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Estimation of genetic and phenotypic parameters of growth curve and their relationship with early growth and productivity in Horro sheep

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Abstract

Weight (kg)-age (days) data of 524 Horro sheep of Ethiopia were fitted to a Brody function to estimate parameters of growth curve and their genetic and phenotypic parameters. Genetic and phenotypic relationships were also estimated between growth curve parameters and weight at birth (BW), weaning (WW) six-month (WT6) and yearling (YW). For ewes Pearson correlations were also calculated between growth curve parameters and ewe productivity over first to fourth parities. Least squares means of growth curve parameters A (asymptotic mature weight, kg), B (proportion of mature weight attained after birth) and K (the rate of maturity, kg gain kg^{-1} body weight) were 37.6, 0.88, and $0.27 \cdot 10^{-2}$, respectively. Heritability estimates were 0.29, 0.18 and 0.14 for A, B, and K, respectively. Genetic correlations between A and B, A and K, and B and K were 0.39, −0.07, and 0.25 respectively. Genetic correlations of A and K with BW, WW, WT6, and YW were 0.27 and −0.13, 0.34 and 0.37, 0.44 and 0.61, and 0.67 and 0.66, respectively. The growth curve parameters have small but positive (r=0.05 to 0.28) relationship with indicators of lifetime productivity. Medium heritability estimates of A and K indicate that progress in improving these traits can be made through selection. WT6 and YW have medium genetic correlations with the growth curve parameters and these may allow the use of these weights as indirect early selection criteria for optimum growth curve.

Keywords: Horro sheep, Brody function, productivity, genetic parameters, growth curve parameters

Zusammenfassung

Schätzung genetischer und phänotypischer Wachstumskurvenparameter und Beziehungen zum Jugendwachstum und der Produktivität bei Horroschafen

Mit Hilfe der Brody-Funktion wurden Gewichts- und Altersdaten von 524 Ethiopischen Horro Schafen zur Schätzung genetischer und phänotypischer Parameter genutzt. Ebenso erfolgte die Schätzung der genetischen und phänotypischen Beziehungen zwischen Wachstumskurvenparametern und dem Geburtsgewicht (BW), dem Absetzgewicht (WW), dem Sechs-Monate-Gewicht (WT6) sowie dem Jährlingsgewicht (YW). Mit Hilfe der Pearson-Korrelation wurden die Wachstumskurvenparameter in Beziehung zur Produktivität der Schafe über einen Vierjahreszeitraum untersucht. Die

Mittelwerte der Wachstumskurvenparameter für A das Gewicht ausgewachsener Tiere als asymtotische Begrenzung des Gewichtes im jeweiligen Alter, B das Verhältnis des ausgewachsenen Gewichtes zum Gewicht nach der Geburt, und K die Wachstumsrate (Zunahme kg je kg Körpergewicht/Tag) betrugen 37,6, 0,88 und $0{,}27 \cdot 10^{-2}$. Die Heritabilitätsschätzwerte für A, B und K waren 0,29, 0,18 bzw. 0,14. Die genetischen Korrelationen für A und B; A und K sowie B und K betrugen 0,39, −0,07 bzw. 0,25. Weitere genetische Merkmalskorrelationen werden diskutiert. Die Wachstumskurvenparameter zeigten geringe bis positive (r=0,05 bis 0,28) Beziehungen zu den Werten für die Produktivität im Vierjahreszeitraum der Schafe. Die Schätzwerte der Heritabilität von A und K zeigen, dass diese Merkmale durch Selektion verbessert werden können. Die Möglichkeiten einer indirekten Selektion werden aus den genetischen Korrelationen der Wachstumskurvenparameter abgeleitet.

Schlüsselwörter: Horroschaf, Brody-Funktion, Produktivität, genetische Parameter, Wachstumskurvenparameter

Introduction

Sheep production in Ethiopia is characterized by smallholder farming. Sale of lambs provides a considerable part of the income of farmers. In the central highlands of Ethiopia, an estimated 75% of small ruminants account for only 6.6% of the capital invested but provide more than 48% of the cash income generated from livestock production (KRIESEL and LEMMA 1989). In order to increase farmers' income, there needs to be improvement in the production of these animals. Slow growth rate resulting in low market weight has been identified to be one of the factors limiting profitability in Ethiopia (MUKASA-MUGERWA and LAHLOU-KASSI 1995) and elsewhere (NOOR *et al.* 2001). Growth rate is related to rate of maturing and mature weight and these latter traits have been suggested to have relationship with other female lifetime productivity parameters in goats (PALA *et al.* 2005). Existence of optimum size to improve productivity has also been suggested for sheep (BEDIER *et al.* 1992, KESBI *et al.* 2008). Because of this rate of gain and mature weight need to be considered in selection programs. Fast early growth on the part of the slaughter generation and smaller mature size (though smaller income in culled ewe value) on the part of the reproducing female are desirable traits. Growth curve parameters provide potentially useful criteria for altering the relationship between body weight and age through selection (KACHMAN and GIANOLA 1984) and an optimum growth curve can be obtained by selection for desired values of growth curve parameters (BATHAEI and LEROY 1998).

Growth curve parameters are usually estimated from non-linear mathematical functions which help to summarize the information in a large longitudinal (weight-age) data from each individual (AKBAŞ *et al.* 2006). Among a number of mathematical models Brody's function (BRODY 1945) has been found to be adequate for comparing individual differences in rate of maturing and mature weight (GBANGBOCHE *et al.* 2008). Additionally this function has advantages of mathematical simplicity and biological interpretability. Recently it has been applied in the study of growth curve in sheep (BATHAEI and LEROY 1998, GBANGBOCHE *et al.* 2008, KARAKUS *et al.* 2008).

The objective of this study was to estimate parameters of growth curve their genetic and phenotypic parameters and the relationship with weights measured early in life and with measures of productivity. These results can then be used in designing breed improvement programs.

Material and methods

Data were obtained from a flock of Horro sheep kept at Bako research center, Ethiopia. Weight-age records have been kept from 1978 to 1997. The Horro sheep breed (and its ecotypes) is the most dominant sheep in the Southwestern areas of the country and is distributed in the area which lies within 35°-38° E and 6°-10° N. The current population size of the breed is estimated at over two million. Features that identify the Horro sheep have been described by GALAL (1983) and SOLOMON *et al.* (2008). 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. The mean height at shoulders is 73 ± 1.3 and 68 ± 0.8 cm for adult rams and ewes respectively. The center where data collection has taken place is located at an altitude of 1650 m in Western Ethiopia and lies at 09° 6′N and 37° 09′E. A detailed description of the environment and flock management is reported in ABEGAZ *et al.* (2002). After editing the data consist of 27488 weight records (recorded at monthly intervals from birth to a minimum of 3.5 years), from 524 sheep (60 male and wethers and 464 female animals) which were progeny of 132 sires and 327 dams. A previous study on Horro sheep shows that body weight starts to stabilize from about 36 months of age (ABEGAZ and DUGUMA 2000). Since parameters describing growth curve can be evaluated only after growth is completed, 42 months was assumed to be the minimum age at which maturity is achieved. All available weights of up to 56 months of age were included in the analyses of body weight measurements which were taken in the morning after an overnight fasting for 12-14 h.

Brody's model was used to estimate parameters of the growth curve for each animal. The mathematical function is:

$$Y_t = A(1 - Be^{-Kt}) + \varepsilon_t \qquad (1)$$

where Y_t is the weight at t days of age, A is the mature weight as asymptotic limit of the weight when age (t) approaches infinity, B is the proportion of mature weight gained after birth, K is the maturing rate, e is the Napier's base for natural logarithms, t is the age expressed in days and ε_t is the deviation of observed value from model estimates.

The function was fitted to weight (kg)-age (days) data of each animal using the least squares nonlinear (NLIN) procedure of SAS (SAS 1999) with the Gauss Newton iterative method. The convergence criteria used was as follows:

$$\frac{SSE_{i-1} - SSE_i}{SSE_i + 10^{-6}} < 10^{-8} \qquad (2)$$

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 included was fitted using the GLM procedure of SAS (SAS 1999) in order to identify environmental effects which affect growth curve parameters. Intact males and wethers were categorized in the same sex group (wethers were few in number and for the major part castration in these sheep was applied when their age had approached maturity). 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 additive genetic effect of the animal as random. Bivariate analysis among the curve parameters and weight at birth (BW), weaning (WW), six-month (WT6) and yearling (YW) were done to estimate corresponding genetic and phenotypic correlations. Additionally Pearson product moment correlations were calculated between growth curve parameters of ewes and their productivity. Ewe productivity was expressed as follows:

- TWW1 = total weight of lamb weaned at first parity
- TWW2 = total weight of lamb weaned over the first two parities
- TWW3 = total weight of lamb weaned over the first three parities
- TWW4 = total weight of lamb weaned over the first four parities
- NLB4 = average number of lambs per parity for ewes with four or more lambing opportunities
- 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 weight of lambs weaned per ewe after adjustments for sex and age at weaning.

Results and discussion

Least squares means of growth curve parameter estimates and immature weights are presented in Table 1. The estimates of mature weight (A) for 16 sheep were found to be biologically impossible and were excluded from subsequent analyses. Year of birth had a significant ($P<0.05$) effect on all growth curve parameters. Sex was a significant source of variation in A ($P<0.01$) and B ($P<0.05$) values while type of birth and age of dam only have a significant ($P<0.01$) effect on B. Least squares means in the different years ranged from 34.5 to 45.3 for A, 0.84 to 0.97 for B and 0.118 to $0.488 \cdot 10^{-2}$ for K. Similar significant effects of year of birth on mature weight of sheep have been reported (STOBART *et al.* 1986, PITCHFORD 1993, BATHAEI and LEROY 1996). Unlike the result in this study, STOBART *et al.* (1986) found a highly significant ($P<0.01$) effect of age of dam on mature weight while BATHAEI and LEROY (1998) have reported significant ($P<0.01$) effect of age of dam only on B. The latter result is similar to what is obtained in the current study. Presence of effect of type of birth on K (derived from Gompertz function) has been reported by PITCHFORD (1993), BATHAEI and LEROY (1998) and UNAL *et al.* (2006). In this study the effect of type of birth has approached significant level ($P=0.077$). Singles were only 2% heavier than twins at maturity. This figure is close to estimates of 3% reported by PICHFORD (1993) but lower than the estimate of 13% reported by BATHAEI and LEROY

(1996). It appears that twins mature slower but achieve similar mature weight to singles. Using the Gompetrz model LEWIS *et al.* (2002) estimated a value of A for males which is about 1.27 times of A for females. This is close to the estimate of 1.24 in the current study. This is 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. Significant effects in slope of growth between male and female kids during post weaning period have also been reported by AKIN *et al.* (2005) and UNAL *et al.* (2006). 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 the proportion of weight gained after birth will amount to about 0.93 as opposed to an estimate of 0.88 for B in this study. Other study using Brody's model for sheep (BATHAEI and LEROY 1998) estimated a B value of 0.95. These values are higher than the estimate in this study. Brody's function fits data poorly for weights prior to inflection point (maximum growth rate) and it appears it overestimated birth weight in this study. Significant differences in B for type of birth and age of dam show that twins and lambs from young ewes are lighter at birth and the proportion of mature weight they may gain after birth is higher compared to singles and lambs born from adult ewes.

Table 1
Least squares means (±SE), coefficient of determination (R^2) and variation (CV) of growth curve parameters
Least squares means (±Standardfehler), R^2 und CV der Wachstumskurvenparameter

Effects	Number	A	B	$K(10)^{-2}$
Overall	508	37.6 ± 0.45	0.88 ± 0.006	0.27 ± 0.011
Sex		**	*	ns
Male	49	41.8 ± 0.84	0.90 ± 0.010	0.258 ± 0.020
Female	459	33.3 ± 0.28	0.87 ± 0.003	0.289 ± 0.007
Rear		ns	**	ns (*P*=0.07)
Singles	270	37.9 ± 0.52	0.86 ± 0.006	0.284 ± 0.012
Multiples	238	37.2 ± 0.50	0.91 ± 0.006	0.264 ± 0.012
Damage, year		ns	**	ns
≤2	124	37.1 ± 0.64	0.90 ± 0.007	0.284 ± 0.015
3	124	37.2 ± 0.65	0.88 ± 0.008	0.285 ± 0.015
4	86	37.2 ± 0.68	0.86 ± 0.008	0.276 ± 0.016
5	70	38.0 ± 0.72	0.87 ± 0.009	0.260 ± 0.017
6	53	37.2 ± 0.79	0.90 ± 0.010	0.291 ± 0.019
≥7	46	38.6 ± 0.88	0.89 ± 0.011	0.246 ± 0.021
Year		**	**	**
R^2		32.8	39.8	42.1
CV, %		14.0	6.7	36.3

A mature weight (kg) as asymptotic limit of the weight when age approaches infinity, B proportion of mature weight gained after birth, K kg gain per kg live weight per day (maturing rate)

The overall estimate of K ($0.27 \cdot 10^{-2} day^{-1}$ and 0.081 $month^{-1}$) in this study was low compared to the estimate of 0.12 ($month^{-1}$) reported for sheep by BATHAEI and LEROY (1998). Singles have a significantly (*P*<0.05) higher maturing rate than twins while females have higher maturing rates than males. Female sheep achieved about 37, 46 and 68% of their mature weight at weaning, six month and yearling while males achieved only 31, 40 and 59%, respectively. GOLIOMYTIS *et al.* (2006) using Richards' model on Karagouniko sheep reported an absence of a significant sex difference in maturation index. Singles have achieved about 36, 45 and 65% of their mature weight while twin born lambs achieved 31, 41 and 61% at weaning, six months and yearling, respectively. For Chios ewes STOBART *et al.* (1986) have reported yearling weight which is about 67% of mature weight. This is very similar to the value in the current study. Coefficient of variations (CV) of A, B and K parameters were 14.0, 6.7 and 36.3 per cent which implies there is more variation in maturing rate, followed by mature weight.

Genetic parameter estimates of A, B and K are presented in Table 2. All three parameters have medium heritability estimates the highest and the lowest being for A and K, respectively. The heritability estimate of A (0.29) is comparable to estimates of 0.30 for Chios sheep (MAVROGENIS and CONSTANTINOU 1990). Very high estimates (0.44 to 0.53) have been reported for sheep by BATHAEI and LEROY (1998) and STOBART *et al.* (1986). CLARKE *et al.* (2000) reported estimates of 0.41, 0.37, and 0.38 for ewe live weight at 3, 4 and 5 years of age, respectively. Heritability estimates for B and K are lower than literature estimates for sheep (BATHAEI and LEROY 1998, SWACZKOWSKI *et al.* 2006). Due to the difference in availability of grazing land in the different years (and concurrent change in stocking rate), highly variable climatic factors and high turn over of the personnel involved in the management of the flock, there were variabilities in grazing and management conditions during the collection of the data used in this study. The large annual difference (ranging from 0.12 to $0.49 \cdot 10^{-2}$) observed in rate of maturing is a manifestation of this variability. Very high environmental variability clearly inflates the environmental variance while deflating the genetic variance and estimate of the heritability.

Table 2
Heritability estimates (±SE) (diagonal) of growth curve parameters and genetic (above diagonal) and phenotypic (below diagonal) correlations (±SE)
Heritabilitätsschätzwerte (±Standardfehler) der Wachstumskurvenparameter, genetische (über) und phänotypische (unter der Diagonalen) Korrelationskoeffizienten (±Standardfehler)

Parameter	A	B	K
A	0.29 ± 0.100	0.39 ± 0.308	−0.07 ± 0.34
B	0.04 ± 0.047	0.18 ± 0.092	0.25 ± 0.39
K	−0.36 ± 0.038	0.25 ± 0.044	0.14 ± 0.089

A mature weight (kg) as asymptotic limit of the weight when age approaches infinity, B proportion of mature weight gained after birth, K kg gain per kg live weight per day (maturing rate)

Genetic correlations between A and B, and B and K were positive while between A and K it was close to zero (−0.07) (Table 2). In all cases standard error estimates were high. The phenotypic correlation between A and B was close to zero while between A and K was medium and negative. For sheep BATHAEI and LEROY (1998) estimated negative genetic correlations of −0.12 and −0.40 between A and B and A and K, respectively. The positive genetic correlation between A and B in the current study is contrary to other reports. However, it is not unconceivable that mature weight could be positively genetically correlated with the proportion of mature weight obtained after birth. The phenotypic correlation of 0.04 between A and B in the current study is higher than the value of −0.20 reported for Mehraban Iranian fat-tailed sheep (BATHAEI and LEROY 1998). The genetic correlation estimate of −0.07 between A and K in the current study is lower than (in absolute value) estimate of −0.40 (BATHAEI and LEROY 1998). Many studies on growth curves 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 fastest have a lower weight 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 (Table 3). Genetic correlations with B, with the exception of yearling weight, were negative while the correlations with K, with the exception of birth weight were positive. In most cases the standard errors were high and inferences should be viewed with caution. In sheep similar positive genetic correlations between the different weights and mature weight and which increased with age at weight measurement had been reported by STOBART *et al.* (1986), BATHAEI and LEROY (1998) and DOBEK *et al.* (2004). Similarly MAVROGENIS and CONSTANTINOU (1990) reported a genetic correlation of 0.34 and 0.55 and a phenotypic correlation of 0.23 and 0.33 for mature weight with birth and weaning weight respectively. Estimates of genetic correlation between mature weight and immature weights in this study, although non significant ($P>0.05$) are in general agreement with literature estimates. 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 most studies 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 weights from weaning to yearling has a medium positive value. This indicates that the genetic potential for maturing rate which depends on growth rate is more positively related to early growth, but has no relationship (or negatively related) with weights which would be achieved until maturity.

Table 3
Genetic and phenotypic (in parenthesis) correlations (±SE) between growth curve parameters and immature weights

Genetische und phänotypische (in Klammern) Korrelationen (±Standardfehler) zwischen Wachstumskurvenparametern einzelner Gewichtsabschnitte

Parameter	Trait			
	Birth weight	Weaning weight	Six-month weight	Yearling weight
A	0.27 ± 0.34 (0.15 ± 0.048)	0.34 ± 0.270 (0.21 ± 0.047)	0.44 ± 0.203 (0.25 ± 0.047)	0.67 ± 0.172 (0.24 ± 0.048)
B	−0.66 ± 0.531 (−0.30 ± 0.043)	−0.48 ± 0.269 (−0.49 ± 0.037)	−0.22 ± 0.262 (−0.34 ± 0.044)	0.78 ± 0.555 (0.06 ± 0.050)
K	−0.13 ± 0.694 (0.03 ± 0.048)	0.37 ± 0.346 (0.31 ± 0.044)	0.61 ± 0.249 (0.35 ± 0.043)	0.66 ± 0.221 (0.50 ± 0.038)

A mature weight (kg) as asymptotic limit of the weight when age approaches infinity, B proportion of mature weight gained after birth, K kg gain per kg live weight per day (maturing rate)

Pearson correlation coefficients between growth curve parameters and ewe productivity traits are presented in Table 4. A has significant (P<0.05 to 0.01) positive correlations with all the traits except with TWW1. B and K are also significantly (P<0.01) correlated with TWW1 and TWW4. TWW4 and NLS4 have significant (P<0.05) relationship with B and K respectively. It appears that ewe performance at a young age is more related to maturing rate than mature weight and with an increase in age, mature weight becomes more important than K. B has a similar trend to K. An analytical attempt to determine if the relationship has a genetic basis failed to converge. However the result indicates that productivity can have positive relationships with growth curve parameters. The estimated average productive life in Horro sheep is about 3 parities and maximizing productivity from young ewes is important in improving flock productivity. Therefore maturing rate may be more important than mature weight in this breed.

Table 4
Pearson's correlations of growth curve parameters with ewe productivity
Pearson-Korrelationen zwischen Wachstumskurvenparametern und Produktionswerten

Traits	Number 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*

TWW1-TWW4 total weight of lambs weaned over the first four parities, NLB4 average number of lambs born per lambing for ewes with 4+ lambing opportunities, NLS4 average number of lambs surviving to weaning per lambing for ewes with 4+ lambing opportunities, A mature weight as asymptotic limit of the weight when age approaches infinity, B proportion of mature weight gained after birth, K kg gain per kg live weight per day (maturing rate)

Except for estimates of B, Brody's function appears to fit the growth curve of Horro sheep fairly accurately. Practically the most important components of the function are A and K. Heritability estimates of the growth curve parameters are medium and 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 seems an important trait worth consideration. 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 medium positive genetic correlations with weight at six-month and yearling, these traits can be used to indirectly select for the growth curve parameters.

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