0.06. This agrees closely with the estimate in the current study. Long *et al.* (1989) fitting a sire model (service sire included as random) and Al-Shorepy & Notter (1996) under an animal model (service sire included either as random or fixed) reported higher heritability

estimates than in this study. In cattle, using linear and threshold sire models, Weller & Ron (1992) estimated (service sire included as random) heritabilities of 0.01 to 0.03.

The heritability estimate for fertility is very low throughout and it becomes much lower as a result of inclusion of service sire as a non-genetic random effect. The data were generated from a single sire controlled mating system where assignment of rams to a group was done randomly after initial choice of rams to be used as sires. Due to this there was a need to include the serving ram as a random effect to separate its contribution to variation in ewe fertility. Estimate of service-sire variance as a ratio of the total phenotypic variance is 0.16, which is higher than estimates of 0.08 and 0.10 reported by Al-Shorepy & Notter (1996). In cattle variation in fertility attributable to service sire was estimated to be less than 1% (Weller & Ron, 1992).

Burfening & Davis (1996) reported a highly significant ($P < 0.01$) service sire effect for number of lambs born per ewe exposed in the Rambouillet breed when it was considered as fixed, but a non-significant ($P > 0.20$) contribution of less than 1% when the effect was considered as random. Besides differences in breed and analytical models, fertility in the current work was an 'all or none' trait, while in the study of Burfening & Davis (1996) it was 'none' against a gradation of number of lambs (1 to 4) for fertile ewes. The relatively higher service sire variance in this study implies that it could be an important source in affecting fertility in Horro sheep. A previous study (Yohannes *et al.*, 1995) showed that this is not related to weight (size) of rams and factors contributing to this variation need identification. Repeatability of fertility was 0.02 and 0.08 when service sire was considered random and fixed. This is lower than repeatability estimates of 0.10 to 0.17 from Finnsheep and Rambouillet sheep by linear sire and animal models and threshold sire models (Matos *et al.*, 1997a). Bunge *et al.* (1990) reported a repeatability of 0.03, while Gabiña (1989) reported zero repeatability.

The estimate of heritability for TWW4 was 0.05. In a review of literature by Fogarty (1995) it was indicated that heritabilities were approximately doubled for average lifetime

ewe performance compared to single-record estimates. However, in this study, the improvement in heritability obtained by TWW4 over TWW was very low (0.05 vs. 0.04). Snyman *et al.* (1997), for two Merino flocks, reported higher heritabilities (0.10 and 0.26) of TWW4 than obtained in this study. In this study the data for TWW4 consisted of records of only 252 ewes. This obviously creates a limitation in the analysis, particularly when one considers the 17 years' period it encompasses. Due to this there was no improvement in the estimate of heritability by the use of TWW4 over TWW and the standard error of the estimate was very high, though the former is expected to have superior statistical properties of approaching normal distribution over records from individual parities.

Phenotypic and genetic relationships from two-trait analysis are presented in Table 4.3. The phenotypic relationships of TBW with TWW, twinning, and number of lambs at weaning were 0.37, 0.77 and 0.45, while genetic correlations were 0.86, 0.83 and 0.62 respectively. Bromley *et al.* (2001) estimated genetic correlations of -0.22 to 0.28 between TBW and TWW, while Matika *et al.* (2001) reported a genetic correlation of 0.46 between individual lamb birth weights and TWW per ewe. These are lower than the estimate of 0.86 in this study. Hansen & Shrestha (1999) using REML procedures, for three breeds of sheep reported genetic correlations of 0.52 to 0.74 for litter size at birth and total birth weight, which are lower than the estimate of 0.83 in the current study. Differences in litter size may account for the difference in correlation.

The phenotypic relationship of litter size at birth with TWW, and litter size at weaning was 0.26 and 0.45 respectively. Genetic correlations for these traits were higher than phenotypic correlations. Rosati *et al.* (2002) reported estimates of genetic correlation between number of lambs born alive and total litter weight at weaning to be 0.51 and that between number of lambs weaned and total litter weight at weaning to be 0.16. The former value is close to an estimate of 0.57 in the current study for twinning and TWW, while the latter value is by far lower than an estimate of 0.76 for number of lambs at weaning and TWW. In a review by Fogarty (1995) there were six values on genetic and phenotypic correlations between number and weights of lambs weaned per ewe lambing

with averages of 0.83 and 0.88 respectively. In the current study estimate of 0.76 for the genetic and 0.84 for the phenotypic correlation between number of lambs weaned and TWW are slightly lower than those estimates. Hansen & Shrestha (1999) reported genetic correlations of 0.19 to 0.94 for litter size at birth and total lamb weight at weaning (91 days) with corresponding phenotypic correlations of 0.48 to 0.55. It appears that there is large between-breed variation with respect to genetic correlations between litter size at birth or weaning and total weaning weight per ewe and at times standard error estimates are very high. In the current study the standard errors are reasonably low. Bromley *et al.* (2000), in four breeds for sheep, estimated genetic correlations ranging from 0.58 to 1.00 between litter size at birth and at weaning while Saboulard *et al.* (1995) reported a genetic correlation of 0.86. The estimate in the current study (0.82) is in the range of the former and is close to the latter estimate.

Residual correlation estimates are in all cases similar to the phenotypic correlations. This is to be expected due to the low genetic variation shown in low heritability estimates. Heritability estimates in all bivariate analyses of each trait were very close to one another and hence were pooled over all bivariate estimates for the trait. These values were similar to univariate estimates, except for litter size at birth, where a decline occurred from 0.15 in the univariate to 0.12 in the bivariate analysis. This could be explained by the use of logit analysis in the univariate analysis while in the bivariate analysis the observed scale was used. Bivariate analysis between total weaning weight in the first one and two parities with TWW4 was attempted and failed to converge.

Table 4.3 Genetic (above diagonal), phenotypic (below diagonal), and residual (below diagonal in parenthesis) correlation and pooled heritability estimates (bold, on diagonal) from a two trait analysis of productivity traits

Trait	TBW	TWW	Twinning	Litter size at weaning
TBW	0.08±0.01	0.86±0.14	0.83±0.05	0.62±0.17
TWW	0.37±0.02 (0.34±0.02)	0.04±0.01	0.57±0.16	0.76±0.10
Twinning	0.77±0.01 (0.76±0.01)	0.26±0.02 (0.24±0.02)	0.12±0.01	0.82±0.12
Litter size at weaning	0.45±0.02 (0.45±0.02)	0.84±0.01 (0.84±0.01)	0.45±0.02 (0.43±0.02)	0.04±0.01

4.4 Conclusions

Mean values and heritability estimates of TBW, TWW, twinning, fertility, number of lambs weaned and TWW4 were found to be low. Direct genetic selection within the breed may therefore not bring about much improvement. However, productivity estimates are aggregate traits and a small improvement in these traits would mean sizeable gain in terms of overall change in the other traits and is usually realized with concurrent change in all components. Genetic correlations were positive in all cases and moderate to high in value. Twinning has medium heritability and moderate to high genetic correlation with number of lambs weaned and TWW. This suggests it can be used as a selection criterion for indirect improvement in productivity. TBW can be used as additional criteria due to its moderate correlation with TWW and number of lambs weaned. Total lifetime productivity as estimated by TWW4 has low heritability. However, data size for this estimate is small and verification of this estimate is required with the availability of additional data. Service sire was found to be an important source of variation in fertility and attributes of the sire which insure higher fertility should be investigated.

Chapter 5

**GENETIC AND PHENOTYPIC PARAMETERS OF GROWTH CURVE AND
THE RELATIONSHIP WITH EARLY GROWTH****5.1 Introduction**

Sheep production in Ethiopia is characterized by smallholder farming. Sale of lambs provides a considerable part of the income of farmers. About 75% of the sheep population in the country is found in the highlands (Mukasa-Mugerwa & Lahlou-Kassi, 1995) and a study in this area indicated that small ruminants, while accounting for only 6.6% of the capital invested, provide more than 48% of the cash income generated from livestock production (Kriesel & Lemma, 1989). To increase farmers' income, there needs to be improvement in the production of these animals. Rate of weight gain to marketing is an important trait determining productivity and efficiency of a meat production enterprise. In the highlands of Ethiopia slow growth rate resulting in low market weight has been identified to be one of the factors limiting profitability (Mukasa-Mugerwa & Lahlou-Kassi, 1995). Fast early growth on the part of the slaughter generation and small mature size (though smaller income in culled ewe value) on the part of the reproducing female are desirable. Because of this, rate of gain and mature weight need to be considered in selection programs. The possibility of selecting for rapid growth rate without necessarily selecting for an increase in mature size has been suggested for beef bulls (Webster *et al.*, 1982). Theron *et al.* (1994) also indicated that feeder-breeder dimorphism (large offspring for slaughter are obtained from small breeding animals) can be genetically induced in beef cattle for different nutritional environments. Growth curve parameters provide potentially useful criteria for altering the relationship between body weight and age through selection (Kachman & Gianola, 1984). An optimum growth curve could be obtained by selection for the desired values of growth curve parameters (Bathaei & Leroy, 1998). Estimation of growth curve parameters requires weight-age data after growth has been completed. This requires a long period of time and increases

the generation interval in selection programs. Thus as a means of obtaining early indicators of these parameters it would be of great importance to look for traits with early expression and at the same time with strong relationship with the growth curve parameters.

Growth curve parameters are usually estimated from non-linear mathematical functions which help to summarize the information in large longitudinal (weight-age) data from each individual. Five such functions, viz. Gompertz, Brody, von Bertalanfy, Richards, and Logistic were compared in cattle by Brown *et al.* (1976). For selection to be effective, accurate estimates of genetic and phenotypic parameters of the growth curve parameters are required.

In Horro sheep weight-age data were collected in the years 1978-1997. Description of the growth curve of a breed and studying the genetic and phenotypic aspects of the parameters provide an opportunity to manipulate the growth curve for improved production. The objective of this study was first to estimate parameters of the growth curve for each animal and use these estimates in subsequent (co)variance analyses to obtain estimates of genetic and phenotypic parameters.

5.2 Material and Methods

The data were generated from a flock of Horro sheep kept at Bako research centre, Ethiopia. After editing data from a total of 524 sheep (60 male and wethers and 464 female animals - the progeny of 132 sires and 327 dams) were used for this study. A total of 27488 weights taken at about monthly intervals from birth to past 3.5 years were used. In Horro sheep body weight starts to stabilize from about 36 months of age (Abegaz & Duguma, 2000). Since parameters describing the growth curve can be evaluated only after growth has been completed, 3.5 years of age was assumed the age of maturity. Birth weight was recorded soon after birth (maximum of 12 hours after birth) while all body weights were recorded in the morning after an overnight fasting of 12-14 hours. A detailed description of the flock and management procedures is given in chapter 2.

Brody's model (Brody, 1945) was used to estimate parameters of the growth curve for each animal. Besides its computational ease and provision of biologically interpretable parameters, Brody's function has been reported to be adequate to describe growth in cattle after the point of inflection (Brown *et al.*, 1976). Recently it has been applied (on cattle (Kaps *et al.*, 2000) and sheep (Bathaei & Leroy, 1998). The mathematical function is:

$$Y_t = A(1 - Be^{-kt}) + \epsilon_t$$

where:

Y_t = weight at t (0 to 1719) days of age, A = mature weight as expressed by asymptotic limit of the weight when age approaches infinity. This estimates the average weight of the mature animal independent of short term fluctuation in weight due to environmental effects (e.g. feed availability) or pregnancy and suckling status. B = proportion of mature weight gained after birth. k = a function of the ratio of maximum growth rate to mature weight, normally referred to as maturing rate. It is related to postnatal rate of maturing and serves both as a measure of growth rate and rate of change in growth rate. High k values indicate early maturing animals and vice versa. e = is Napier's base for natural logarithms, t = age expressed in days and ϵ_t = deviation of observed value from model estimates (predicted value).

The function was fitted to weight (kg)-age (days) data from each animal using the least square nonlinear procedure (NLIN) of SAS (SAS, 1994) with the Gauss Newton iterative method. The convergence criterion used was as follows:

$$\frac{(SSE_{i-1} - SSE_i)}{(SSE_i + 10^{-6})} < 10^{-8}$$

where SSE_i is the residual sum of squares for the i^{th} iteration.

A fixed effect model where year of birth (1978 to 1997), sex (male and female), type of birth (singles and twins) and age of dam (≤ 2 , 3, 4, 5, 6 and ≥ 7 years) were fitted using the GLM procedure of SAS (SAS, 1994) in order to identify environmental effects which affect growth curve parameters. Intact males and wethers were categorized in the same

sex group. Interactions between main effects (particularly between sex and year) were found to be significant, but the amount of variation accounted by these interactions was low. Thus interactions were avoided from subsequent analysis. The ASREML program of Gilmour *et al.* (1999) was used to estimate genetic parameters of growth curve parameters. The mixed model included fixed effects which were found to be significant ($P < 0.05$) for each parameter along with the random effect of additive genetic effect of the animal. Bivariate analyses among the curve parameters and immature body weight (birth, weaning, six-month and yearling) were done to estimate genetic and phenotypic correlations. Additionally, Pearson correlations were calculated between growth curve parameters of ewes and their productivity. Ewe productivity was expressed as follows:

1. TWW1= total weight of lamb weaned at first parity
2. TWW2= total weight of lamb weaned over the first two parities
3. TWW3= total weight of lamb weaned over the first three parities
4. TWW4= total weight of lamb weaned over the first four parities
5. NLB4= average number of lambs per parity for ewes with four or more lambing opportunities
6. NLS4= average number of lambs survived to weaning per parity for ewes with four or more lambing opportunities.

Total weight of lamb weaned per ewe per lambing was calculated as the sum of weights of lambs weaned per ewe after adjustments for sex and age at weaning.

5.3 Results and Discussion

An estimate of the asymptotic mature weight (A) in some of the sheep was found to be biologically impossible. It appears that the solution for these particular animals (16 animals) had converged to a local maximum and records of these sheep were excluded from subsequent analyses. Least squares means of the growth curve parameter estimates and immature weights are presented in Table 5.1. Year of birth had a significant ($P < 0.05$) effect on all parameters of the growth curve. Sex had a significant effect on A ($P < 0.01$) and B ($P < 0.05$). Type of birth and age of dam had a significant ($P < 0.01$) effect only on B. Least squares means in the different years ranged from 34.5 kg to 45.3 kg for A, 0.84 to

0.97 for B and 0.118 to 0.488×10^{-2} for k. The coefficient of determination (R^2) for all traits indicated that the fixed model fitted, explained only less than half of the total variability.

Similar significant effects of year of birth on mature weight of sheep have been reported by Stobart *et al.* (1986), Pitchford (1993) and Bathaei & Leroy (1996) and for cattle (López de Torre & Rankin, 1978). Unlike in this study, Stobart *et al.* (1986) found a highly significant ($P < 0.01$) effect of age of dam on mature weight. Bathaei & Leroy (1998) reported a significant ($P < 0.01$) effect of age of dam only on B which is similar to what was obtained in the current study. Significant effect of type of birth on k has been reported by Pitchford (1993; from Gompertz function) and Bathaei & Leroy (1998). In this study the effect of type of birth on k had approached the significant level ($P = 0.077$). Singles were only 2% heavier than twins at maturity. This figure is in agreement with the estimate of 3% reported by Pitchford (1993), but lower than the 13% reported by Bathaei & Leroy (1996). It appears that twins mature more slowly than, but achieve similar mature weights to singles. Using the Gompertz function Lewis *et al.* (2002) have estimated values of A for males which is about 1.27 times of that for females. This is in close agreement to the estimate of 1.24 in the current study, but below the generally assumed ratio of 1.3 (Hammond, 1932 as cited by Zygoyiannis *et al.*, 1997). In a number of European sheep breeds, Friggens *et al.* (1997) and Zygoyiannis *et al.* (1997) have also estimated the ratio of weight at maturity to be 1.3 while Bathaei & Leroy (1996) reported a ratio of 1.33. Breed differences may account for the discrepancy. Chickens from different lines have ratios of mature weight ranging from 1.25 to 1.36 (Mignon-Grasteau *et al.*, 2000). Significant differences in B for type of birth show that singles are heavier at birth and the proportion of mature weight they may gain after birth is lower as compared to twins which were born lighter. Similarly lambs from young and first parity ewes are born with lighter weights than lambs from older and advanced parity ewes, and a higher proportion of their mature weight is gained after birth. The overall estimate of k was $0.27 \times 10^{-2} \text{ day}^{-1}$ or 0.081 month^{-1} . Estimates of k from other functions are not comparable to estimates from Brody's function due to the use of different inflection points.

Table 5.1 Descriptive statistics for birth, weaning, six-month and yearling weight and growth curve parameters

Effects	Number	Trait						
		Birth weight(kg)	Weaning weight(kg)	Six-month weight(kg)	Yearling weight(kg)	A (kg)	B	k(x10 ²) [†]
R ²		33.4	37.0	33.0	46.1	32.8	39.8	42.1
CV(%)		17.3	20.2	19.8	17.3	14.0	6.7	36.3
Overall	508	2.72±0.04	12.6±0.2	16.1±0.3	23.7±0.4	37.6±0.5	0.88±0.01	0.27±0.01
Sex		NS	NS	**	**	**	*	NS
Male	49	2.79±0.08	12.9±0.5	16.8±0.6	24.8±0.8	41.8±0.8	0.90±0.01	0.258±0.020
Female	459	2.66±0.03	12.3±0.2	15.4±0.2	22.6±0.3	33.3±0.3	0.87±0.00	0.289±0.007
Type of birth		**	**	**	**	NS	**	NS (P=0.07)
Single	270	2.96±0.05	13.7±0.3	17.0±0.4	24.5±0.5	37.9±0.5	0.86±0.02	0.284±0.012
Twin	238	2.49±0.05	11.5±0.3	15.2±0.4	22.8±0.5	37.2±0.5	0.91±0.01	0.264±0.012
Dam age		*	NS	NS	NS	NS	**	NS
≤2	124	2.59±0.06	12.3±0.4	15.9±0.5	24.1±0.6	37.1±0.6	0.90±0.01	0.284±0.015
3	124	2.71±0.06	12.8±0.4	16.6±0.5	23.8±0.6	37.2±0.7	0.88±0.01	0.285±0.015
4	86	2.83±0.06	13.2±0.4	16.3±0.5	23.6±0.6	37.2±0.7	0.86±0.01	0.276±0.016
5	70	2.80±0.06	12.9±0.3	16.7±0.5	23.7±0.6	38.0±0.7	0.87±0.01	0.260±0.017
6	53	2.67±0.07	12.3±0.4	15.5±0.5	23.4±0.7	37.2±0.8	0.90±0.01	0.291±0.019
≥7	46	2.74±0.08	12.1±0.5	15.8±0.6	23.3±0.8	38.6±0.9	0.89±0.01	0.246±0.021
Year		**	**	**	**	**	**	**

* P<0.05 **P<0.01 NS=not significant †k=growth rate constant

Because of this, the only comparable estimate available for sheep is an estimate of 0.12 month^{-1} by Bathaei & Leroy (1998) which is much higher than the estimate in the current study.

Singles and females have significantly ($P < 0.05$) higher maturing rates than twins and males respectively. Females had achieved about 37, 46 and 68 per cent of their mature weight at weaning (≈ 90 days), six month and yearling, while males had achieved only 31, 40 and 59 per cent respectively. Singles had reached about 36, 45 and 65 per cent of their mature weight, while twin born lambs had achieved 31, 41 and 61 per cent at weaning, six month and yearling respectively. For ewes from three different breeds Stobart *et al.* (1986) reported yearling weights which were about 67% of mature weight. This is similar to the value in the current study. However in their two consecutive articles Bathaei & Leroy (1996; 1998) reported values of yearling weight which provide high (close to 75%) percentage of mature weight. As opposed to the finding in the current study Brown *et al.* (1972a) found that in Hereford and Angus cattle, males mature faster than females. Coefficient of variations (CV) of A, B and k parameters were 14.0, 6.7 and 36.3 per cent, which implies there is much more variation in maturing rate, followed by mature weight. Similar high CVs for k in cows were reported by López de Torre *et al.* (1992), but in this instance CV was lowest for mature weight. It appears that animals achieve similar mature weight though their rate of growth (maturity) varies.

Comparison of observed and predicted values for weight at birth and at different age intervals are presented in Table 5.2. It is shown that the function had overestimated mean birth weight by about 1.6 kg. Afterwards the difference narrowed and stabilized resulting in increased correlations between the observed and predicted values. Brody's function is intended to describe growth occurring after point of inflection (a period of maximum growth rate some time during early growth) (Beltrán *et al.*, 1992). The function overestimated birth weight when it was fitted to data including pre-inflection points in cattle (Brown *et al.*, 1976; Beltrán *et al.*, 1992). The weight difference between birth and mature weight represents the proportion of weight gained after birth (B). With an average birth weight of about 2.7 kg and a mature weight of 37.6 kg (Table 5.1) the proportion of

weight gained after birth will amount to about 0.93, as opposed to 0.88, which is the estimate of B in this study. Other studies using Brody's model for sheep (Bathaei & Leroy, 1998) and for cattle (Beltrán *et al.*, 1992) estimated B values of 0.95 and 0.91 respectively. These values are higher than the current estimates. For weights from the first month through maturity the correlation was 0.94 and the difference between mean of predicted and observed weight was only 0.04 kg (Table 5.2). However inclusion of birth weight is extremely important for a good fit to the other parts of the curve (DeNise & Brinks, 1985).

Table 5.2 Mean observed and predicted weights for the different age intervals and correlation between observed and predicted weights

Age (days)	Mean weight (kg)		Correlations between observed and predicted
	Observed	Predicted	
0	2.7	4.3	0.29
12-30	6.31	6.84	0.71
31-60	8.78	8.12	0.88
61-90	11.62	10.37	0.90
91-180	14.47	13.91	0.89
181-360	19.48	19.83	0.90
361-540	24.68	24.88	0.88
541-720	28.35	27.98	0.86
721-900	30.09	30.04	0.84
901-1080	32.01	31.11	0.86
1081-1260	31.51	32.07	0.81
1261-1719	32.60	32.99	0.78
12-1719(excluding birth weight)	27.06	27.03	0.94

Genetic parameter estimates of A, B and k are presented in Table 5.3. All three parameters have a medium heritability with the highest and the lowest being for A and k respectively. Heritability estimates of mature weight (A) in this study is comparable to an estimate of 0.30 for Chios sheep reported by Mavrogenis & Constantinou (1990) and 0.32 to 0.34 for Hereford cattle (Brown *et al.*, 1972a; MacNeil & Urick, 1999). For Angus cattle Brown *et al.* (1972a) reported a heritability of 0.21 for mature weight which is lower than the current estimate. Very high estimates (0.44 to 0.53) of heritability for mature weight were reported for sheep by Stobart *et al.* (1986) and Bathaei & Leroy (1998), and for cattle by Northcutt & Wilson (1993) and Kaps *et al.* (1999). Clarke *et al.* (2000) reported heritability estimates of 0.41, 0.37 and 0.38 for ewe body weight at three, four and five years of age respectively. For mature weight (A) derived from Gompertz function in chicken, Mignon-Grasteau *et al.* (2000) estimated a heritability of 0.54. Heritability estimates for B and k in the current study are lower than literature estimates for sheep (Bathaei & Leroy, 1998) and for cattle (Brown *et al.*, 1972a; DeNise & Brinks, 1985). MacNeil & Urick (1999) reported heritability estimates of 0.27 for B and 0.10 for k. The estimate for k is in close agreement with the current estimate of 0.14. The sheep flock in this study was managed under variable grazing and management conditions. Stocking rate varied because of large annual differences in the grazing land available and other management conditions were also variable, depending on the availability of supplementary feed and personnel involved in the management. This can be seen from the high annual variation in rate of maturing, ranging from 0.12 to 0.49×10^{-2} . This might have rendered genetic parameter estimates of k to be low.

The genetic and phenotypic correlations among the growth curve parameters and weaning, six-month and yearling weight are presented in Table 5.3. Genetic correlations between A and B, and B and k were positive, while those between A and k were close to zero (-0.07). In all cases standard error estimates were high. The phenotypic correlation between A and B was close to zero and between A and k medium and negative. For sheep Bathaei & Leroy (1998) estimated negative genetic correlations of -0.12 and -0.40 between A and B and A and k respectively. In cattle, genetic correlation estimates between A and B were all negative, but highly variable: -0.02 to -0.97 (Brown *et al.*,

Table 5.3 Heritability estimates (diagonal) of growth curve parameters and genetic (above diagonal) and phenotypic correlations (below diagonal) between the growth curve parameters and with weights from birth to yearling

	Parameter			Trait			
	A value	B value	k value	Birth weight	Wean weight	Six-month weight	One year weight
A value	0.29±0.10	0.39±0.31	-0.07±0.34	0.27±0.34	0.34±0.27	0.44±0.20	0.67±0.17
B value	0.04±0.05	0.18±0.09	0.25±0.39	-0.66±0.53	-0.48±0.27	-0.22±0.26	0.78±0.56
k value	-0.36±0.04	0.25±0.04	0.14±0.09	-0.13±0.69	0.37±0.35	0.61±0.25	0.66±0.22
Birth weight	0.15±0.05	-0.30±0.04	0.03±0.05	-	-	-	-
Wean weight	0.21±0.05	-0.49±0.04	0.31±0.04	-	-	-	-
six month weight	0.25±0.05	-0.34±0.04	0.35±0.04	-	-	-	-
One year weight	0.24±0.05	0.06±0.05	0.50±0.04	-	-	-	-

Table 5.4 Pearson correlations (r) between growth curve parameters and ewe productivity traits

Traits	No. of observation	Curve parameters		
		A	B	k
TWW1	341	0.05	0.29**	0.26**
TWW2	284	0.28**	0.21**	0.20**
TWW3	229	0.25**	0.18**	0.18**
TWW4	155	0.27**	0.16*	0.05
NLB4	233	0.27**	0.09	0.05
NLS4	233	0.14*	0.10	0.13*

* $P < 0.05$ ** $P < 0.01$

TWW1-4= total weight of lambs weaned over the first to fourth parities

NLB4= average number of lambs born per lambing for ewes with at least four lambing opportunities

NLS4= average number of lambs weaned per lambing for ewes with at least four lambing opportunities

1972a; DeNise & Brinks, 1985). The positive genetic correlation between A and B in the current study is contrary to the other reports. However it is conceivable that mature weight could have a positive genetic correlation with the proportion of mature weight obtained after birth. The estimate of phenotypic correlation of 0.04 between A and B falls within the range of -0.30 to 0.33 reported for cattle (Brown *et al.*, 1972a; López de Torre & Rankin, 1978; DeNise & Brinks, 1985). For sheep Bathaei & Leroy (1998) reported a phenotypic correlation of -0.20. The genetic correlation estimate of -0.07 between A and k in the current study is lower than (in absolute value) the estimate of -0.40 for sheep (Bathaei & Leroy, 1998) and -0.29 to -1.16 for cattle (Brown *et al.*, 1972a; DeNise & Brinks, 1985; Glaze & Schalles, 1999). The phenotypic correlation of -0.36 between A and k agrees well with the estimate of -0.45 for sheep (Bathaei & Leroy, 1998) and -0.48 to -0.72 for cattle (Brown *et al.*, 1972a; Brown *et al.*, 1976; López de Torre & Rankin, 1978; DeNise & Brinks 1985). Estimate of genetic correlation between B and k (0.25) in this study is low compared to estimates 0.95 for Mehraban Sheep (Bathaei & Leroy, 1998) and 0.82 to 1.00 for cattle (DeNise & Brinks, 1985; Brown *et al.*, 1972a).

Many studies on growth curve show that the maturing rate parameter (k) which is related to growth rate of animals, is negatively correlated with A. This suggests that animals maturing the fastest have lower weights at maturity than slowly maturing animals. However, in this study the relationship between A and k is close to zero, implying selection for either one has no effect on the other.

Genetic correlations between A and early growth parameters were positive and increased from birth to yearling weight. Genetic correlations with B, with the exception of yearling weight were negative while the genetic correlations with k (with the exception of birth weight) were positive. In most cases standard errors were high. In sheep, similar positive genetic correlations which increased with age at measurement, (between the different weights and mature weight) had been reported by Stobart *et al.* (1986) and Bathaei & Leroy (1998). Similarly Mavrogenis & Constantinou (1990) reported a genetic correlation of 0.34 and 0.55 and a phenotypic correlation of 0.23 and 0.33 between

mature weight and birth and weaning weights respectively. Brown *et al.* (1972b) reported very high positive correlations between immature weights at 4, 8 and 12 months of age and mature weight for Hereford cattle, but very low positive estimates for Angus cattle. The phenotypic correlations were higher for Angus in most cases. MacNeil & Urick (1999) in cattle reported a genetic correlation of 0.65, -0.17 and 0.11 between yearling weight and A, B and k respectively, while López de Torre & Rankin (1978) estimated phenotypic correlations of 0.33 and 0.32 between 14 month and mature weight for Hereford and Brangus cattle respectively. For Angus cattle Kaps *et al.* (1999) estimated direct genetic correlations of 0.63 to 0.85 between weaning and mature weight, while Northcutt & Wilson (1993) reported a genetic correlation of 0.45 between yearling and mature weight. Estimates of genetic correlations between mature weight and immature weights in this study are in general agreement with estimates in the literature. However, unlike in other studies, the genetic correlation between yearling weight and B is positive and high. The genetic correlation between A and B in the current study is positive as opposed to estimates in most other studies (e.g. Denise & Brinks, 1985; Bathaei & Leroy, 1998) and this might have influenced the relationship of yearling weight with B. The genetic relationship between A and k is close to zero, while the correlation of k with weaning to yearling weight has a medium positive value. This may indicate that the genetic potential for maturing rate, which depends on growth rate, is more positively related to early growth, but has no relationship with weights which would be achieved afterwards until maturity.

Pearson correlation coefficients between growth curve parameters and TWW1, TWW2, TWW3, TWW4, NLB4 and NLS4 are presented in Table 5.4. A has significant ($P < 0.05$) positive correlations with all the traits, except with TWW1. B and k are also significantly ($P < 0.01$) correlated with TWW1, TWW2 and TWW3. TWW4 and NLS4 have a significant ($P < 0.05$) relationship with B and k respectively. It appears that ewe performance at a young age is more closely related to maturing rate than mature weight and with an increase in age, mature weight becomes more important than k. B has a trend similar to k. Analytical attempts to investigate the possible genetic basis (genetic correlations) failed to reach convergence. However the results indicate that productivity

can have some relationship with growth curve parameters. In cattle López de Torre *et al.* (1992) reported significant regression coefficients of number of calves weaned per cow during a 5-year period on A (-0.005) and k (0.53). The average productive life in the Horro sheep flock used in this study covers about three parities. Therefore, improving productivity from young ewes can have a sizeable contribution in increasing flock productivity.

5.4 Conclusions

Except for birth weight, Brody's function appears to estimate body weight in Horro sheep fairly accurately. Only about 6.2 per cent of predicted values of birth weight fall within the 10% limit of observed weights, while this value is about 70 per cent for weight taken after 3.5 years of age. The shortcoming of the function has more impact on the B parameter. The A and k parameters, represent the mature weight and the growth rate (maturing rate) respectively, thus being practically the most important components of the function. Heritability estimates were medium and the genetic correlation between A and k was close to zero. This allows for independent selection for each trait. Due to its positive correlation with productivity in young ewes, maturing rate (k) seems an important trait worth considering. The parameters of growth curve require weights of an animal to be measured from birth until weight stabilizes at maturity. Selection for these traits obviously increases the generation interval and direct selection would be difficult. Since A and k have moderate positive genetic correlations with immature weights, these weights may be used as indirect selection criteria. Development of mathematical functions which can predict mature weight and maturing rate from weights taken early in life is an area worth investigating.

Genetic evaluation of early growth using a random regression model

6.1 Introduction

Growth as represented by body weights at different ages is an important trait which contributes to the productivity in sheep. Genetic improvement of this trait is one of the means to raise productivity and this requires accurate estimation of genetic parameters. Weights of an animal measured at different stages are usually considered as repeated measurements of a single trait with homogenous variances or as different traits. Analysis in the former case requires fitting of repeatability models, while in the latter case multivariate models are conventionally used. In reality, however, these traits are an expansion of the same trait measured along a trajectory of time. The other conventional approach is to fit a standard growth curve and analyze the parameters of the growth curve as traits (Chapter 5). The growth curve approach assumes a certain standard curve (e.g. Brody's function) equally fits the growth of all animals. Each animal, however, normally has a different growth curve.

Currently random regression models are being applied in the analysis of longitudinal "infinite-dimensional" data (e.g. growth, test day milk yield) (Jamrozik & Schaeffer, 1997; Meyer, 1998b; Albuquerque & Meyer, 2001). Such models use polynomials (fixed and random) to describe mean profiles with random coefficients and to generate correlation structures among the repeated observations on each individual (Robert-Granié *et al.*, 2002). Since repeated measurements on the same animal are normally more correlated than two measurements on different animals and the correlation between repeated measurements may decrease as the time between them increases, analysis of such data must address the issue of covariation between measures on the same animal (Robert-Granié *et al.*, 2002). Analysis where the measurements along the trajectory are

modelled as a function that defines that trajectory (time) may be more appropriate in the estimation of growth parameters for selection purposes. Such an approach has an additional advantage of studying change and increasing statistical power.

In the tropics where large fluctuation in environmental variables (particularly in availability of feed) is common, concurrent fluctuations in weight (growth rate) of animals is likely to occur. Under these conditions random regression analyses, where the trait is the whole set of measurements along the trajectory, may have advantages above univariate or multivariate analyses of weight traits at specific time intervals in obtaining reliable variance estimates.

Univariate and bivariate analyses on weights recorded at different ages during early growth were carried out on data from a flock of Horro sheep (Chapter 2). Due to its superior statistical properties, a random regression model was thought worth investigating in the belief that the analysis would result in more accurate estimates of the genetic and environmental parameters. Additionally the random regression analysis allows estimation of parameters at all points along the trajectory and provide a wider option in choosing the right age for selection to take place. Therefore, the objective was to estimate genetic and permanent environmental parameters using different random regression models.

6.2 Material and methods

Data: The data used in this study were collected from a flock of Horro sheep during the period 1978 to 1997 (excluding 1984) at Bako research centre, Ethiopia. In order to explore the possibility of fitting polynomials of higher order (up to six) 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 used. A total of 22149 records from 1951 animals were eventually available. Body weight recorded at monthly intervals from birth to a maximum of 408 days of age was used. Roughly 8.0, 7.0, 6.0, 6.0, 12.0, 16.0 and 45.0 per cent of the animals have 7, 8, 9, 10, 11, 12 and 13 weight measurements respectively. Description of the data is presented in Table 6.1.

Table 6.1 Description of data used for random regression analysis

Measurement	Range	Mean	S.D.
Age(days)	0 – 408	161.5	106.9
Weight (kg)	1 – 48	14.3	7.01
No. records	22149	-	-
No. animals	1951	-	-
No. dams	641	-	-
No. Sires	158	-	-

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 (1978-1997, except 1984), type of birth (single and multiple), sex (male and female) and age of dam (one to seven+ years). To determine the most appropriate polynomial order to be fitted for fixed effects, 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. Thus weight as a function of age in days at weighing (test day) 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 data.

Data at all ages were analyzed simultaneously by fitting a set of regression coefficients on age as random effects. The software ("DXMRR": Meyer, 1998a) used has the ability to fit only direct additive and the animal's permanent environmental effects (Meyer, 1998c) in addition to the residual effect. Orthogonal polynomials of varying degree were fitted only for these two effects. The animal's permanent environmental effect represented the environmental variance between repeated records of an animal. The general model in matrix notation is:

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

where \mathbf{y} is a vector of weights of each animal, \mathbf{b} is a vector of fixed effects including year, sex, type of birth and age of dam and a polynomial of age in days, \mathbf{a} is the vector of additive genetic regression, \mathbf{p} is the vector of permanent environmental random regression coefficients and \mathbf{e} is the vector of residual effects. \mathbf{X} , \mathbf{Z} and \mathbf{W} are corresponding design matrices. In all cases orthogonal (legendre) polynomials were used. These polynomials are appropriate for analyzing a covariance function of longitudinal growth data (Kirkpatrick *et al.*, 1990) and are also easy to manipulate. In addition they have good convergence properties and correlations between coefficients are lower than between the coefficients of ordinary polynomials (Lewis & Brotherstone, 2002).

A total of six models (Table 6.2) varying in the order of polynomial fit for the random effects and assumptions about the distribution of the error variance were used. Error variances were considered either to be homogenous (uniform distribution) for weight at all ages (one error measure) or heterogeneous (variable distribution) between measurements at different growth stages (four error measures). In models where heterogeneity of error variance was assumed, separate error measures were fitted for weights at birth, 10 to 90 (weaning), 91 to 180 and 181 to 408 days of age. The four groups were formed to represent phases of growth to birth, pre-weaning, post-weaning and post-pubertal stages. Analyses were carried out using the DXMRR program (Meyer, 1998a). The AI-REML algorithm was used with a subsequent analysis using the derivative free Powel method to check for convergence to a global maximum. Comparison for better order of fit of the different models was done by likelihood ratio tests (LRT) and Akaike's Information criteria (AIC). For model comparisons under highly differing number of degrees of freedom (number of parameters) the use of LRT at constant levels of α (level of significance) is questionable and AIC was suggested as an alternative (Burnham & Anderson, 1998). In this study both methods were used in the comparison. A model with the highest ($P < 0.05$) LRT and with the lowest AIC was considered to be the most appropriate model.

Table 6.2 Description of models used in random regression analysis

Model	Order of polynomial fit		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).

Eigenfunctions of the additive genetic and permanent environmental effect were obtained as

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

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

Eigenfunctions of genetic covariance function are especially of interest as they represent possible deformations of the mean (growth) trajectory which can be affected by selection, while corresponding eigenvalues describe the amount of genetic variation in that direction. In particular the eigenfunction associated with the largest eigenvalue gives the direction in which the mean trajectory will change most rapidly (Kirkpatrick *et al.*, 1990; Meyer, 1998b)

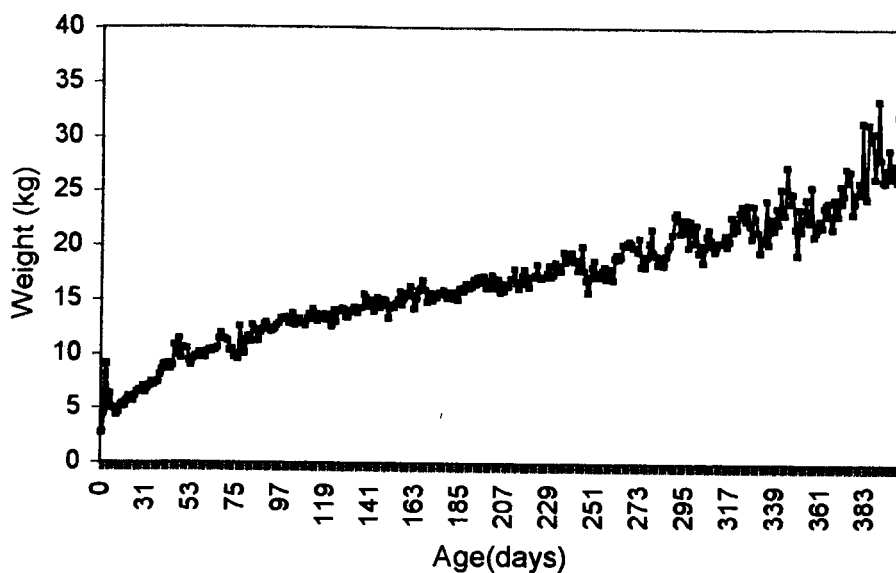


Figure 6.1 Average of the recorded weights within the range of ages used in this study.

6.3 Results and Discussion

Weight measurements across the age range in this study are presented in Figure 6.1. Weight increased from 2.7 kg at birth to 34 kg at about 400 days of age. Fluctuation in mean weight at consecutive ages was observed. This is due to measurements for consecutive ages (days) being from different sets of animals.

Log-likelihood estimates for models with different orders of polynomial fit and number of error measures are presented in Table 6.3. Significant ($P < 0.05$) increases in log-likelihood were observed with an 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. A superior fit ($P < 0.05$) was observed for heterogeneity in models with lower order of fit implying that part of the residual variance would be taken up by the increase in the order of polynomial fit. In this study, maternal effects were not considered. Previous univariate analyses (Chapter 2) have shown that this effect has a significant ($P < 0.05$) contribution up to about

eight months of age. Ignoring this effect might have contributed to heterogeneity in the error variance since difference in estimates of the error variance between successive groupings reduced progressively with an increase in age. Under both LRT and AIC methods, Model 6 was found to be significantly superior to all other models.

Table 6.3 Log-likelihood values for different models and likelihood ratio (LRT) and Akaike's information criteria (AIC) values

Model	No. of parameters ^{a)}	Log L	LRT	AIC
1	13	-25845.9	0.0	51717.8
2	16	-24712.7	2266.4	49457.4
3	21	-25136.4	1419.0	50314.8
4	24	-24060.8	3570.2	48169.6
5	31	-23931.4	3829.0	47924.8
6	34	-22915.3	5861.2	45898.6

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

Estimates of heritability and ratio of permanent environment to the phenotypic variance obtained from the different models are presented in Table 6.4. Estimates differed between models of different polynomial order and number of 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 similar. Order of polynomial fit as well as appropriate modelling of the error variance may contribute to accurate estimation of parameters. Olori *et al.* (1999), found no significant differences in estimates of additive genetic and

Table 6.4 Heritability and ratio of permanent environmental variance from models with different orders of polynomial and error measures

Age(days)	Model					
	1	2	3	4	5	6
	Heritability					
0	0.00	0.14	0.01	0.13	0.03	0.14
30	0.08	0.12	0.18	0.25	0.26	0.32
60	0.16	0.21	0.28	0.31	0.30	0.32
90	0.21	0.24	0.30	0.31	0.29	0.30
120	0.23	0.25	0.29	0.28	0.28	0.28
150	0.24	0.26	0.27	0.27	0.28	0.27
180	0.25	0.26	0.25	0.25	0.27	0.26
210	0.26	0.26	0.25	0.25	0.26	0.26
240	0.27	0.26	0.25	0.26	0.27	0.27
270	0.28	0.27	0.27	0.28	0.31	0.31
300	0.30	0.29	0.30	0.31	0.34	0.34
330	0.32	0.31	0.34	0.34	0.36	0.35
360	0.34	0.33	0.38	0.39	0.35	0.35
390	0.36	0.35	0.41	0.44	0.36	0.37
	Permanent environmental ratio ^{a)}					
0	0.01	0.16	0.01	0.19	0.01	0.42
30	0.23	0.27	0.29	0.36	0.36	0.44
60	0.42	0.45	0.45	0.50	0.51	0.55
90	0.52	0.54	0.53	0.56	0.58	0.61
120	0.57	0.58	0.57	0.58	0.61	0.61
150	0.61	0.61	0.62	0.62	0.64	0.63
180	0.63	0.63	0.65	0.65	0.66	0.65
210	0.64	0.62	0.67	0.65	0.68	0.67
240	0.64	0.63	0.67	0.66	0.67	0.66
270	0.64	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	0.62	0.62	0.60	0.61	0.61
360	0.62	0.61	0.59	0.57	0.62	0.62
390	0.61	0.60	0.56	0.53	0.62	0.61
	Error variance ^{b)}					
1	1.9861	0.1597	1.5611	0.1465	1.1689	0.0907
2	-	1.8067	-	1.2310	-	0.8257
3	-	1.9218	-	1.7293	-	1.4195
4	-	2.7416	-	2.1049	-	1.4893

^{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.

environmental variances of test day records in dairy cows when fitting different numbers of measurement error variances. Similarly Snyder *et al.* (2000 as cited by Meyer, 2000) reported only minor differences in estimates of variances for daily feed intake in pigs between models fitting a single measurement error variance and assuming the log error variance was described by a quadratic function of age of measurement. Meyer (2000) also reported little difference in estimates of between-animal standard deviations for higher (≥ 12) orders of fit with widely varying number of error measures (1 to 66). Therefore, for sufficient order of fit, different regression curves to model between-animal 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. For weight at birth and at about 12 months of age heritability estimates from Model 6 in the current study were close to the total heritability estimate from univariate analyses (Chapter 2). For weights between these periods heritability estimates from univariate analyses were low. This is reasonable to expect, since in the current random regression analysis maternal effects were not included. Ignoring maternal effects in traits that are likely to be influenced by this effect would result in overestimation of heritability. Similarly Lewis & Brotherstone (2002) reported higher heritability estimates from models ignoring maternal effects than models which included them, with a decline in the difference as age increased. The animals' permanent environmental effect has accounted for 0.42 to 0.67 per cent 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. In addition to the possibility of improved partitioning of the total variance into environmental and genetic origin, the permanent environmental effect (and the repeatability) may indicate how reliable estimates at a specified age could be. The repeatability value obtained in this study for weights at later ages was very high. 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.

Additive genetic, permanent environmental, phenotypic and residual variance estimates from Model 6 for the whole period are presented in Figure 6.2. Except for the residual variance that stabilized after weaning at 90 days of age, all variance components showed a steady increase with age. Towards the end of the growth period estimates increased drastically. Similarly, implausible values of variance and covariance components at the 'edges', i.e. the extremes of the age were reported by Meyer (1999) from analyses on mature weight of beef cows. This is most likely due to the small number of observations with weight records at this age. In the current study, from a total of 1951 animals only six had weight records above 400 days of age. A drastic change in residual and phenotypic variance was observed at about 90 days of age. This is the result of creating 'fixed' age classes of homogenous variance. Though the assumption of heterogeneity was found to be significant ($P < 0.05$) modelling such heterogeneity is better done by using a continuous function than fitting fixed classes of error measures. Large classes of homogeneity with a narrow range along the trajectory may also solve the problem. In the current study the attempt to fit 13 error variances (birth and one to ≥ 12 months) failed due to a lack of convergence to a global maximum.

The heritability estimates for the entire period obtained from Model 6 are presented in Figure 6.3. The estimate has increased from about 0.14 at birth to about 0.33 around two months of age and declined again to about 0.26 at roughly 200 days of age and then increased to about 0.35 at yearling and 0.4 at about 400 days of age. As was the case with the variance components, heritability estimates showed a drop at about 90 days of age, but drastic increases towards the end of the period.

Correlation estimates for additive genetic, permanent environmental and phenotypic effects from Model 6 are presented in Figure 6.4. Correlations between weight at birth and at other ages were low in all cases (bottom line of the three dimensional curve). Previous bivariate analyses (Chapter 2) has also resulted in low direct additive and

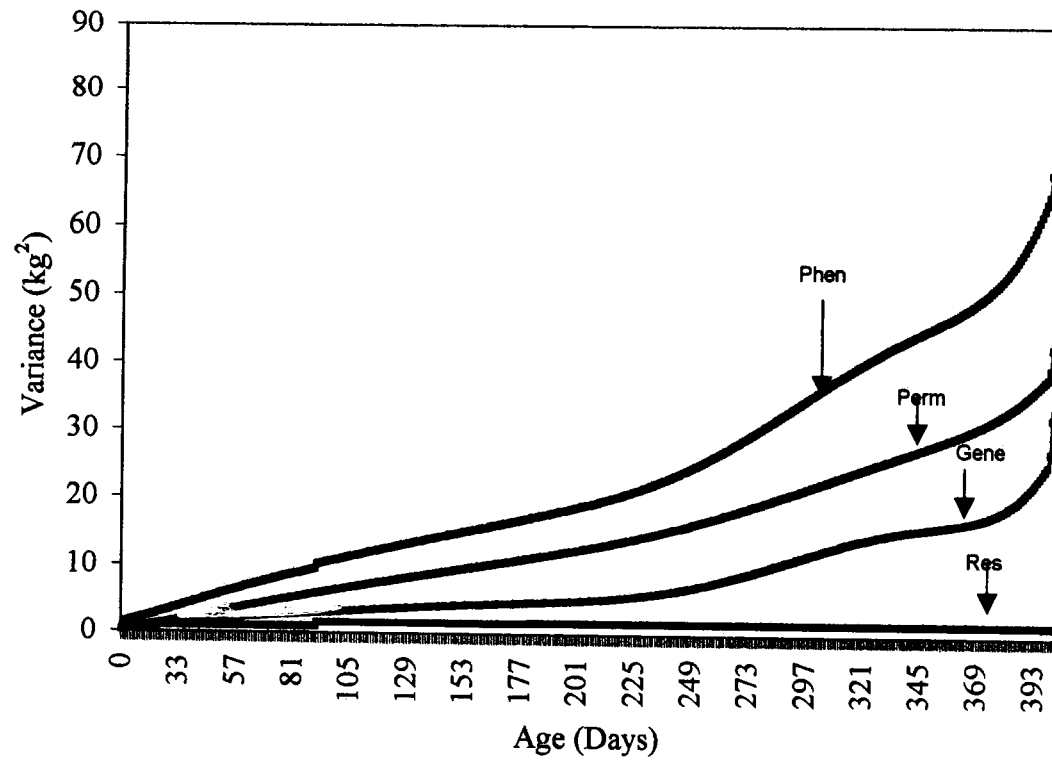


Figure 6.2 Additive genetic (Gene), permanent environmental (Perm), phenotypic (Phen) and residual (Res) variance estimates from Model 6 over the entire period.

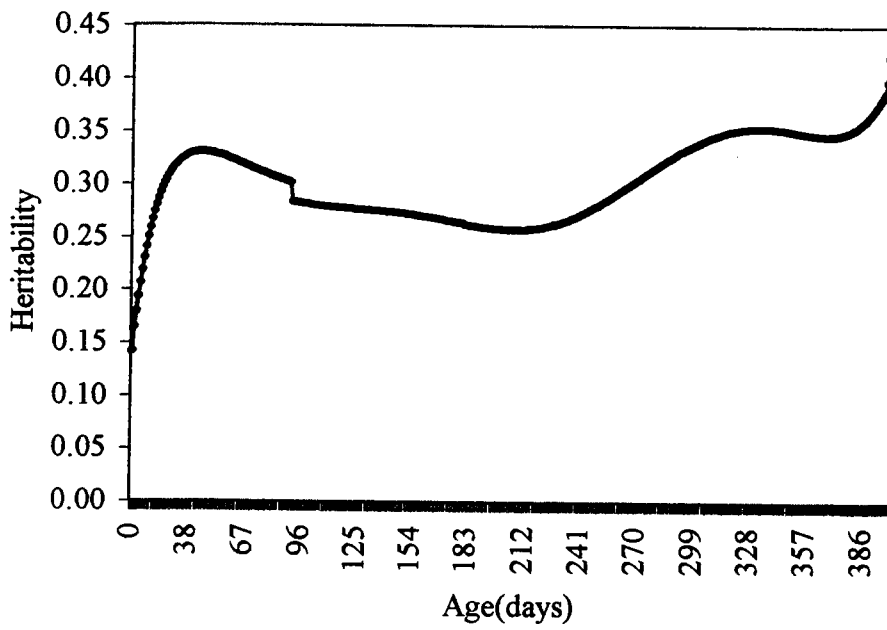


Figure 6.3 Trend in heritability estimates along the range of the trajectory.

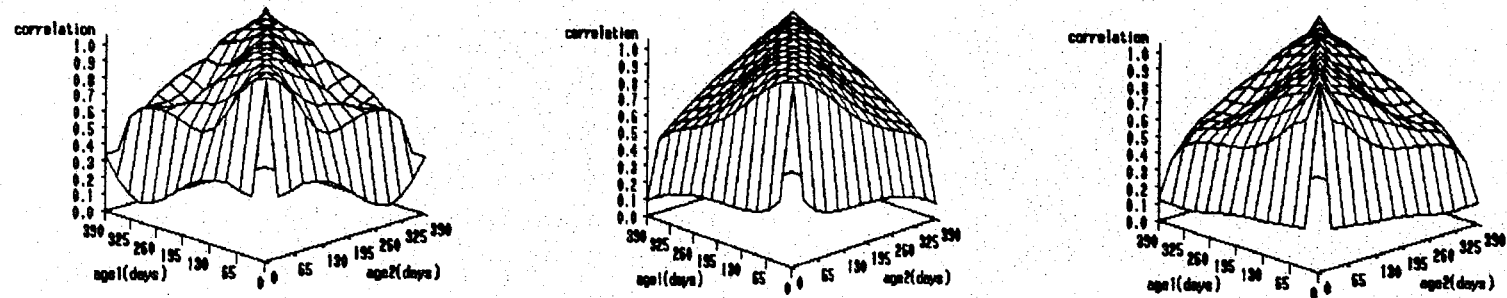


Figure 6.4 Additive genetic (left), permanent environmental (centre) and phenotypic (right) correlations between weights at different ages.

phenotypic correlations between birth weight and weight at about three, six and 12 months of age. Genetic correlation estimates showed a fluctuating trend. This might have been caused by inappropriate modelling of the genetic effects as a result of ignoring the maternal effect. 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 were reported by Meyer (1998b). For permanent environmental correlations and to a lesser degree for phenotypic correlations, estimates increased steadily as the difference in age at measurements decreased. Genetic correlation estimates between weaning (about 90 days of age) and six months and yearling weight from previous work (Chapter 2) were in the range of 0.76 to 0.98. Estimates in the current study is lower (0.60 to 0.87). Phenotypic correlation estimates are similar. Inclusion of the permanent environmental effect in the current random regression analysis and maternal effect in the previous bivariate analysis, makes straightforward comparison impossible.

Coefficients of covariance function and eigenvalues for additive genetic and permanent environmental effect are presented in Tables 6.5 and 6.6 respectively. For additive genetic covariance function the first, second and fourth eigenvalues accounted for about 80, 8 and 10 per cent of the total sum, while for permanent environmental effect they accounted for 86.6, 9.0 and 3.3 per cent respectively. The third eigenvalues for both additive genetic and permanent environmental effects were close to zero, while the fourth one has a value comparable to the second eigenvalue of the additive genetic covariance function. This calls for analysis under a reduced rank fixing the third (and probably the fifth) eigenvalue to zero. The contribution of the first eigenvalue to the total in this study is lower than the value of 95% reported by Lewis & Brotherstone (2002) for a similar order of fit. This indicates a sizeable variation (about 20%) that needs to be explained by functions higher than the first order (intercept). In analyzing test day milk records using a third order fit, Van der Werf *et al.* (1998) estimated about 84 and 11 per cent for the first and the second eigenvalues of the covariance function of the coefficient matrix. This is close to the estimate in the current study, but growth and lactation curves have a different shape and the comparison should be seen in this light.

Table 6.5 Coefficients of covariance functions between random regression coefficients (0: intercept, 1:linear, 2:quadratic, 3:cubic and 4:quartic) for additive genetic effect and the eigenvalues under Model 6

Coefficients of covariance function						
	0	1	2	3	4	Eigenvalues
0	4.877	2.283	-0.489	1.699	-0.308	12.628
1	2.283	14.154	16.773	-14.381	-19.395	1.260
2	-0.489	16.773	35.951	-21.372	-40.117	0.002
3	1.699	-14.381	-21.372	22.714	28.286	1.583
4	-0.308	-19.395	-40.117	28.286	49.468	0.255

Table 6.6 Coefficients of covariance functions between random regression coefficients (0: intercept, 1:linear, 2:quadratic, 3:cubic and 4:quartic) for animals' permanent effect and the eigenvalues under Model 6

Coefficients of covariance function						
	0	1	2	3	4	Eigenvalues
0	12.568	6.875	-3.917	0.901	-0.635	25.821
1	6.875	17.343	6.723	-11.160	-7.310	2.698
2	-3.917	6.723	20.977	-6.057	-16.426	0.006
3	0.901	-11.160	-6.057	15.724	9.623	0.997
4	-0.635	-7.310	16.426	9.623	19.262	0.293

Corresponding eigenfunctions for eigenvalues of the additive covariance function are presented in Figure 6.5. The first eigenfunctions were positive throughout, implying positive genetic correlations across all stages and that selection for weight at any age would result in an increase at all other ages. The increasing trend shows that the direct genetic variance component can have a more pronounced contribution to the total variance with an increase in age. This is reasonable to expect, since the contribution of other effects (maternal genetic and environmental) would decrease with age. The second eigenfunction was negative up to about 300 days of age and positive afterwards. This suggests genetic effects acting differently (probably different genes) before and after about 300 days of age and selection on this variable decreases weight at early ages, but increases weight at later ages. Had the eigenvalue represented by this value been large enough, selection on this variable would have been used to change the growth curve (e.g. select for lower weight at start and higher weight towards the end of trajectory). This may have an implication on finishing practices and on maintenance at adult age. The third eigenfunction has no practical value because of the very low eigenvalue associated with it. Eigenfunctions with very small (or zero) eigenvalues represent deformations for which there is little (or no) additive genetic variation (Kirkpatrick *et al.*, 1990).

A more parsimonious fit of the covariance functions might be obtained by estimating a reduced rank of the coefficient matrix, forcing the third eigenvalue to zero. The fourth eigenfunction has negative values for about the first 240 days and then increases drastically afterwards. The trend in the fifth eigenfunction is somewhat similar to the trend in the fourth one. However the corresponding eigenvalue for the fifth is not large enough to be of practical importance. Change in the eigenfunctions of the second and fourth eigenvalue from negative to positive may be related to genetic effects, namely the maternal genetic effect, which was not considered in this model.

Corresponding eigenfunctions for eigenvalues of the permanent environmental covariance function are presented in Figure 6.6. Except for the eigenfunction of the fourth eigenvalue which is positive throughout, trends in all of the eigenfunctions are

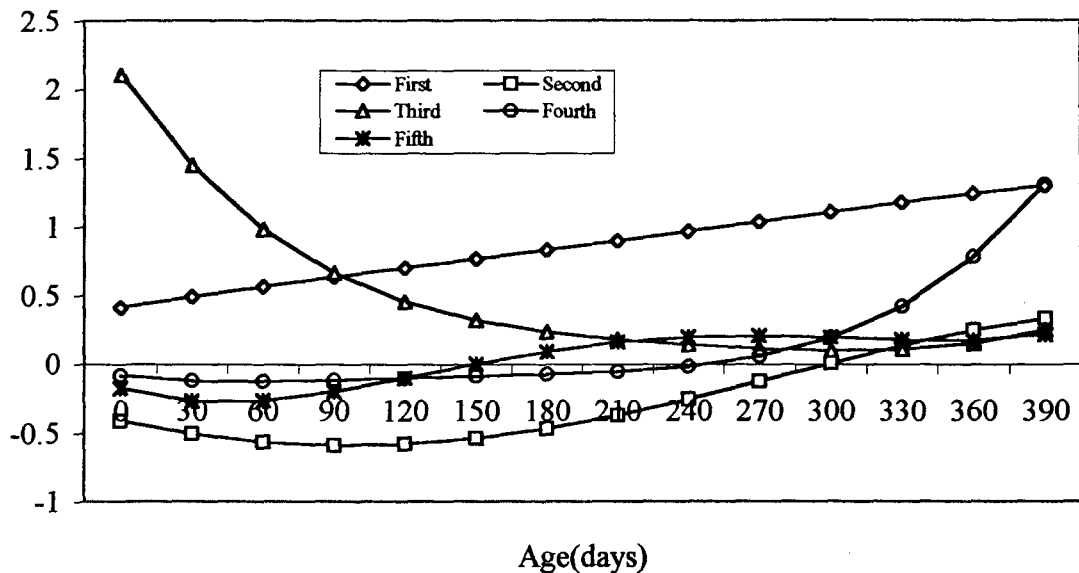


Figure 6.5 Eigenfunctions of the additive covariance function corresponding to the first to fifth eigenvalues from Model 6.

similar to that of the additive covariance function. The positive value and increasing trend of the eigenfunction of the first eigenvalue indicates that environmental factors which have an influence at an earlier age also have a sizeable effect at later ages. This is in line with the high positive correlations obtained between the weights at different ages (Figure 6.4). Similarly change in the eigenfunctions of the second eigenvalue from negative to positive may be related to environmental effects associated with the dam. The temporary maternal environment has been found to have a significant contribution to the total variance to weights until about six months of age (Chapter 2).

Figure 6.7 shows estimated breeding values for four sires used in the same season having more than 30 progeny each. Two of the sires were below average throughout, while two were above average from about 70 to 240 days of age and below average afterwards. Notwithstanding limitations in not including maternal genetic and environmental effects in this study, the figure shows that ranking of animals on breeding values may vary at different ages. This may reflect that growth at different ages may be related to different genes.

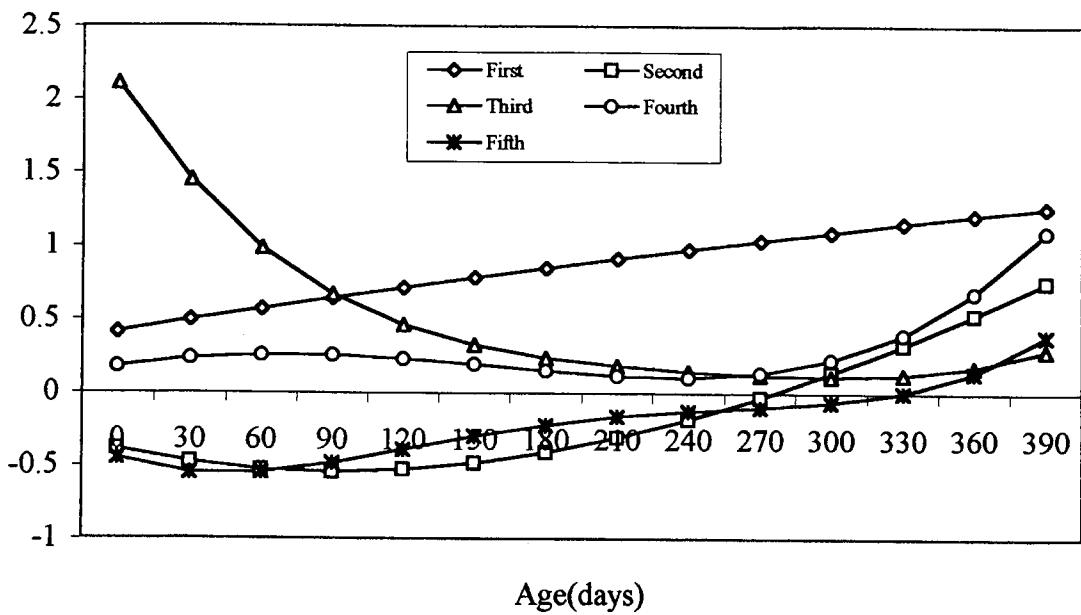


Figure 6.6 Eigenfunctions of the permanent environmental covariance corresponding to the first to fifth eigenfunctions from Model 6.

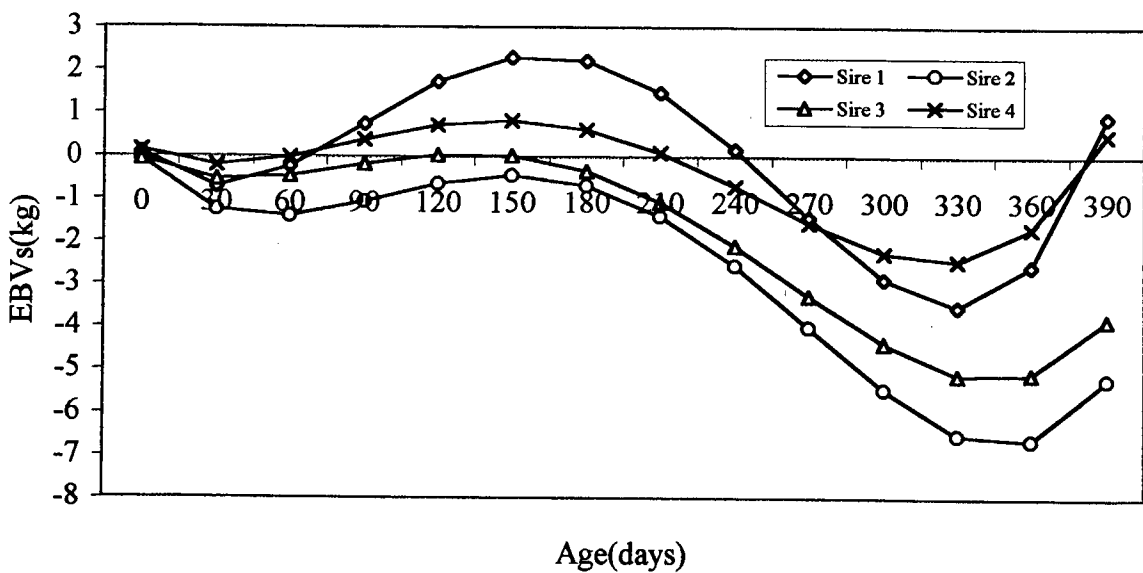


Figure 6.7 Estimated breeding values (EBVs) of four sires (sire 1,2,3,4 with 35, 31, 36 and 32 progeny) along the trajectory of age.

6.4 Conclusions

The use of appropriate polynomial order and modelling the residual variance were found to be very important in affecting estimates of the variance components. The variance components at the edge has shown drastic increases indicating the importance of number of records in the analysis at each stage of growth where ages with low number of records may lead to a biased estimate. Increased order of polynomials may decrease bias in estimates. In situations with incomplete records, increasing order of polynomials may have a benefit in estimation of covariance functions to situations with complete records (Pool & Meuwissen, 2000). In spite of difference in data editing criteria used, close estimates of heritability were obtained between univariate and random regression models for weight at birth and at about one year of age. For weights between these ages the estimates from random regression model were higher than estimates from univariate analyses. This may be related to maternal genetic and environmental effects (temporary and permanent) which were not included in the current random regression analysis. Further research with inclusion of these effects is required. Though it is difficult to make firm recommendations or conclusions from the current results, it appears that random regression can have advantages in modelling longitudinal growth data. This is due to the ability of the models to formulate covariance functions among records over time. The eigenvalues and eigenfunctions of the covariance functions provide insight into how effective selection at different stages could be. More benefit of the random regression model can be accrued in situations where there is change in ranking of animals at different growth stages and under conditions where there are seasonal weight fluctuations, as in most tropical extensive production systems. Considering the overall continuous set of weight data rather than weight at a specific age may reduce bias in estimates of important parameters. Modeling the residual variance with a continuous function may avoid problems which arise from the use of fixed classes of error measures.

General conclusions and recommendations

Under smallholder farming conditions where resources and production inputs are limited, indigenous animals should form the basis of livestock improvement. Due to their adaptability to the environment and performance under low input systems these populations can be used as purebreds or in crossing programs with improved breeds (Olivier *et al.*, 2002). Characterizing these indigenous breeds would contribute towards the designing of appropriate improvement strategies. Any genetic improvement study on these animals should however take into consideration the socio-economic environment and the entire production system. The recommendations from this study should be viewed with this in mind.

Due to a relatively higher heritability of body weight traits and the presence of positive and high correlations with daily gain and Kleiber ratio in most cases, it seems more practical to select on body weight traits to improve gain and efficiency. The conclusions are therefore solely based on results of body weight. The maternal environmental effects (the permanent environmental effect due to the dam and the temporary environmental (litter) effect) were found to be significant sources of variation for body weight of lambs at an early age. The temporary environmental effect was also important in the analysis of survival. In addition to avoiding bias in estimates of the different parameters, inclusion and quantification of the temporary environmental effect is important in designing management practices which could improve the growth and survival of twins. Twinning rate in this flock is 34% and the results from this study show that with a twinning rate of as low as 30%, inclusion of the temporary environmental (litter) effect in analytical models could be important. Literature review reveals that this effect was largely ignored in analytical models, even when the rate of multiple births was much higher than attained in the flock in the current study.

Results from analyses of early growth traits have shown that there are sizeable genetic variations within the breed for these traits which can be exploited to improve the productivity of the breed. A number of findings from the current and a previous study (Abegaz *et al.*, 2002a) indicate that weight at about one year of age is the most important trait to consider in improving productivity in Horro sheep. These include: high and relatively consistent estimates of heritability from different models of analyses (univariate, bivariate, random regression); strong correlation with weights, daily gain and Kleiber ratio at earlier ages; significant effect on estimates of ewe lifetime productivity; and strong correlation with growth curve parameters. In Ethiopia the great majority of sheep for slaughter are unfinished milk tooth lambs weighing 10 to 20 kg (Galal *et al.*, 1979; Kassahun, 2000). This weight is achieved from about the age of six months to one year of age. The existence of high correlations between body weight at one year of age and earlier ages allow earlier weights to respond to improvement protocols based on yearling weight, and it also permits some initial culling on performance at an earlier age.

Genetic variation for lamb survival and ewe reproduction and productivity is low. The only exception is the ability to bear twins. This result indicates that since the additive genetic variation in these traits is very low, environmental (management) interventions which improve lamb survival and ewe reproduction should receive attention. This study indicated that service sire is an important source of variation in ewe fertility. Attributes of sires which insure higher fertility need to be investigated. Despite the possibility of increase in lamb mortality twinning has a medium heritability and moderate correlation with total weight of lamb weaned. Thus it can be considered as an additional trait in improvement programs. Birth weight was found to have a moderate and positive genetic correlation with lamb survival and it should be used as an indirect selection criterion to improve survival. Previous studies on non-genetic aspects of survival in Horro sheep have shown that no decrease in survival was observed at higher birth weights and there appears to be a critical body weight (about 2.6 kg) below which a drastic increase in lamb mortality occurs (Abegaz *et al.*, 2000; Abegaz *et al.*, 2002c).

Growth curve parameters provide potentially useful criteria for altering the relationship between body weight and age through selection (Kachman & Gianola, 1984). Heritability estimates of growth curve parameters from this study are medium and progress can be expected if selection is applied on these parameters. Due to the need for weight-age data from birth to maturity to obtain the curve parameters, it will be very difficult under present circumstances to exercise such improvement programs or to consider this in the breeding objectives. All the growth curve parameters have a moderate correlation with yearling weight and selection for the latter can result in an indirect response in the parameters. Random regression models used in this study considered direct additive genetic and animal permanent environmental effects and fixed residual variance classes. The results show overestimation of genetic variances at early ages. Subsequent work to address inclusion of maternal genetic and environmental effects and modelling the residual effect for linear change is required.

In the mixed farming systems where Horro sheep are kept, flock size per household rarely exceeds 10 sheep and no controlled mating is practised. Under these circumstances it will be difficult to implement improvement programs, even via open nucleus breeding systems (ONBS) which require minimal field recording. At higher altitudes, flock sizes increase to 30 sheep or more per household. With a close look at the production system, flocks in these areas could form the basis of ONBS which may also contribute (spill over) to improvement in the other areas. Experimental stations or ranches could play a role in managing the nucleus flock and in dissemination of rams. In all cases substantial funding for such programs is a prerequisite. At the current management level it would be difficult to introduce exotic sheep germ plasm to these areas either for purebred purposes or in crossbreeding programs. However, experimental on-station investigation to evaluate different breeds and their crosses with Horro sheep for their suitability under low input management system warrants attention. Market incentives are the main driving forces to increase production and improvement in the current marketing systems and efforts to open additional marketing channels should be attended to concurrently with or in advance of the improvement programs.

Abstract

Genetic analyses of economically important traits were carried out using data collected for 20 years (1978-1997) from a flock of Horro sheep at Bako Research Center, Ethiopia. (Co)variance components and genetic and environmental parameters were estimated for pre- and post-weaning average daily gain (ADG1, ADG2) and Kleiber ratio (KR1, KR2), birth weight (BWT), weaning weight (WWT) and bi-monthly weights to 12 months of age (WT2 to WT12), and weight at 18 months of age (WT18). using ASREML. Twelve models, formed with inclusion or exclusion of the maternal genetic, permanent environmental, and temporary (litter) environmental variance components and the covariance between the direct and maternal additive effect on the basic direct additive genetic model, were used. Bivariate analyses were also done. Maternal genetic and temporary environmental components were found to be important ($P < 0.05$) sources of variation for ADG1 and KR1 while only the temporary environmental component was found to be important for ADG2 and KR2. Total heritability estimates for ADG1, ADG2, KR1 and KR2, were 0.13 ± 0.04 , 0.04 ± 0.03 , 0.13 ± 0.03 , and 0.01 ± 0.02 respectively. For weights to about six months of age, the inclusion of the temporary maternal effect in the models was found to have significant ($P < 0.05$) contribution to the total variance. Maternal genetic components were important for weights until about eight months of age, while the direct-maternal covariance was important for BWT, WT2, WWT and ADG1. Direct genetic correlations of ADG1 with BWT, WWT and WT6 were 0.04 ± 0.21 , 0.96 ± 0.02 and 0.92 ± 0.09 while with KR1 they were -0.41 ± 0.21 , 0.74 ± 0.10 and 0.66 ± 0.16 respectively. The inclusion of maternal genetic, temporary and permanent environmental effects in analytical models for early weights improved model fit. Heritability estimates of average daily gains and Kleiber ratios are low to moderate. The correlations with weight traits, with the exception of BWT, are moderate to high. Thus, it seems more practical to select on weight traits to improve gain and efficiency.

Genetic and maternal environmental parameters of perinatal, pre- and post-weaning survival in Horro lambs were studied using 3864 lamb records. The perinatal period covered the first three days after birth (3DS) while pre-weaning (3MS) and post-weaning

(3-6MS) survival were taken as survival in the pre- and post-weaning three-month periods respectively. Cumulative survival to six months of age (6MS) was also considered. The same twelve linear genetic models used for growth traits were applied. Additionally logit and probit analyses were carried out. The most appropriate model was chosen which was consistently superior in all of the analytical methods and used to estimate genetic and environmental parameters. A bivariate analyses between survival on the observed scale and birth weight was carried out. For survival to all ages, the model, which included the direct genetic and maternal temporary (litter) environmental effect was found to be the most consistent of all the models compared. Heritability estimates for 3DS, 3MS, 6MS and 3-6MS were 0.00 ± 0.00 , 0.02 ± 0.03 , 0.05 ± 0.03 and 0.07 ± 0.03 respectively. Genetic correlations with birth weight were 0.20 ± 0.23 , 0.68 ± 0.34 , 0.26 ± 0.17 and 0.45 ± 0.26 respectively, for 3DS, 3MS, 6MS and 3-6MS. The low heritability estimates of survival in this study suggest acceptable progress with respect to this trait through selection will be difficult to attain. The relatively higher genetic correlation of 3MS with birth weight indicates survival may be improved indirectly through selection for birth weight. Despite the low rate of prolificacy (34% twinning) there exists a sizeable litter effect on survival. This should be looked into, since this may entail a separate management for twin born lambs.

Genetic parameters of productivity expressed as ewe fertility, incidence of twinning, number of lambs weaned, and total lamb weight at birth (TBW) and at weaning (TWW) per ewe per lambing were estimated using direct additive and repeatability models. Fertility and twinning were analyzed by a logit analysis, using similar models. In the analysis of fertility, service sire was included either as random or fixed effect. Additionally cumulative total weight of lamb weaned in the first four parities (TWW4) was also analyzed, using the direct additive model. Except for fertility where service sire was considered as random effect, the repeatability model was found to have a better fit than ($P < 0.05$) the direct animal model. Bivariate analyses were done, using the direct animal model. Direct heritability estimates for fertility, twinning and total weight of lambs at birth and at weaning were 0.02 ± 0.02 , 0.15 ± 0.03 , 0.08 ± 0.02 and 0.04 ± 0.02 respectively. Where service sire was considered as fixed effect, heritability estimate of

fertility from a direct model increased to 0.06. Heritability estimates for number of lambs weaned were 0.03 and 0.00 for the direct and repeatability models respectively. Repeatability estimates were 0.10, 0.07, 0.16, 0.06, 0.02 and 0.08 for TBW, TWW, twinning, litter size weaned and fertility under random and fixed sire models respectively. Estimate of the variance ratio in fertility attributed to service sire was 0.16 ± 0.02 . Heritability estimate for TWW4 was 0.05. Genetic correlations among TBW, TWW, twinning and number of lambs at weaning were in the range of 0.57 to 0.86. Except for twinning, heritability estimates were very low. Twinning was found to have medium heritability and repeatability, and moderate to high genetic correlation with number of lambs weaned, TBW, and TWW. These suggest that twinning can be used as a selection criterion for improvement in productivity despite increase in lamb mortality with increase in twinning.

Weight (kg)-age (days) data of 524 Horro sheep surviving past 3.5 years of age were fitted to Brody's function to estimate growth curve parameters. Genetic and phenotypic parameters of the curve parameters and their relationships among themselves and with birth weight (BW), weaning weight (WW), 6-month weight (WT6) and yearling weight (YW) were estimated using direct univariate and bivariate animal models. Least squares means of growth curve parameters: A (asymptotic mature weight, kg), B (proportion of mature weight attained after birth) and k (rate of maturity, $\text{kg gain kg}^{-1} \text{ body weight day}^{-1}$) were 37.6, 0.88 and 0.27×10^{-2} respectively. Female and male Horro sheep have asymptotic mature weights of 33.3 kg and 41.8 kg respectively. Heritability estimates were 0.29 ± 0.10 , 0.18 ± 0.09 and 0.14 ± 0.09 for A, B and k respectively. Genetic correlations between A and B, A and k, and B and k were 0.39 ± 0.31 , -0.07 ± 0.34 and 0.25 ± 0.39 respectively. Genetic correlations of A with BW, WW, WT6 and YW were 0.27 ± 0.34 , 0.34 ± 0.27 , 0.44 ± 0.20 and 0.67 ± 0.17 respectively. Genetic correlations of k with BW, WW, WT6, and YW were -0.13 ± 0.69 , 0.37 ± 0.35 , 0.61 ± 0.25 and 0.66 ± 0.22 respectively. Presence of medium heritability for A and k indicates that progress in improving these traits can be made through selection. WT6 and YW have medium genetic correlations (with reasonable standard error) with the growth curve parameters

and these may allow the use of these weights as an indirect selection criterion to shorten generation interval.

Weight data from birth to about one year (maximum of 408 days) were analyzed using the random regression model. A total of 22149 weight records of 1951 lambs were used. Three different orthogonal (legendre) polynomial orders (three, four and five) of fit for additive genetic and animal permanent environmental effect were considered along with two different error measures. The residual error for weight at the different ages was assumed to be either homogeneous (one error measure) throughout the growing period or heterogeneous (four error measure classes: birth, 10 to 90 days, 91 to 180 days and >180 days). Likelihood ratio test (LRT) and Akaike's Information Criteria (AIC) were used for model comparison. Model fit improved with increased order of fit and with assumption of heterogeneity of error variance. Sizeable differences were found in heritability estimates from the different models, particularly for weight at birth and early age. Components for both additive genetic and animal permanent environmental covariances increased with an increase in age. Heritability estimates from the 'best' model have shown declining and increasing values at different parts of the trajectory. The lowest estimate was 0.14 for weight at birth, while the highest estimate was 0.40 for weight at about 400 days of age. The ratio of permanent environmental variance to the total variance increased from 0.42 at birth to 0.67 at about 270 days and decreased slightly thereafter. With the exception of weight at birth and at about yearling, heritability estimates from this study were lower than estimates from univariate studies where maternal effects were considered. The difference between estimates decreased with age, implying the higher estimates from this study are a result of ignoring maternal genetic and environmental (temporary and permanent) effects. Therefore consideration of maternal genetic and environmental effects needs attention. Choice of appropriate order of polynomial has significant influence and increased order of polynomial may need to be tested to refine estimates with a larger data set (additional weights per animal).

===== Opsomming =====

Genetiese analises van ekonomies belangrike eienskappe is uitgevoer op data ingesamel vir 'n periode van 20 jaar (1978-1997) van 'n kudde Horro skape te Bako Navorsingsentrum, Etiopië. (Ko)variensie-komponente en omgewingsparameters is beraam vir voor- en naspeense gemiddelde daaglikse toename (GDT1 en GDT2) en Kleiberverhouding (KV1,KV2) deur gebruik te maak van ASREML. Twaalf modelle is gebruik, wat opgebou is deur in- of uitsluiting van die maternaal genetiese permanente en tydelike (werpsel) omgewingsvariensiekomponente en die ko-variensie tussen die direk- en maternaal additiewe effek op die basiese direk-additiewe genetiese model. Dieselfde modelle is aangewend om die beste model te identifiseer en die belangrikheid te bereken van maternale omgewingseffekte op geboortegewig (Ggew), speengewig (Sgew) en tweemaandelikse gewigte tot 12 maande ouderdom (Gew2 tot Gew12), en gewig op 18 maande ouderdom (Gew 18). Dubbelveranderlike ontledings is gedoen tussen GDT1, GDT2, KV1 en KV2 en met Ggew, Sgew Gew6, Gew12 en Gew18. Maternaal-genetiese en tydelike omgewingskomponente het geblyk belangrike ($P < 0.05$) bronne van variasie vir GDT2 en KV1 te wees. Onder die beste model was direk-additiewe, maternaal-additiewe en tydelike omgewingskomponente verantwoordelik vir ongeveer 15, 20 en 13 persent onderskeidelik van die totale fenotipiese variensie vir GDT1 en 9, 8 en 19 persent onderskeidelik vir KV1. Vir GDT2 en KV2 was die bydrae tot die totale variensie van tydelike omgewingseffek 22 en 20 persent onderskeidelik. Totale oorerflikheidsberamings vir GDT1 en GDT2, KV1 en KV2 was 0.13 ± 0.04 , 0.04 ± 0.023 , 0.13 ± 0.03 en 0.01 ± 0.02 onderskeidelik. Vir gewigte tot ongeveer sesmaande ouderdom is gevind dat die insluiting van die tydelike omgewingsvariensiekomponent in die modelle betekenisvolle ($P < 0.05$) bydrae tot die geheelvariensie gelewer het. Die permanente omgewingskomponent was betekenisvol ($P < 0.05$) belangrik vir Gew2 en Sgew. Maternale genetiese komponente was belangrik vir gewigte tot ongeveer agtmaande ouderdom, terwyl die direk-maternale ko-variensie belangrik was vir Ggew, Gew2, Sgew en GDT1. Direkte genetiese korrelasies van GDT1 met Ggew, Sgew en Gew6 was 0.04 ± 0.21 , 0.96 ± 0.02 en 0.92 ± 0.09 , terwyl met KV1 dit -0.41 ± 0.214 , 0.74 ± 0.10 en 0.66 ± 0.16 onderskeidelik was. Die insluiting van maternale genetiese en

tydelike en permanente omgewingseffekte in ontledingsmodelle vir vroeë gewigte het die pas van die model verbeter. Oorerflikheidsberamings van gemiddelde daaglikse toenames en Kleiberverhoudings is laag tot matig. Die korrelasies met gewigseienskappe, geboortegewig uitgesluit, is matig tot hoog. Seleksie op gewigseienskappe blyk dus 'n beter opsie te wees vir verbetering in toename en doeltreffendheid.

Genetiese en maternale omgewingsparameters van na-geboortelike en voor- en naspeense oorlewing in Horro-lammers is van 3864 lamrekords bestudeer wat gedurende die periode 1978 – 1997 versamel is. Die na-geboortelike periode het oor die eerste drie dae na geboorte (3D) gestrek, terwyl voorspeense (3M) en na-speense (3-6M) oorlewing beskou is as oorlewing in die voor- en naspeense driemaande-periodes onderskeidelik. Kumulatiewe oorlewing tot by sesmaande ouderdom is ook in aanmerking geneem. Dieselfde twaalf lineêre genetiese modelle wat op groei-eienskappe toegepas is, is gebruik. Logit- en probit-ontleding is bykomend uitgevoer. Die model wat deurgaans voortreflik in drie van die ontledingsmetodes vertoon het, is as die mees geskikte gekies. Genetiese en omgewingsparameters is van die betrokke model beraam met 'n logit-ontleding (beramings van probit-ontleding was dieselfde). 'n Dubbelveranderlike ontleding tussen oorlewing op die waargenome skaal en geboortegewig is uitgevoer. Vir oorlewing tot by alle ouderdomme is die model wat die additief-direkte en additief-maternale (wepsele) omgewing en die foutkomponent ingesluit het as die mees konsekwente van al die modelle wat vergelyk is bevind. Oorerflikheidsberamings was 0.00 ± 0.00 , 0.02 ± 0.03 , 0.05 ± 0.03 en 0.07 ± 0.03 vir 3D, 3M, 6M en 3-6M onderskeidelik. Genetiese korrelasies met geboortegewig was 0.20 ± 0.23 , 0.68 ± 0.34 , 0.26 ± 0.17 en 0.45 ± 0.26 onderskeidelik vir 3D, 3M, 6M, en 3-6M. Die lae oorerflikheidsberamings van oorlewing in hierdie studie dui daarop dat aanvaarbare vordering ten opsigte van hierdie eienskap deur kunsmatige seleksie moeilik haalbaar sal wees. Die relatief hoë genetiese korrelasie van 3M met geboortegewig dui aan dat oorlewing indirek verbeter kan word deur seleksie vir geboortegewig. Ten spyte van die lae vrugbaarheidsgraad (34% tweeling) is daar 'n aansienlike werpseleffek op oorlewing. Dit regverdig verdere aandag, aangesien dit aparte bestuur vir tweelinggebore lammers mag behels.

Genetiese parameters van produktiwiteit uitgedruk as ooivrugbaarheid, voorkoms van tweeling, aantal lammers gespeen en totale lamgewig met geboorte (TGgew) en met speen (TSgew) per ooi per lamkans is beraam. Direkte additiewe en herhaalbare modelle is gebruik. Vrugbaarheid en voorkoms van tweeling is ontleed deur 'n logit-ontleding waar eners modelle gebruik is. In die ontleding van vrugbaarheid is diensvaar òf as toevallige òf as vaste effek ingesluit. Bykomend is die kumulatiewe totale gewig lammers gespeen in die eerste vier lamkans (TSgew4) ook ontleed, deur die direkte additiewe model te gebruik. Op die basis van log-aanneemlikheid verhoudingstoets is die herhaalbaarheidsmodel betekenisvol ($P < 0.05$) verskillend van die direkte model in alle gevalle gevind. Behalwe vir vrugbaarheid waar diensvaar as toevallige effek gereken is, is gevind dat die herhaalbaarheidsmodel beter gepas het as die direkte dieremodel. Dubbelveranderlike ontledings is gedoen, deur gebruikmaking van die direkte dieremodel. Direkte oorerflikheidsberamings vir vrugbaarheid, voorkoms van tweeling en totale gewig van lammers met geboorte en speen was 0.02 ± 0.02 , 0.15 ± 0.03 , 0.08 ± 0.02 en 0.04 ± 0.02 onderskeidelik. Waar diensvaar as vaste effek gereken is, het oorerflikheidsberaming van vrugbaarheid van 'n direkte model verhoog na 0.06. Oorerflikheidsberamings vir aantal lammers gespeen was 0.03 en 0.00 vir die direkte en herhaalbaarheidsmodelle onderskeidelik. Herhaalbaarheidsberamings was 0.10, 0.07, 0.16, 0.06, 0.02 en 0.08 vir TGgew, TSgew, tweelinggeboortes, grootte van werpsel gespeen en vrugbaarheid onder toevallige en vaste modelle onderskeidelik. Beraming van die variansie-verhouding in vrugbaarheid wat aan diensvaar toegeskryf is was 0.16 ± 0.02 . Die oorerflikheidsberaming vir TSgew4 was 0.05. Genetiese korrelasies tussen TGgew, TSgew, voorkoms van tweeling en aantal lammers met speen was tussen 0.57 en 0.86. Behalwe vir tweelinggeboortes, was oorerflikheidsberamings baie laag. Tweelinggeboortes het geblyk medium oorerflikheid en herhaalbaarheid te hê en matige tot hoë genetiese korrelasie met aantal lammers gespeen, TGgew en TSgew. Dit dui daarop dat voorkoms van tweeling as 'n seleksiekriterium vir verbetering in produktiwiteit gebruik kan word.

Gewigs (kg)-ouderdom (dae) data van 524 Horro-skape wat tot na 3.5 jaar oorleef het, is in Brody se funksie ingebou om groeikurweparameters te beraam. Genetiese en

fenotipiese parameters van die kurwe-parameters en hul verhouding met hulself en met geboorte-gewig (Ggew), speengewig (Sgew), sesmaande-gewig (Gew6) en jaaroudgewig (Jgew) is beraam. 'n Direkte dieremodel is in alle enkel- en dubbelveranderlike ontledings gebruik. Lineêre korrelasies is bereken tussen groeikurwe-parameters en totale gewig gespeen per ooi vir die eerste tot vierde lamkanse (TGS1, TGS2, TGS3 en TGS4) en tussen die gemiddeld van aantal lammers gebore (ALG4) en aantal wat oorlewe het (ALO4) per lamkans by ooie wat vier en meer lamkanse gehad het. Kleinste kwadraatgemiddeldes van groeikurweparameters: A (asimptotiese volwasse gewig, kg), B (proporsie van volwasse gewig bereik na geboorte) en k (tempo van volwassenheid, kg toename kg^{-1} liggaamsgewig dag^{-1}) was 37.6, 0.88 en 0.27×10^{-2} onderskeidelik. Die asimptotiese volwasse gewig van vroulike en manlike Horro-skape is 33.3 kg en 41.8 kg onderskeidelik. Oorerflikheidsberamings was 0.29 ± 0.10 , 0.18 ± 0.09 en 0.14 ± 0.09 vir A, B en k onderskeidelik. Genetiese korrelasies tussen A en B, A en k en B en k was 0.39 ± 0.31 , -0.07 ± 0.34 en 0.25 ± 0.39 onderskeidelik. Genetiese korrelasies van A met Ggew, Sgew, Gew6 en Jgew was 0.27 ± 0.34 , 0.34 ± 0.27 , 0.44 ± 0.20 en 0.67 ± 0.17 onderskeidelik. Genetiese korrelasies van k was -0.13 ± 0.69 , 0.37 ± 0.35 , 0.61 ± 0.25 en 0.66 ± 0.22 met Ggew, Sgew, Gew6 en Jgew onderskeidelik. Lineêre korrelasies van A en k met TSgew1, TSgew2, TSgew4, ALG4 en ALO4 was 0.05 & 0.26, 0.28 & 0.20, 0.27 & 0.05, 0.27 & 0.05 en 0.14 & 0.13 onderskeidelik. Die voorkoms van 'n medium oorerflikheid vir A en k toon aan dat vordering gemaak kan word in die verbetering van hierdie eienskappe deur seleksie. Die groeikurwe-parameters blyk positiewe verhoudings te hê met aanwysers van leeftydproduksie. Gew6 en Jgew het medium genetiese korrelasies (met redelike standaardfout) met die groeikurwe-parameters, wat dit moontlik maak dat hierdie gewigte as 'n indirekte seleksie-kriterium gebruik kan word om generasie-interval te verkort.

Gewigdata vanaf geboorte tot ongeveer een jaar (maksimum 408 dae) is ontleed deur die toevallige regressiemodel te gebruik. 'n Totaal van 22149 gewigrekords van 1951 lammers is gebruik. Drie verskillende ortogonale (legendre) veeltermige ordes, (drie, vier en vyf) wat geskik was vir additiewe genetiese en dier- permanente omgewingseffek is in aanmerking geneem, tesame met twee verskillende foutterme. Die

fout vir gewig op die verskillende ouderdomme was veronderstel om òf homogeen te wees (een foutterm) reg deur die groeiperiode, òf heterogeen (vier fouttermklasse: geboorte, 10 tot 90 dae, 91 tot 180 dae en >180 dae). Aanneemlikheidsverhoudingstoets (AVT) en Akaike se Inligtingskriteria (AIK) is gebruik vir modelvergelyking. Pas van die model het verbeter met verhoging in rangorde van passing en met aanname van ongelyksoortigheid van foutvariensie. Aansienlike verskille is in oorerflikheidsberamings van die verskillende modelle gevind, veral vir gewig met geboorte en op vroeë ouderdom. Komponente vir beide additiewe genetiese en dier-permanente omgewingskovariensie het toegeneem met 'n toename in ouderdom. Oorerflikheidsberamings van die "beste" model het afnemende en toenemende waardes getoon in verskillende dele van die trajek. Die laagste beraming was 0.14 vir gewig met geboorte, terwyl die hoogste beraming 0.40 was vir gewig op ongeveer 400-dae ouderdom. Die verhouding van permanente omgewingsvariensie tot die totale variensie het toegeneem van 0.42 by geboorte tot 0.67 op ongeveer 270-dae ouderdom en weer effens afgeneem daarna. Met die uitsondering van gewig by geboorte en teen jaaroud was oorerflikheidsberamings verkry in hierdie studie laer as beramings van enkelveranderlike studies waar maternale effekte in aanmerking geneem is. Die verskille tussen beramings het afgeneem met ouderdom, wat impliseer dat die hoër beramings van hierdie studie 'n gevolg is van die verontagsaming van maternale genetiese en omgewings- (tydelike en permanente) effekte. Inagneming van maternale genetiese en omgewingseffekte behoort dus aandag te geniet. Keuse van gepaste orde van veelterme het betekenisvolle invloed en toenemende orde van veelterme moet miskien getoets word om beramings met 'n groter datastel te verfyn (bykomende gewigte per dier).

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