

Environmental and genetic effects on growth in Timahdite and crossbred lambs in Morocco

M. El Fadili^{1*} C. Michaux²
B. Boulanouar¹ P.L. Leroy²

Key words

Sheep - Timahdite - D'man - Cross-breeding - Heritability - Growth - Genetic correlation - Morocco.

Summary

Knowledge of genetic parameters for growth traits of economic importance is required for the development of sheep populations in Morocco. Records on 544 lambs of the Timahdite (T) breed and of 756 D'man x Timahdite (DT) lambs, all born from 1992 to 1998, were used to estimate genetic parameters for lamb weights at birth, at 30, 70 and 90 days and daily gains from 10-30 days, 30-70 days and 30-90 days for each trait. Separate REML (co)variance component estimates were obtained assuming animal models that included the fixed effects of birth year, sex, age of dam, birth type or rearing types and the interaction of birth year by sex, the animal direct genetic effect and the maternal genetic effect. Genetic and phenotypic correlations between traits were estimated with models including the same fixed effects and only additive direct genetic effects. All fixed effects influenced growth traits. The direct heritability estimates for the various body weight and daily gain traits were low to medium and varied between 0.07 and 0.25 in T, and between 0.02 and 0.18 in DT. Maternal heritability ranged from 0.20 to 0.36 in DT, and from 0.01 to 0.10 in T lambs, except for the birth weight (0.53). For all traits the direct and maternal genetic correlations were high and negative in DT (-0.80 and -1.00) and in T (-0.90 and -1.00) lambs. However, the accuracy of such estimates is low due to the small data set used in the present study. The estimates of genetic and phenotypic correlations were positive for all traits, they were particularly high for genetic correlations between weights and weight gains after birth, both in DT and T lambs, and they showed no genetic antagonisms among the growth traits.

INTRODUCTION

The Timahdite breed is the most important native breed of Morocco in number (about 17% of the total ewe population) and geographical distribution. This native breed is well adapted to a wide range of pastoral and mixed farming environments, where it is used mainly in purebreeding, but has poor prolificacy, less than 1.2 lamb per ewe lambing (7). Prolificacy determines the number of lambs available for sale, directly affecting productivity and profitability of the Timahdite flocks. To enhance lambing rate and productivity, a crossbreeding program with D'man prolific rams

was carried out at El Koudia experimental station. Previous results reported by El Fadili *et al.* (8) showed that productivity of D'man x Timahdite ewes and growth of their progeny sired by meat breed were higher than in both parental purebreds, and that D'man x Timahdite first cross lambs showed similar growth rates as Timahdite ones. From a national perspective utilization, D'man x Timahdite crossbred dams might lead to an increase in productivity and profitability in sheep production as a whole. Therefore, interest arises in breeding D'man x Timahdite crossbred as a viable economic alternative to improve both ewe reproductive performances and lamb production, while maintaining their adaptability to grazing. However, development of efficient breeding programs that take into account the different structures of Moroccan breeds requires the knowledge of the genetic variability and genetic correlations between lamb weights and daily gains, which are important components of market lamb production.

Only Tijani and Boujenane (21) reported estimates of paternal half-sib heritabilities for growth traits in Timahdite lambs, but no information on genetic parameters are available for the D'man

1. Département de zootechnie, Institut national de la recherche agronomique, BP 415, Rabat, Maroc

2. Département de génétique, Faculté de médecine vétérinaire, Université de Liège, Sart Tilman, Bat. 43, 4000, Liège, Belgique

* Current address of the corresponding author: same as in 2

Tel: 32 4 366 41 28; Fax: 32 4 366 41 22

E-mail: elfadili@stat.fmv.ulg.ac.be

x Timahdite lambs. Furthermore, there is no report on genetic parameters in Moroccan breeds estimated using animal model methodology and accounting for maternal additive genetic effect. However, studies showed that both direct and maternal genetic influences are of importance for lamb growth and that ignoring the maternal genetic effect in the models leads to larger estimates of direct genetic heritabilities (5, 19, 22). Therefore, the genetic correlation between the additive direct and additive maternal components are important, particularly in situations where selection programs include traits affected by both direct and maternal effects.

The purpose of this paper was to quantify the effects of some environmental factors on body weights and daily gains of Timahdite and D'man x Timahdite lambs from birth to 90 days, and to estimate additive direct and maternal genetic heritabilities and genetic correlations for the traits of interest.

■ MATERIALS AND METHODS

Animals

Data came from Timahdite (T) and D'man (D) x Timahdite (DT) lambs born to ewes 1.5 to 6 years old between 1992 and 1998 at the National Institute and Agricultural Research experimental station of El Koudia located 30 km south of Rabat, on the Atlantic Coast, at an altitude of 150 m. The T flock was established in El Koudia station at the beginning of 1980. All D sires and some T sires were purchased outside from the national association of sheep and goat flocks. Data on the T breed included 544 records on the progeny of 322 ewes and 15 sires. Data on the DT (D male x T female) crossbreed included 756 records on the progeny of 467 ewes and 24 sires. In DT genetic groups, 201 crossed lambs were F2 (DT x DT) progeny of 116 ewes and 5 sires. Seven sires in T and 12 sires in DT genetic groups had progeny in various years. A total of 102 T and 161 DT dams lambed in various years. All lambs had complete records for all traits from birth to weaning. The available pedigree was used to form the numerator relationship matrix.

Management

Both T and DT ewes were raised under similar management conditions and an annual breeding cycle. Ewes were allocated to individual rams at random with an average mating ratio of 25 to 27 ewes per ram. Starting in July, young ewes were exposed to rams at an average age of 1.5 year. No culling was performed for the dams except for infertility, old age, and health problems. During lambing and suckling periods (December-May), ewes grazed on green pasture. Otherwise, they grazed on dry pasture and cereal crop residues. During the mating period of about 45 days, and for 5 to 10 days after lambing, ewes were kept indoors, with a ration composed of cereals (barley, triticale), molasses, sunflower meal, straw, hay, minerals and vitamins. Ewes were supplemented, depending upon available resources, pasture conditions and ewes requirements (maintenance, pregnancy, lactation). Lambs were kept indoors during the day and had free access to hay and commercial creep feed that contained about 16% of crude proteins, 0.8 forage units, minerals and vitamins. An annual program of vaccinations, deworming and dipping was carried out for all animals.

Lambs were born from December to January. The identities of newborn lambs and their dam, the date of birth, sex, birth type, birth weight within 24 hours and rearing type were all recorded.

Lambs were weighed individually every 20 days, until weaning at around 90-100 days of age. The first weighing occurred 21 days after the birth of the first lambs in the flock. Lambs' birth weight (BW), age-standardized weights at 30 days (W30), 70 days (W70) and 90 days (W90) and average daily gains from 10 to 30 days (ADG10-30), 30 to 70 days (ADG30-70) and 30 to 90 days (ADG30-90) were analyzed.

Statistical analysis

Environmental effect analysis

Fixed linear models were applied to the data using GLM procedure in SAS (20). Preliminary analyses were used to assess all first order interactions among all fixed effects (genotype of lamb, birth year, sex of lamb, birth type, rearing types and dam age). The interaction between year of birth and sex of lamb was the only significant interaction and was fitted in final models, both in T and DT genetic groups.

In T lambs, final models for BW, W30 and ADG10-30 included the main fixed effects of birth year (1992-1998), sex of lamb (male, female), birth type of lamb (single, twin), and dam age (≤ 1.5 , 1.5-2.5, 2.5-3.5, 3.5-4.5, > 5.5 years). For W70, W90, ADG30-70 and ADG30-90 traits, final models included the same fixed effects as for BW, but the birth type was replaced by the effect of rearing type (single, twin).

In DT lambs, final models for BW, W30 and ADG10-30 included the same fixed effects as in the T models for the same traits, but the birth type contained one more subclass (lambs born triplet and greater), and the genotype of the lamb (F1, F2) was added to the models. Final models for W70, W90, ADG30-70 and ADG30-90 included the same fixed effects as for BW, W30 and ADG10-30, but the birth type was replaced by the rearing type of lambs (single, twin, triplet). In T and DT lambs, the rearing type was equal to the birth type if the lamb was alive at 40 days of age. But, if the lamb died before 40 days, the rearing type was different from the birth type and equal to the number of lambs still alive.

Genetic parameters

To estimate genetic parameters, data for each trait and for T and DT groups were analyzed separately. The same fixed effects as the ones used in fixed analyses were included in mixed models, except in DT lambs where the genotype effect was replaced by the heterozygosity in individual DT lambs (1.0 in F1 and 0.5 in F2 lambs), which was fitted as a covariate. The maternal heterosis and recombination loss effects in the second generation (F2) were omitted, because the available genetic group did not allow their estimation. Furthermore, Boujenane *et al.* (2) reported negligible and nonsignificant effects of these genetic components in D'man x Sardi crossbred.

The random effects were the animal effects for the additive direct genetic effect and the maternal genetic effect, and the residual effect. The linear mixed models used to analyze growth traits were in matrix notation:

$$\text{in DT: } y = X\beta + bH + Zd + Mm + e$$

$$\text{in T: } y = X\beta + Zd + Mm + e$$

where: y is a vector of observations, β is a vector of fixed effects, b is a vector of the partial regression coefficients of observation y on level of heterozygosity in the lambs, H is the vector of heterozygosity coefficients in DT lambs, $d \sim N(0, A\sigma_d^2)$ is a vector

of direct additive genetic values, $m \sim N(0, A\sigma_m^2)$ is a vector of maternal additive genetic values, $e \sim N(0, I\sigma_e^2)$ is a vector of residual effects including both random environmental and non additive genetic effects. The X, Z and M are incidence matrices that assign the appropriate effects to the vector of observations, A is the matrix of additive numerator genetic relationship matrix among animals and I is the identity matrix of order equal to the number of records. The σ_d^2 and σ_m^2 are the additive direct and additive maternal genetic variances, and σ_e^2 is the residual variance.

The REML estimates of (co)variance components were obtained using the program MTDFREML (1). Direct and maternal heritabilities, and correlation between direct and maternal genetic effects were first estimated using single-trait analyses. Next, genetic correlations between all traits were estimated using two-trait analyses with only the direct genetic effect in the model. The starting values for additive genetic and residual variances in the two-trait analyses were those estimated under single-trait analyses. A minimum of two cold restarts were performed to check for global maxima. A variance of 10^{-8} of simplex function values was chosen as the convergence criterion. Standard errors of genetic correlations were calculated using the approximate formula given by Falconer and Mackay (9).

RESULTS AND DISCUSSION

Environmental effects

Overall means (and standard deviations), test of significance (F) and the proportion of variation explained by the fixed model (R^2) are given in table I. The fixed models explained 42 to 64% of the phenotypic variances in all traits in DT lambs, and 47 to 51% in T lambs. Birth year, sex of lambs, birth type, rearing types were all important environmental sources of variation on all growth traits ($p < 0.01$), both in T and DT lambs. Ewe age was an important effect ($p < 0.01$) for BW, W30, ADG10-30, but its influence decreased for W70 and ADG30-70 and became non significant for W90 and ADG30-90, both in T and DT lambs. The year by sex of lamb interaction was significant only for W70, W90, ADG30-70 and ADG30-90 in T lambs ($p < 0.05$) and in DT lambs ($p < 0.01$). The genotype influence in DT lambs was not significant for BW, W30 and ADG10-30, but highly significant for the other traits ($p < 0.01$). In general, these results are in agreement with those reported for growth traits, particularly for sex of lamb, year of birth and for the type of birth in previous studies on Moroccan breeds such as the Timahdite (21), the D'man (3), and the Beni Guil breeds (4).

Tableau I

Overall means (standard deviation) and test of significance (F) for growth traits of Timahdite and D'man x Timahdite lambs - Fixed effects only

Fixed effects	df	BW (kg)	W30 (kg)	W70 (kg)	W90 (kg)	ADG10-30 (g)	ADG30-70 (g)	ADG30-90 (g)
Timahdite								
Overall means		3.69	9.27	16.67	20.03	175	184	179
Standard deviation		(0.54)	(1.55)	(2.55)	(2.97)	(48)	(40)	(35)
Year of birth	6	**	**	**	**	**	**	**
Sex	1	**	**	**	**	ns	**	**
Birth type	1	**	**			**		
Rearing type	1			**	**		**	**
Ewe age	5	**	**	**	*	**	ns	ns
Year x sex	6	ns	ns	*	*	ns	*	*
R^2 (%)		47	52	57	56	42	51	51
D'man x Timahdite								
Overall means		3.50	9.07	16.56	20.20	187	187	185
Standard deviation		(0.55)	(1.49)	(2.52)	(2.98)	(48)	(37)	(34)
Genotype	1	ns	ns	**	**	ns	**	**
Year of birth	6	**	**	**	**	**	**	**
Sex	1	**	**	**	**	**	**	**
Birth type	2	**	**			**		
Rearing type	2			**	**		**	**
Ewe age	5	**	**	**	*	ns	**	ns
Year x sex	6	ns	ns	**	**	ns	**	**
R^2 (%)		42	55	63	64	47	62	62

df = degree of freedom

BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age

ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age

ns = $p > 0.05$; * $p < 0.05$; ** $p < 0.01$

The number of observations and least-square means (\pm standard errors) are shown for T lambs (table II) and DT lambs (table III). The effect of the year of birth on lamb weights and daily gains both in T and DT are drawn in figures 1 and 2.

Differences between male and female lambs were 0.23 and 0.12 kg at birth and 2.09 and 3.30 kg at 90 days of age in T and DT lambs, respectively. For ADGs, the differences between male and female lambs were 12 and 13 g/d for ADG10-30 and 24 and 38 g/d for ADG30-90 in T and DT lambs, respectively. Observed weight differences between male and female were consistent with other results (3, 4, 6, 11).

In T breed, single-born lambs were 0.82 kg heavier than twins were at birth. Similarly, single-born lambs were 2.95 kg heavier at 30 days, 3.86 kg at 70 days, and 4.18 kg at 90 days than twins. In DT, single-born lambs were heaviest by 1.12, 3.67, 4.30, and 6.01 kg, respectively at birth, 30, 70, and 90 days (table III). However, the ADGs between each subclass decreased with the age of lambs, both in T and DT. The least-square means showed that the effects of rearing types on the lamb body development tend to decrease as the lamb became older. This declining age trend can be attributed to a decreasing maternal effect including nursing and milk feeding of the lambs by their mothers. The differences between single and multiple lambs in weights and daily gains at birth and at 90 days have been reported in Barbarine (11), D'man (3) and Beni Guil (4) breeds.

The weights and ADGs of lambs born from dams in first parity were lower ($p < 0.05$) than those born in subsequent parities, but the differences in ADGs were significant only for ADG10-30 in T

lambs and for ADG30-70 in DT lambs. In general, lambs were heavier and grew faster with increased age of dam until an optimum age of 4.5-5.5 years, then decreased both in T and DT lambs (tables II and III). Similar results were reported in the literature (6, 11).

In DT lambs, the differences between F1 and F2 lambs were not significant for BW, W30, and ADG10-30 ($p > 0.05$), but for advanced ages the differences were significant ($p < 0.01$). The F2 were lighter and showed lower daily gains than F1 lambs: -2.51 kg for W90 and -38 g/d for ADG30-90. The superiority of F1 crossbred lambs can be explained by the heterosis effect for growth traits. Nitter (15), reviewing heterosis for growth in sheep, reported average estimates of individual heterosis to be about 3.2 and 5% for birth and weaning weights, respectively. In F2 lambs, the expected individual heterosis is halved, but the difference in the number of lambs born from F1 dams (prolificacy of 185%) compared to that of F1 lambs born from T dams (prolificacy of 120%) may explain the superiority of F1 lambs. Indeed, single-born lambs represented 53.17 vs. 40%, twins 20.24 vs. 15.34% and triplets and greater 0 vs. 45%, respectively in F1 and F2 lambs.

Lamb weights were heavier during the favorable years (1992, 1993, 1995) than during the unfavorable birth years of dryness (1994, 1996, 1997, 1998). Weight differences reached 0.13, 0.16 kg at birth, 1.18, 1.12 kg at 30 days, 3.37, 3.13 kg at 70 days, 3.58, 3.42 kg at 90 days, 44, 39 g/d for ADG10-30 and 46, 36 g/d for ADG30-90 in T and DT, respectively. The great influence of the year of birth on sheep performances in North Africa regions was observed in other studies (3, 4, 11).

Table II

Number of observations and least square means (\pm standard errors) for growth traits in Timahdite lambs

Fixed effect	Number	BW (kg)	W30 (kg)	W70 (kg)	W90 (kg)	ADG10-30 (g)	ADG30-70 (g)	ADG30-90 (g)
Sex								
Male	292	3.54 \pm 0.04 ^a	8.80 \pm 0.12 ^a	15.98 \pm 0.19 ^a	19.65 \pm 0.22 ^a	166 \pm 4	182 \pm 3 ^a	183 \pm 3 ^a
Female	252	3.31 \pm 0.04 ^b	8.33 \pm 0.12 ^b	14.56 \pm 0.20 ^b	17.66 \pm 0.24 ^b	157 \pm 4	160 \pm 3 ^b	159 \pm 3 ^b
Birth type								
Single	352	3.83 \pm 0.03 ^a	10.04 \pm 0.10 ^a			195 \pm 3 ^a		
Twin	192	3.01 \pm 0.04 ^b	8.09 \pm 0.12 ^b			159 \pm 4 ^b		
Rearing type								
Single	377			17.20 \pm 0.16 ^a	20.77 \pm 0.19 ^a		183 \pm 3 ^a	181 \pm 2 ^a
Twin	167			13.34 \pm 0.22 ^b	16.54 \pm 0.26 ^b		160 \pm 3 ^b	159 \pm 3 ^b
Ewe age (years)								
Age \leq 1.5	107	3.07 \pm 0.06 ^a	7.50 \pm 0.18 ^a	13.73 \pm 0.30 ^a	16.89 \pm 0.36 ^a	140 \pm 6 ^a	161 \pm 5	160 \pm 4
1.5 < age \leq 2.5	71	3.28 \pm 0.07 ^b	8.43 \pm 0.20 ^b	15.16 \pm 0.33 ^b	18.67 \pm 0.38 ^b	156 \pm 6 ^{ba}	171 \pm 5	172 \pm 5
2.5 < age \leq 3.5	76	3.56 \pm 0.07 ^c	8.68 \pm 0.19 ^b	15.86 \pm 0.32 ^b	19.25 \pm 0.37 ^b	159 \pm 6 ^b	179 \pm 5	176 \pm 4
3.5 < age \leq 4.5	94	3.65 \pm 0.06 ^c	9.23 \pm 0.18 ^c	15.76 \pm 0.30 ^b	19.02 \pm 0.35 ^b	178 \pm 6 ^b	172 \pm 5	169 \pm 4
4.5 < age \leq 5.5	109	3.46 \pm 0.06 ^c	8.96 \pm 0.18 ^c	15.80 \pm 0.32 ^b	19.40 \pm 0.33 ^b	172 \pm 6 ^b	175 \pm 5	176 \pm 4
Age > 5.5 years	87	3.51 \pm 0.07 ^c	8.60 \pm 0.19 ^{b,c}	15.33 \pm 0.32 ^b	18.71 \pm 0.37 ^b	164 \pm 6 ^b	173 \pm 5	172 \pm 4

BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age

ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age

Means within a column that do not have a common subscript differ ($p < 0.05$)

Table III

Fixed effect	Number	BW (kg)	W30 (kg)	W70 (kg)	W90 (kg)	ADG10-30 (g)	ADG30-70 (g)	ADG30-90 (g)
Genotype								
F1	555	3.13 ± 0.05	7.81 ± 0.15	14.70 ± 0.27 ^a	18.46 ± 0.32 ^a	158 ± 5	173 ± 4 ^a	178 ± 4 ^a
F2	201	3.01 ± 0.07	7.79 ± 0.21	13.16 ± 0.36 ^b	15.95 ± 0.43 ^b	154 ± 7	140 ± 5 ^b	140 ± 5 ^b
Sex								
Male	334	3.16 ± 0.04 ^a	8.09 ± 0.12 ^a	14.66 ± 0.22 ^a	18.32 ± 0.26 ^a	162 ± 4 ^a	167 ± 3 ^a	172 ± 3 ^a
Female	422	2.98 ± 0.04 ^b	7.50 ± 0.12 ^b	13.21 ± 0.22 ^b	16.10 ± 0.26 ^b	149 ± 4 ^b	146 ± 3 ^b	145 ± 3 ^b
Birth type								
Single	442	3.63 ± 0.04 ^a	9.78 ± 0.11 ^a			201 ± 4 ^a		
Twin	269	3.07 ± 0.04 ^b	7.51 ± 0.10 ^b			166 ± 3 ^b		
Triplet	45	2.51 ± 0.09 ^c	6.11 ± 0.25 ^c			121 ± 8 ^c		
Rearing type								
Single	478			16.73 ± 0.18 ^a	20.28 ± 0.21 ^a		179 ± 3 ^a	178 ± 2 ^a
Twin	244			13.63 ± 0.18 ^b	17.07 ± 0.22 ^b		155 ± 3 ^b	161 ± 3 ^b
Triplet	34			11.43 ± 0.47 ^c	14.27 ± 0.56 ^c		134 ± 7 ^c	137 ± 6 ^c
Ewe age (years)								
Age ≤ 1.5	72	2.78 ± 0.07 ^a	7.15 ± 0.20 ^a	13.04 ± 0.36 ^a	16.44 ± 0.42 ^a	145 ± 7	151 ± 5 ^a	157 ± 5
1.5 < age ≤ 2.5	119	3.04 ± 0.06 ^b	7.80 ± 0.16 ^b	13.70 ± 0.28 ^{a,b}	17.11 ± 0.33 ^{b,a}	162 ± 5	151 ± 4 ^a	157 ± 4
2.5 < age ≤ 3.5	169	3.13 ± 0.05 ^b	7.87 ± 0.14 ^b	13.91 ± 0.24 ^b	17.15 ± 0.29 ^{b,a}	156 ± 4	155 ± 4 ^{a,b}	157 ± 4
3.5 < age ≤ 4.5	181	3.13 ± 0.05 ^b	7.97 ± 0.13 ^b	14.52 ± 0.23 ^c	17.72 ± 0.28 ^b	157 ± 4	165 ± 3 ^b	163 ± 3
4.5 < age ≤ 5.5	112	3.22 ± 0.06 ^b	8.12 ± 0.17 ^b	14.49 ± 0.30 ^{c,b}	17.82 ± 0.36 ^b	161 ± 5	164 ± 4 ^b	165 ± 4
Age > 5.5	101	3.14 ± 0.06 ^b	7.87 ± 0.19 ^b	13.93 ± 0.32 ^{c,b}	17.00 ± 0.38 ^{b,a}	153 ± 6	154 ± 5 ^{a,b}	154 ± 4

BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age

ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age

Means within a column that do not have a common subscript differ ($p < 0.05$)

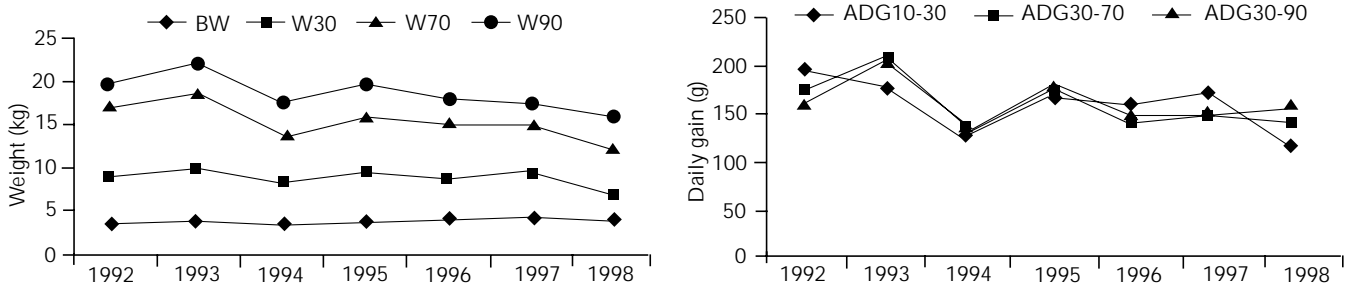


Figure 1: Effect of the birth year on weights and daily gains in Timahdite lambs. BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age; ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age.

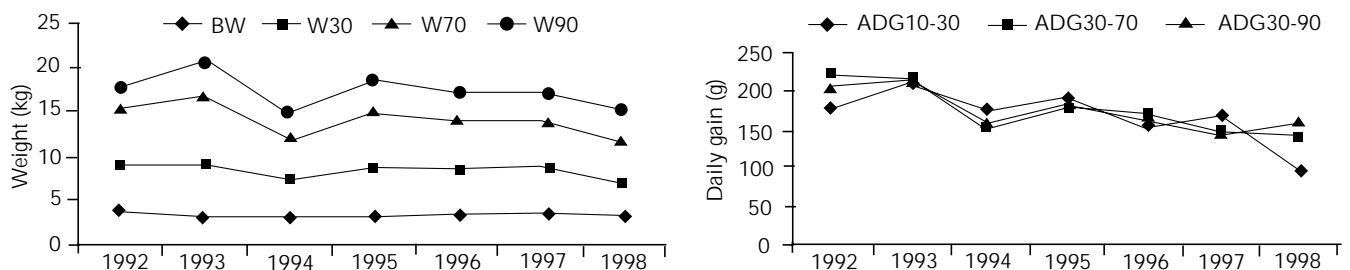


Figure 2: Effect of the birth year on weights and daily gains in D'man x Timahdite lambs. BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age; ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age.

Genetic parameters estimation

Single-trait analyses

Direct (h^2_d), maternal (h^2_m) heritabilities and direct-maternal additive correlation (r_{dm}) for lamb weights and ADGs obtained from the single-trait analyses are given in table IV. These estimates should be taken with caution due to the small data set used both in T and DT lambs.

Heritability estimates fluctuated across traits and within the T and DT lambs, taking a wide range of values. For daily gains, h^2_d estimates were slightly larger in T than in DT lambs, except for ADG10-30. On the other hand, h^2_m estimates were larger in DT than in T lambs, except for BW.

For both T and DT, h^2_d estimates for lamb weights fall within the range of values reported in the literature. In the Barbarine breed, Khaldi and Boichard (11) found an h^2_d of 0.02 to 0.04 for weight at birth to 90 days. Using an animal model, Maria *et al.* (13) reported in the Romanov breed an h^2_d of 0.04 to 0.34 for weights at birth to 90 days, and Tosh and Kemp (22) found values of 0.05 to 0.39 for weight at birth to 100 days in three breeds of sheep. Estimates of heritability in models, which did not consider maternal effects, as reported by Boujenane and Kerfal (3) in D'man breed, were larger and ranged from 0.23 to 0.56. In the T breed, our estimates of h^2_d were higher than those observed by Tijani and Boujenane (21) for the same breed. Their estimates were of 0.02 for BW and 0.06 for W90. These discrepancies could be due to differences in animals, models and computational methods. These authors used data from a T flock raised in the medium Atlas area of Morocco, a paternal half-sib model, and a computational method III of Henderson (10).

Estimates of h^2_m were low in T to moderate in DT lambs, but high for BW in both genotypes (table IV). Burfening and Kress (5) also found a large maternal effect on BW that ranged from 0.30 to 0.65. In DT, the estimates of h^2_m (0.20 to 0.36) were larger than those for h^2_d (0.02 to 0.18). Poivey *et al.* (17) reported h^2_m estimates of 0.30 for W30 and W90 in Ile de France lambs. In DT lambs, the estimates of h^2_m of the present study were higher than those observed by Khaldi and Boichard (11) for Barbarine lambs, with h^2_m of 0.04 (W30) and 0.03 (W90). They were also higher than those reported by Maria *et al.* (13) in Romanov lambs for BW ($h^2_m = 0.22$) and W90 ($h^2_m = 0.01$), by Tosh and Kemp (22)

in Hampshire for BW ($h^2_m = 0.22$) and W90 ($h^2_m = 0.19$), in Polled Dorset for BW ($h^2_m = 0.31$) and W90 ($h^2_m = 0.09$), and in Romanov lambs for BW ($h^2_m = 0.13$) and W90 ($h^2_m = 0.02$). On the other hand, the estimates in T lambs are similar to those observed by Maria *et al.* (13) and by Khaldi and Boichard (11). The results for body weights show that within breed groups, estimates tend to increase for h^2_d and to decline for h^2_m from birth to 90 days of age. This was expected because maternal influence, expressed during gestation and lactation, decreases in importance as lambs become independent of their dams (increasing expression of genes with direct additive effects on body development). This tendency was also observed in other studies (5, 13, 14, 16, 22).

For average daily gains, the h^2_d estimates in DT and T lambs were lower than those observed by Djemali *et al.* (6) in Barbarine lambs with $h^2_d = 0.24$ (ADG30-70) and $h^2_d = 0.31$ (ADG30-90), and by Boujenane and Kerfal (3) in D'man lambs with $h^2_d = 0.56$ (ADG30-90), and they were higher than those reported for the Barbarine breed (11) and T lambs (21).

High h^2_m estimates of 0.29 (ADG10-30) and 0.27 (ADG30-90) were reported by Poivey *et al.* (17) in Ile de France lambs. The h^2_m estimates for ADG30-90 in this study were higher than those observed by Khaldi and Boichard (11) and by Maria *et al.* (13), who reported low estimates of h^2_m ranging from 0.01 to 0.06 for growth traits in Barbarine and Romanov sheep. Maternal heritability decreases with age, which confirms the finding of Notter and Hough (16), Tosh and Kemp (22), and Yazidi *et al.* (23), who observed that maternal effects are substantial in young animals but diminish with age. Small estimates of h^2_m in T breed indicate a much lower proportion of genetic variation in T than in DT crossbred lambs. The greater maternal genetic effect on weights and daily gains in DT lambs is expressed through the variation in the uterine environment, litter size and milk production of prolific DT dams.

Estimated genetic correlations (r_{dm}) between direct additive and additive maternal effects were negative, but unreasonably high, both in T and DT lambs, ranging from -0.80 to -1.0 for body weights and from -0.90 to -1.0 for daily gains. It is difficult to find a biological explanation for this high correlation. It may be due to the small data size and to the structure of this data set (i.e., the number of generations for which animals were measured both directly and as dams was limited). In general, to avoid this type of

Table IV

Estimates of direct (h^2_d) and maternal (h^2_m) heritability and additive-maternal genetic correlation (r_{dm}) for growth traits in D'man x Timahdite and Timahdite lambs - Single character model

Traits	D'man x Timahdite			Timahdite		
	h^2_d	h^2_m	r_{dm}	h^2_d	h^2_m	r_{dm}
BW	0.02	0.36	-1.00	0.07	0.53	-1.00
W30	0.12	0.33	-0.85	0.15	0.02	-0.96
W70	0.08	0.34	-0.80	0.21	0.01	-1.00
W90	0.16	0.23	-0.80	0.21	0.01	-0.93
ADG10-30	0.13	0.20	-1.00	0.13	0.05	-0.95
ADG30-70	0.04	0.29	-1.00	0.13	0.07	-1.00
ADG30-90	0.18	0.22	-0.90	0.25	0.10	-0.98

BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age

ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age

problem, three generations and large grandparent offspring relationships in the data are needed (12). However, our estimates were obtained after rerunning the program with different starting values and with two or three cold restarts, and they still converged to the same estimates. Negative estimates for direct-maternal covariance for early growth traits are numerous in the literature for sheep. Maria *et al.* (13) reported strong negative correlations (r_{dm}) between direct and maternal additive effects for lamb body weights of -0.99 (BW), -0.98 (W30), -0.97 (W90), and -0.99 (ADG). Poivey *et al.* (17) also reported high negative estimates of r_{dm} ranging from -0.61 to -0.70 for growth traits to weaning in Ile de France lambs. Other authors (5, 11, 22) found important correlations between additive direct and additive maternal effects for body weight traits, ranging from -0.74 to -0.18.

In a simulation study Robinson (18) found that a large proportion of the negative correlation between direct and maternal for weaning weight could be caused by a sire by year interaction, which is especially important when a large proportion of sires are introduced into the population each year. This was the case in the present study as some T and D sires were bought out of the flock.

Other studies found that correlation between direct and maternal genetic effects could not be important or favorable. Indeed, Saatci

et al. (19) observed no correlation between direct and maternal additive effects for 12-week weights of Welsh Mountain lambs. Nasholm and Danell (14) and Yazidi *et al.* (23) observed positive direct-maternal additive correlations for BW (0.11 and 0.18) and the weaning weight (0.47 and 0.50).

Two-trait analyses

The estimates of the genetic (r_G) and phenotypic (r_P) correlations between traits in DT and T lambs are presented in tables V and VI, respectively. These estimates were obtained using only an additive direct animal model because, in the complete model, the genetic correlation between direct and maternal additive effects was high. Medium to high genetic correlations in DT ($r_G = 0.61$ to 0.81) and T ($r_G = 0.52$ to 0.81) were found between BW and other growth traits. The corresponding phenotypic correlations ranged from 0.12 to 0.55 in T, and from 0.27 to 0.58 in DT. All genetic correlation estimates were positive and high among W70, W90, ADG10-30, ADG30-70 and ADG30-90 traits, and exceeded 0.62 and 0.75 in T and DT lambs, respectively. The phenotypic correlation estimates among these traits were low to high ranging from 0.26 to 0.92 in DT, and from 0.13 to 0.94 in T lambs. In general, the largest genetic and phenotypic correlations were between chronologically

Table V

Genetic \pm error standard (above diagonal) and phenotypic (below diagonal) correlations between growth traits in D'man x Timahdite lambs

Traits	BW	W30	W70	W90	ADG10-30	ADG30-70	ADG30-90
BW		0.81 \pm 0.05	0.79 \pm 0.05	0.78 \pm 0.07	0.63 \pm 0.20	0.70 \pm 0.10	0.61 \pm 0.14
W30	0.58		0.98 \pm 0.04	0.95 \pm 0.06	0.97 \pm 0.11	0.91 \pm 0.08	0.81 \pm 0.13
W70	0.54	0.84		0.98 \pm 0.05	0.98 \pm 0.10	0.98 \pm 0.06	0.96 \pm 0.08
W90	0.50	0.75	0.92		0.94 \pm 0.16	0.98 \pm 0.07	0.97 \pm 0.10
ADG10-30	0.27	0.80	0.68	0.26		0.90 \pm 0.22	0.75 \pm 0.39
ADG30-70	0.30	0.40	0.83	0.59	0.33		0.95 \pm 0.11
ADG30-90	0.28	0.35	0.71	0.88	0.30	0.78	

BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age

ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age

Table VI

Genetic \pm standard error (above diagonal) and phenotypic (below diagonal) correlations among growth traits in Timahdite lambs

Traits	BW	W30	W70	W90	ADG10-30	ADG30-70	ADG30-90
BW		0.81 \pm 0.20	0.85 \pm 0.18	0.85 \pm 0.22	0.58 \pm 0.31	0.52 \pm 0.19	0.60 \pm 0.27
W30	0.55		0.95 \pm 0.14	0.94 \pm 0.09	0.96 \pm 0.18	0.75 \pm 0.28	0.87 \pm 0.24
W70	0.45	0.79		0.98 \pm 0.10	0.92 \pm 0.12	0.96 \pm 0.16	0.78 \pm 0.29
W90	0.40	0.69	0.94		0.97 \pm 0.10	0.86 \pm 0.27	0.94 \pm 0.23
ADG10-30	0.12	0.81	0.61	0.56		0.87 \pm 0.27	0.62 \pm 0.27
ADG30-70	0.19	0.26	0.81	0.77	0.18		0.85 \pm 0.25
ADG30-90	0.16	0.28	0.72	0.85	0.13	0.87	

BW = weight at birth; W30 = weight at 30 days of age; W70 = weight at 70 days of age; W90 = weight at 90 days of age

ADG10-30 = average daily gains from 10-30 days of age; ADG30-70 = average daily gains from 30-70 days of age; ADG30-90 = average daily gains from 30-90 days of age

adjacent weights rather than non-adjacent ones. As was reported in other sheep populations (Beni Guil, D'man, and Barbarine), there was a close association between postnatal weights and ADGs, as reflected by the high genetic and phenotypic correlations of W30 and ADG10-30, W70 and ADG30-70, and W90 and ADG30-90. In the literature, the values of genetic correlations ranged from 0.59 to 0.92 between W30 and ADG10-30, from 0.67 to 0.88 between W70 and ADG30-70 or ADG30-90, and from 0.79 to 0.98 between W90 and ADG30-90 (3, 4, 6). Our estimates for genetic and phenotypic correlations were comparable to those found by Djemali *et al.* (6) and higher than those reported by Boujenane and Mharchi (4) and Khaldi and Boichard (11).

■ CONCLUSION

The environmental factors investigated in this study had a high influence on T and DT lamb weights and on growth rates from birth to 90 days of age. Therefore, it is necessary to consider these environmental factors to obtain accurate estimates of breeding values. The direct heritability estimates obtained in this study were medium, except for the low values of BW both in T and DT lambs. The genetic and phenotypic correlations among growth traits of T and DT lambs were positive and high indicating that selection for one of those traits could result in genetic improvement in all other traits. Estimates of additive direct-maternal correlations were high and negative but the accuracy of such estimates is low due to the small size of the data set. In general, negative direct-maternal genetic correlation may complicate selection programs in sheep when farmers want to improve both an animal's own performances for growth and its dam's maternal genetic contribution to that growth. This is the case in the local Moroccan sheep where lamb growth depends closely on the milk production of their dams in the first 3-4 months.

Acknowledgments

Acknowledgments are given to the staff of the experimental station of El Koudia for the management and recording of animals. The support of the Administration générale de la Coopération au développement, Brussels, Belgium, and financial support of the Institut national de la recherche agronomique, Rabat, Morocco, are acknowledged.

REFERENCES

- BOLDMAN K.G., KRIESE A., VAN VLECK L.D., KACHMAN S.D., 1993. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances. Washington, DC, USDA, ARS.
- BOUJENANE I., CHAFIK A., BENBIHI M., 1999. Heterosis retained in different generation of inter se mating between D'man and Sardi sheep. *J. Anim. Breed. Genet.*, **116**: 151-159.
- BOUJENANE I., KERFAL M., 1990. Estimates of genetic and phenotypic parameters for growth traits of D'man lambs. *Anim. Prod.*, **51**: 173-178.
- BOUJENANE I., MHARCHI A., 1992. Estimation des paramètres génétiques et phénotypiques des performances de croissance et de viabilité des agneaux de race Beni Guil. *Actes Inst. agron. vét.*, **12**: 15-22.
- BURFENING P.J., KRESS D.D., 1993. Direct and maternal effects on birth and weaning weight in sheep. *Small Rumin. Res.*, **10**: 153-163.
- DJEMALI M., ALOULOU R., BEN SASSI M., 1994. Adjustment factors and genetic and phenotypic parameters for growth traits of Barbarine lambs in Tunisia. *Small Rumin. Res.*, **13**: 41-47.
- EL FADILI M., 1996. Amélioration de la productivité des ovins par croisement. In : Convention de recherche n°33/DE/91 (Rapport final). Rabat, Maroc, Institut national de la recherche agronomique, 62 p.
- EL FADILI M., MICHAUX C., DETILLEUX J., LEROY P.L., 1999. Comparison of matings using Moroccan Timahdite and D'man purebreds, first and terminal crosses. 1. Ewe productivity, lambs survival and growth performances. In: Proc. 50th Annual meeting of EAAP, Zurich, Switzerland, 22-26 August, p. 176-177 (Abstr.).
- FALCONER D.S., MACKAY T.F.C., 1996. Introduction to quantitative genetics, 4th Ed. London, UK, Longman, 464 p.
- HENDERSON C.R., 1953. Estimation of variance and covariance components. *Biometrics*, **9**: 192-218.
- KHALDI G., BOICHARD D., 1989. Direct and maternal effects on growth characteristics of Barbarine breed. *Ann. INRAT-ARIANA (Tunisia)*, **62**: 1-20.
- MARIA G.A., 1995. Estimates of variances due to direct and maternal effects for reproductive traits of Romanov sheep. *Small Rumin. Res.*, **18**: 69-73.
- MARIA G.A., BOLDMAN K.G., VAN VLECK L.D., 1993. Estimates of variances due to direct and maternal effects for growth traits of Romanov sheep. *J. Anim. Sci.*, **71**: 845-849.
- NASHOLM A., DANELL O., 1996. Genetic relationship of lambs weight, maternal ability and mature ewe weight in Swedish Finewool sheep. *J. Anim. Sci.*, **74**: 329-339.
- NITTER G., 1978. Breed utilization for meat production in sheep. *Anim. Breed. Abstr.*, **46**: 131-143.
- NOTTER D.R., HOUGH J.D., 1997. Genetic parameter estimates for growth and fleece characteristics in Targhee sheep. *J. Anim. Sci.*, **75**: 1729-1727.
- POIVEY J.P., JULLIEN E., BIBE B., 1994. Utilisation du modèle animal chez les ovins allaitants. In : Foulley J.L., Molénat M. eds, Séminaire Modèle animal, La Colle sur Loup, France, 26-29 septembre 1994, p. 99-114.
- ROBINSON D.L. 1996. Models which might explain negative correlations between direct and maternal genetic effects. *Livest. Prod. Sci.*, **45**: 111-122.
- SAATCI I., DEWIS A.P., ULUTAS Z., 1999. Variance components due to direct and maternal effects and estimation of breeding values for 12-week weight of Welsh Mountain lambs. *Anim. Sci.*, **69**: 345-352.
- SAS, 1989. SAS/STAT user's guide (version 6, 4th ed.). Gary, NC, USA, SAS Institute Inc.
- TIJANI A., BOUJENANE I., 1993. Estimates of genetic and phenotypic parameters for growth traits of Timahdite lambs in Morocco. In: Proc. 44th Annual meeting of the EAAP, **1**: 176-177 (Abstr.).
- TOSH J.J., KEMP R.A., 1994. Estimation of variance components for lamb weights in three sheep populations. *J. Anim. Sci.*, **72**: 1184-1190.
- YAZIDI M.H., ENGSTROM G., NASHOLM A., JOHANSON K., JORJANI H., LIDJEDAHL L.E., 1997. Genetic parameters for lamb weight at different ages and wool production in Baluchi sheep. *Anim. Sci.*, **65**: 247-255.

Reçu le 30.09.99, accepté le 27.07.00

Résumé

El Fadili M., Michaux C., Boulanouar B., Leroy P.L. Effets du milieu et génétiques sur la croissance des agneaux Timahdite et croisés au Maroc

La connaissance des paramètres génétiques pour les caractères de croissance d'intérêt économique est nécessaire à l'évolution des populations ovines au Maroc. Les données sur 544 agneaux de race Timahdite (T) et 756 agneaux D'man x Timahdite (DT), tous nés de 1992 à 1998, ont été utilisées pour estimer les paramètres génétiques des poids des agneaux à la naissance, à 30, 70 et 90 jours, ainsi que des gains de poids journaliers de 10 à 30, 30 à 70 et 30 à 90 jours, pour chaque caractère. Les variances-covariances ont été estimées séparément par la méthode du REML, utilisant un modèle animal qui incluait les effets fixes de l'année de naissance, du sexe, de l'âge de la brebis, du type de naissance ou du mode d'allaitement et de l'interaction année de naissance x sexe, effet génétique direct et effet génétique maternel. Les corrélations génétiques et phénotypiques entre les caractères ont été estimées avec des modèles comportant tous les mêmes effets fixes et seulement les effets génétiques directs additifs. Tous les effets fixes ont eu une influence sur les caractères de croissance. Les estimations des héritabilités directes pour les différents caractères poids et gains de poids journaliers ont été faibles à modérées et ont varié de 0,07 à 0,25 chez les T, et de 0,02 à 0,18 chez les DT. Les héritabilités maternelles ont été de 0,20 à 0,36 chez les DT et de 0,01 à 0,10 chez les T, à l'exception du poids à la naissance (0,53). Pour tous les caractères, les corrélations génétiques directes et maternelles ont été élevées et négatives chez les DT (-0,80 et -1,00) et chez les T (-0,90 et -1,00). Cependant, la précision de telles estimations est faible étant donné la petite taille du fichier des données utilisé dans cette étude. Les estimations des corrélations génétiques et phénotypiques ont été positives pour tous les caractères et particulièrement élevées pour les corrélations génétiques entre les poids et les gains de poids après la naissance à la fois chez les agneaux DT et T montrant l'absence d'antagonismes génétiques entre les différents caractères étudiés.

Mots-clés : Ovin - Timahdite - D'man - Croisement - Héritabilité - Croissance - Corrélation génétique - Maroc.

Resumen

El Fadili M., Michaux C., Boulanouar B., Leroy P.L. Efectos ambientales y genéticos sobre el crecimiento en corderos Timahdite y cruces en Marruecos

Para el desarrollo de las poblaciones de ovinos en Marruecos, son necesarios conocimientos sobre los parámetros genéticos de los caracteres de crecimiento que presentan importancia económica. Se utilizaron registros de 544 corderos de la raza Timahdite (DT), nacidos entre 1992 y 1998, con el fin de estimar los parámetros genéticos de los corderos para el peso al nacimiento, a 30 días, 70 días y 90 días y ganancias diarias de 10-30 días, 30-70 días y 30-90 días para cada carácter. Se obtuvieron estimaciones de los componentes de (co)varianza REML, asumiendo modelos animales que incluyeron efectos fijos del año de nacimiento, sexo, edad de la madre, tipo de parto o tipo de crianza y la interacción entre año de nacimiento y sexo, el efecto genético directo del animal y el efecto genético materno. Se estimaron correlaciones fenotípicas y genotípicas entre caracteres con modelos que incluyeron los mismos efectos fijos y únicamente efectos genéticos aditivos directos. Todos los efectos fijos tuvieron influencia en los caracteres de crecimiento. Las estimaciones de herencia directa para los diversos caracteres de pesos y ganancias diarias fueron de bajas a medias y variaron entre 0,07 y 0,25 en la raza T y entre 0,02 y 0,18 en los corderos DT. La herencia materna vario entre 0,20 y 0,36 en DT y entre 0,01 y 0,10 en los corderos T, con excepción de los pesos al nacimiento (0,53). Para todos los caracteres, las correlaciones genéticas materna y directa fueron elevadas y negativas en DT (-0,80 y -1,0) y en T (-0,90 y -1,0) corderos. Sin embargo, la exactitud de estas estimaciones es baja, debido a la pequeña cantidad de datos utilizados en el presente estudio. Las estimaciones de las correlaciones fenotípicas y genotípicas fueron positivas y altas en ambos corderos, DT y T, y no mostraron antagonismos genéticos entre los caracteres de crecimiento.

Palabras clave: Ovino - Timahdite - D'man - Cruzamiento - Heredabilidad - Crecimiento - Correlación genética - Marruecos.