

Phenotypic and Genetic Analysis of Lori-Bakhtiari Lamb's Longevity Up to Yearling Age for Autosomal and Sex-Linked Chromosomes

Research Article

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Received on: 7 Aug 2016

Revised on: 1 Nov 2016

Accepted on: 15 Nov 2016

Online Published on: Mar 2017

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Online version is available on: www.ijas.ir

ABSTRACT

The data set used in this study contained 8793 records of lamb's longevity (days) from 320 sires and 2349 dams collected during 1989 to 2014, from the Lori-Bakhtiari flock at Shooli station in Shahrekord, Iran. Genetic parameters (partitioned into autosomal, sex-linked and maternal) and breeding values of cumulative lamb's longevity from birth up to yearling age (at 1, 2, 3, 6, 9 and 12 months) were estimated using restricted maximum likelihood procedure. The results showed that the overall mean of the cumulative longevity of lamb up to yearling (12 months of age) was 295.87 days. The effect of fixed factors; year and month of birth, sex of lamb, age of dam, lamb birth weight as quadratic covariate and dam body weight as linear covariate were significant ($P < 0.05$) on lamb's longevity. The heritability estimates of lamb's longevity were low and ranged from 0.01 to 0.08 for autosomal, 0.01 for sex-linked and 0.02 to 0.03 for maternal additive genetic effects. The estimates of autosomal, sex-linked and maternal genetic correlations of lamb's longevity in different ages were high. The Pearson and Spearman correlation coefficients between autosomal breeding values and sex-linked breeding values in lamb's longevity at different ages were 0.15 to 0.46 and 0.11 to 0.43 respectively. Thus, lamb's longevity up to yearling can be improved by farm management practices and improving environmental factors at first. Genetic analysis using linear models which able to estimate breeding values in direct (autosomal and sex-linked chromosomes separately) and maternal effects, could be more effective to improve longevity in lambs.

KEY WORDS autosomal and sex-linked, longevity, Lori-Bakhtiari lambs.

INTRODUCTION

Improved ewe productivity would be achieved by increasing the number of lambs successfully reared per ewe in a given year. The high mortality rates obtained greatly reduce the efficiency and profitability of a lamb production enterprise. According to Fogarty *et al.* (1985), the mortality of lambs from birth to weaning is a major factor affecting the number of lambs weaned per lambing. Poor survival of lambs up to weaning time is a major source of reproductive inefficiency in most sheep flocks around the world (Hinch

and Brien, 2014). To obtain an ethically acceptable increase in the net reproductive rate, a strategy to reduce lamb mortality is required. Young *et al.* (2014) concluded that research on improving survival of lambs is likely to have a higher payoff than research on improving the number of lambs conceived. Lamb survival is a complex trait influenced by many different factors associated with management, climate, behavior of the ewe and lamb, and genetic effects (Smith, 1977; Christley *et al.* 2003; Everett-Hincks *et al.* 2008). Further, the rate of survival is higher in female lambs compared to male lambs in the same flock.

Nash *et al.* (1996) reported that after adjusting for birth weight, male lambs to be at greater risk of postnatal mortality. The higher mortality rate in ram lambs, compared to females is also reported in the other findings (Mukasa-Mugerwa *et al.* 2000; Mandal *et al.* 2007; Vatankhah and Talebi, 2009).

Lamb survival can be analyzed as a binary trait (Fogarty, 1995), but it suffers from a severe information loss because it ignores the continuity of the survival process and the precise time of death. This simplification implies that dead animals in 5 days or 5 months after birth are treated alike and contribute the same amount of information. However, longevity (days) can be analyzed as a continuous trait and accounted the precise time of death in breeding programs to improve survival rate in lambs.

The Lori-Bakhtiari sheep is one of the most common native breeds in the southwestern part of Iran (the Zagros Mountains), with a population of more than 1.7 million head, having the largest fat-tail size among all of the breeds in Iran. The animals of this breed are usually kept in villages under semi intensive systems. The Ministry of Jihad-Agriculture in Iran has found it important to increase the efficiency of sheep production, because the output of sheep in this system is low and the relative economic weights of lamb survival rate at pre- and post- weaning in Lori-Bakhtiari sheep were higher than growth traits (Vatankhah and Akhondi, 2015). Improving lamb's longevity in male lambs is economically beneficial as the replacement rate in male lambs is lower than for female lambs and the majority of male lambs are fattened for sale. The lower longevity in male lambs may be due to sex-linked determinants, which have not yet been researched and identified (Mandal *et al.* 2007). Thus, the objective of this study was to determine the non-genetic factors affecting on lamb's longevity and estimation of genetic parameters for lamb's longevity up to yearling age in Lori-Bakhtiari sheep for autosomal, sex-linked and maternal additive genetic effects.

MATERIALS AND METHODS

Data and flock management

The data set used in this study was collected from 8793 lambs descended from 320 rams and 2349 ewes born between 1989 and 2014 in the Shooli station, Shahrekord, Iran (Table 1). The flock is managed under a semi-migratory or village system. The animals are kept in the range on cereal pastures from mid-spring to late-autumn and kept indoors from December to May at the station and fed a ration composed of alfalfa, barley and wheat stubble. The breeding period extends from late August to late October (ewes were assigned randomly to the rams) and consequently, lambing starts in late January.

From 15 days of age, lambs have access to creep feed *ad libitum* and are weaned at an average age of 90 ± 5 days. After weaning, male and female lambs were separated. Surplus male lambs chosen for fattening were separated from the rest of the animals. Female lambs were kept in the pasture of cultivated alfalfa, while the rest of the males were kept indoors and fed a maintenance and growth ration (45% alfalfa hay, 39% barley, 7% beet pulp, 8% cottonseed meal, 1% salt and mineral supplements which containing 13.5% crude protein and 2.5 Mcal/kg metabolizable energy) to 12 months of age. The animals were monitored daily and dates of death in lambs were recorded. Traits studied were longevity of lamb in days from birth up to 1, 2, 3, 6, 9 and 12 months of age with the day of birth equal to 1 day of age. For calculate each cumulative time period, the birth date minus the removed date of lamb from the flock. Then for example the longevity of all lambs up to 2 months set equal to 60 days except for lambs that left the flock before 60 days.

Statistical analysis

The GLM procedure of SAS (2000) was applied to identify the important fixed effects to be considered in the final linear model. The final statistical model included year of birth, age of dam, birth type, month of birth and sex of lamb as fixed effects and the birth weight of lamb (linear and quadratic) and the mother's body weight of each lamb (as linear) were fitted as covariates in the following model.

$$Y_{ijklmn} = \mu + A_i + B_j + T_k + S_l + M_m + b_1(W_{ijklmn} - W_{000000}) + b_2(W_{ijklmn} - W_{000000})^2 + b_3(EW_{ijklmn} - EW_{000000}) + e_{ijklmn}$$

Where:

Y_{ijklmn} : observed longevity in days of n^{th} lamb.

μ : overall mean.

A_i : effect of i^{th} age of dam ($i=2, \dots, \geq 7$).

B_j : effect of j^{th} year of lambing ($j=1989$ to 2014).

T_k : effect of k^{th} birth type (k =single, twin or triplet).

S_l : effect of l^{th} sex of lamb (l =male and 2=female).

M_m : effect of m^{th} month of lamb birth (m =Jan, Feb or Mar).

W_{ijklmn} : birth weight of n^{th} lamb.

W_{000000} : overall mean of lamb birth weight.

EW_{ijklmn} : mother's body weight of n^{th} lamb.

EW_{000000} : overall mean of mother's body weight.

b_1, b_2 : linear and quadratic regression coefficients of lamb birth weight, respectively.

b_3 : linear regression coefficient of mother's body weight.

e_{ijklmn} : residual effects.

Variance components and genetic parameters were estimated from a linear animal model in a multi-variate analysis using the restricted maximum likelihood (REML)

method by WOMBAT program (Meyer, 2013). The animal model included all fixed effects described above, random effects of animal (separated to autosomal and sex-linked) and random maternal effects. The following multi-variate animal model was fitted to analyze the data set:

$$y_i = X_i b_i + Z_{1i} a_i + Z_{1i} s_i + Z_{2i} m_i + e_i$$

Where:

i : longevity of lamb up to i^{th} age ($i=1, 2, 3, 6, 9$ and 12 months).

y, b, a, s, m and e : vectors of observations, fixed effects, direct additive genetic effects in autosomal chromosomes, direct additive genetic effects in sex-linked, maternal additive genetic effects and residual random effects, respectively.

X, Z_1, Z_2 and Z_3 : incidence matrices relating the observations to the respective effects.

The average information (AI) REML algorithm was used to maximize the likelihood (convergence criterion was 10^{-8}) and additional restarts were performed until no further improvement in log likelihood occurred. With one record for each individual, the BLUP breeding values of longevity at different ages of lambs for autosomal effects ($\hat{\mathbf{a}}$, sex-linked effects ($\hat{\mathbf{s}}$) and maternal effects ($\hat{\mathbf{m}}$) are obtained using mixed model equations as follow:

$$\begin{bmatrix} \mathbf{X}\mathbf{X} & \mathbf{X}\mathbf{Z}_1 & \mathbf{X}\mathbf{Z}_1 & \mathbf{X}\mathbf{Z}_2 \\ \mathbf{Z}_1\mathbf{X} & \mathbf{Z}_1\mathbf{Z}_1 + \mathbf{A}^{-1} \frac{\sigma_e^2}{\sigma_a^2} & \mathbf{Z}_1\mathbf{Z}_1 & \mathbf{Z}_1\mathbf{Z}_2 \\ \mathbf{Z}_1\mathbf{X} & \mathbf{Z}_1\mathbf{Z}_1 & \mathbf{Z}_1\mathbf{Z}_1 + \mathbf{S}^{-1} \frac{\sigma_e^2}{\sigma_F^2} & \mathbf{Z}_1\mathbf{Z}_2 \\ \mathbf{Z}_2\mathbf{X} & \mathbf{Z}_2\mathbf{Z}_1 & \mathbf{Z}_2\mathbf{Z}_1 & \mathbf{Z}_2\mathbf{Z}_2 + \mathbf{A}^{-1} \frac{\sigma_e^2}{\sigma_m^2} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{a} \\ \mathbf{s} \\ \mathbf{m} \end{bmatrix} = \begin{bmatrix} \mathbf{X}\mathbf{y} \\ \mathbf{Z}_1\mathbf{y} \\ \mathbf{Z}_1\mathbf{y} \\ \mathbf{Z}_2\mathbf{y} \end{bmatrix}$$

Where:

$\mathbf{A} \sigma_a^2$: A covariance matrix of $\hat{\mathbf{a}}$.

\mathbf{A} : matrix of the co-ancestries between relative for autosomal loci (Henderson, 1976). And

σ_a^2 : variance of additive genetic values for autosomal loci.

$\mathbf{S} \sigma_F^2$: covariance matrix of $\hat{\mathbf{s}}$.

\mathbf{S} : a matrix whose elements are functions of co-ancestries between relative for X-chromosomal loci.

σ_F^2 : additive genetic variance for X-chromosomal loci for noninbred females (Fernando and Grossman, 1990).

$\mathbf{A} \sigma_m^2$: covariance matrix of $\hat{\mathbf{m}}$.

\mathbf{A} : matrix of the co-ancestries between relative.

σ_m^2 : variance of maternal additive genetic values.

The inverse of \mathbf{A} obtained by an algorithm described by Henderson (1976). The construction of \mathbf{S} and its inverse obtained by an algorithm described by Fernando and Grossman (1990). The total direct BLUP breeding values of animals calculated by summation of autosomal and sex-linked breeding values. The correlation coefficients (Pearson and Spearman) between total, autosomal and sex-linked breeding values of animals were obtained using correlation procedure of SAS (2000).

RESULTS AND DISCUSSION

The values in Table 2 indicate that the cumulative longevity decrease by 0.7, 1.88, 3.39, 18.66, 41.06 and 69.13 days up to 1, 2, 3, 6, 9 and 12 months of age respectively (the differences between observed overall mean of longevity from expected longevity if all of lambs were live and mortality were equal to zero). For example, if all of the lambs were live and could reach to yearling age, the mean of longevity had been 365 days, but due to death some of them at different ages the mean of longevity estimated as 295.87 days. These values indicated that the lamb's longevity decrease by 3.39, 15.27, 22.40 and 28.07 days in the first, second, third and fourth quarter of age, respectively.

The least squares mean for the longevity of lamb for different levels of non-genetic factors are shown in Table 2. There was significant ($P < 0.01$) variation in lamb's longevity between birth years, although, no clear trend was observed during 1989 and 2014. The least squares mean of longevity was lower in lambs born from the younger and older ewes compared to 4-5 years old, but these differences were not significant ($P > 0.05$) up to 1, 2 and 3 months of age and significant for 6, 9 and 12 months of ages ($P < 0.05$). The birth type did not have significant effect on lamb's longevity when corrected for lamb birth weight ($P > 0.05$). Although, the longevity of lambs was lower in triplet lambs, but due to the high standard error of the means the differences were not significant with singleton and twin lambs. The month of birth had a significant effect ($P < 0.01$) on lamb's longevity.

The least square means of lamb's longevity decreased with increasing month of birth. However, the differences between these values were not significant for the first and middle third of the lambing period up to 3 months of age, but the differences increased and were significant after 3 months of age. Female lambs were found to have a higher longevity than males at all the considered ages. The differences between lamb's longevity in females and males were significant ($P < 0.05$). This study showed a quadratic relationship between lamb's birth weight and longevity at all ages (Table 2).

Table 1 Pedigree structure for longevity analysis data set in Lori-Bakhtiari lambs

Item	Number	Item	Number
Original animals	9310	Sires with progeny	320
Animals with record	8793	Sires with record and progeny	246
Animals without offspring	6501	Dams with progeny	2349
Animals with offspring	2669	Dams with record and progeny	2046
Animals with offspring and record	2292	Founders	455
Animals with unknown sire	567	Inbred animals	4153
Animals with unknown dam	466	Average inbreeding coefficient in inbred animals	0.025

Table 2 The least squares means (\pm SE) of fixed effect for longevity (days) in Lori-Bakhtiari lambs

Factor	Number	1 mo	2 mo	3 mo	6 mo	9 mo	12 mo
Overall mean	8793	29.30	58.12	86.61	161.34	228.94	295.87
Birth year		**	**	**	**	**	**
Age of dam (yr)		NS	NS	NS	*	**	**
2	2355	28.91 \pm 0.18	57.05 \pm 0.43	84.86 \pm 0.69	150.96 \pm 2.41 ^{ab}	213.33 \pm 4.16 ^b	277.47 \pm 6.24 ^a
3	1873	28.96 \pm 0.18	57.34 \pm 0.41	85.42 \pm 0.67	153.70 \pm 2.36 ^a	218.85 \pm 4.07 ^a	285.46 \pm 6.10 ^a
4	1729	29.00 \pm 0.18	57.27 \pm 0.41	85.22 \pm 0.67	152.33 \pm 2.38 ^a	216.75 \pm 4.10 ^{ab}	281.53 \pm 6.15 ^a
5	1301	29.05 \pm 0.18	57.55 \pm 0.43	85.83 \pm 0.70	154.04 \pm 2.45 ^a	217.82 \pm 4.22 ^{ab}	282.00 \pm 6.33 ^a
6	935	28.94 \pm 0.20	57.27 \pm 0.46	85.19 \pm 0.75	150.95 \pm 2.62 ^b	213.42 \pm 4.51 ^{ab}	275.70 \pm 6.77 ^a
7	600	28.82 \pm 0.22	56.93 \pm 0.52	84.55 \pm 0.85	146.31 \pm 3.03 ^a	203.33 \pm 5.22 ^c	260.74 \pm 7.83 ^b
Birth type		NS	NS	NS	NS	NS	NS
Single	6377	29.07 \pm 0.07	57.54 \pm 0.16	85.47 \pm 0.27	153.46 \pm 0.94	216.05 \pm 1.61	279.83 \pm 2.42
Twin	2320	29.23 \pm 0.11	57.95 \pm 0.25	86.29 \pm 0.41	155.20 \pm 1.40	216.90 \pm 2.42	278.19 \pm 3.63
Triplet	96	28.53 \pm 0.43	56.23 \pm 1.01	83.77 \pm 1.64	145.47 \pm 5.92	208.80 \pm 10.21	273.43 \pm 15.30
Month of birth		**	**	**	**	**	**
Jan-Feb	4422	29.21 \pm 0.16 ^a	57.97 \pm 0.37 ^a	86.64 \pm 0.60 ^a	161.19 \pm 2.14 ^a	231.50 \pm 3.70 ^a	300.92 \pm 5.54 ^a
Feb-Mar	3411	29.18 \pm 0.16 ^a	57.77 \pm 0.38 ^a	86.13 \pm 0.62 ^a	155.66 \pm 2.19 ^b	221.46 \pm 3.78 ^b	286.69 \pm 5.67 ^b
Mar-Apr	960	28.44 \pm 0.20 ^b	55.97 \pm 0.46 ^b	82.77 \pm 0.75 ^b	137.28 \pm 2.65 ^c	188.79 \pm 4.57 ^c	243.84 \pm 6.86 ^c
Sex of lamb		**	**	**	**	**	**
Male	4403	28.79 \pm 0.16 ^b	56.81 \pm 0.37 ^b	84.47 \pm 0.60 ^b	144.17 \pm 2.17 ^b	200.99 \pm 3.75 ^b	258.52 \pm 5.62 ^b
Female	4390	29.10 \pm 0.16 ^a	57.67 \pm 0.38 ^a	85.89 \pm 0.63 ^a	158.59 \pm 2.21 ^a	226.85 \pm 3.81 ^a	295.78 \pm 5.71 ^a
LRBW		3.84 \pm 0.44 ^{**}	9.30 \pm 1.03 ^{**}	15.49 \pm 1.68 ^{**}	49.82 \pm 5.53 ^{**}	83.17 \pm 9.53 ^{**}	121.73 \pm 14.29 ^{**}
QRBW		-0.32 \pm 0.04 ^{**}	-0.78 \pm 0.10 ^{**}	-1.29 \pm 0.16 ^{**}	-3.84 \pm 0.55 ^{**}	-6.32 \pm 0.94 ^{**}	-9.19 \pm 1.41 ^{**}
LRDW		-0.02 \pm 0.01 ^{**}	-0.04 \pm 0.02 ^{ns}	-0.07 \pm 0.03 ^{**}	-0.26 \pm 0.10 ^{**}	-0.31 \pm 0.17 ^{ns}	-0.29 \pm 0.26 ^{ns}

LRBW: linear regression of birth weight; QRBW: quadratic regression of birth weight and LRDW: linear regression of dam weight.

The means within the same column with at least one common letter, do not have significant difference ($P > 0.05$).

* ($P < 0.05$) and ** ($P < 0.01$).

NS: non significant.

The positive and negative signs for linear and quadratic regression coefficients showed that longevity increased with lamb birth weight, reached an optimum level and then decreased with increasing lamb birth weight. The negative signs of linear regression coefficients of the mother's body weight showed that lamb's longevity decreased with increasing mother's body weight, however, some regression coefficients were not significant from zero (Table 2).

Genetic parameters of lamb's longevity (days) from birth to yearling age estimated by linear animal model including direct additive genetic effects of animal (autosomal and sex-linked) and maternal additive genetic effects are set out in Table 3. The autosomal heritability estimates for lamb's longevity were low, but these values increased with age of lamb (0.01 to 0.08). The estimates of sex-chromosome heritabilities of lamb's longevity were equal to corresponding autosomal heritabilities up to 3 months of age and constant with increasing age of lamb.

The estimates of maternal heritability of lamb's longevity were constant up to 9 months of age (0.03) and then decreased slightly for 12 months of age (0.02). The autosomal and sex-chromosome genetic correlations between lamb's longevity at different ages were positive and ranged from 0.42 to 0.97, while, maternal genetic correlation were higher relatively (0.85 to 0.99). All genetic correlations between longevity at cumulative time periods close to each other were high and reduced with increasing distance between them.

The estimates of phenotypic correlations between lamb's longevity at different ages were positive, but lower than corresponding genetic correlations relatively. A summary of autosomal and sex-chromosome breeding values of lamb longevity at different ages are shown in Table 4. This Table shows the average breeding values of autosomal and sex-linked effects at different ages, of lamb longevity were greater than zero.

Table 3 Heritability estimates (diagonal), genetic (below diagonal) and phenotypic (above diagonal) correlation estimates for autosomal, sex-linked and maternal effects of longevity in Lori-Bakhtiari lambs

Stay to	1 mo	2 mo	3 mo	6 mo	9 mo	12 mo
Autosomal						
1 mo	0.01±0.01	0.95±0.01	0.90±0.01	0.65±0.01	0.55±0.01	0.47±0.01
2 mo	0.89±0.16	0.01±0.01	0.98±0.01	0.83±0.01	0.65±0.01	0.58±0.01
3 mo	0.85±0.21	0.99±0.02	0.01±0.01	0.88±0.01	0.70±0.01	0.63±0.01
6 mo	0.80±0.25	0.98±0.18	0.96±0.09	0.06±0.02	0.94±0.01	0.86±0.01
9 mo	0.60±0.35	0.71±0.18	0.77±0.13	0.91±0.03	0.07±0.02	0.97±0.01
12 mo	0.42±0.34	0.55±0.15	0.65±0.13	0.80±0.07	0.97±0.01	0.08±0.02
Sex-linked						
1 mo	0.01±0.01	-	-	-	-	-
2 mo	0.99±0.13	0.01±0.01	-	-	-	-
3 mo	0.99±0.23	0.99±0.07	0.01±0.01	-	-	-
6 mo	0.97±0.22	0.98±0.12	0.98±0.10	0.01±0.01	-	-
9 mo	0.95±0.20	0.91±0.13	0.97±0.12	0.97±0.21	0.01±0.01	-
12 mo	0.90±0.25	0.90±0.12	0.92±0.10	0.91±0.18	0.93±0.20	0.01±0.01
Maternal						
1 mo	0.03±0.01	-	-	-	-	-
2 mo	0.98±0.01	-	-	-	-	-
3 mo	0.97±0.02	0.99±0.01	0.03±0.01	-	-	-
6 mo	0.90±0.10	0.93±0.04	0.94±0.03	0.03±0.01	-	-
9 mo	0.85±0.11	0.90±0.15	0.95±0.12	0.99±0.02	0.03±0.01	-
12 mo	0.85±0.14	0.86±0.17	0.90±0.13	0.95±0.05	0.97±0.01	0.02±0.01

Table 4 Summary of autosomal and sex-linked breeding values of longevity (days) in Lori-Bakhtiari lambs

Stay to	Autosomal				Sex-linked			
	Mean	SD	Min	Max	Mean	SD	Min	Max
1 mo	0.0037	0.0670	-0.3149	0.2291	0.0014	0.0626	-0.3000	0.2667
2 mo	0.0654	0.2545	-1.3905	0.9992	0.0032	0.1448	-0.6936	0.6165
3 mo	0.1409	0.5118	-2.9429	2.0115	0.0062	0.2818	-1.3496	1.9970
6 mo	1.1520	3.6522	-16.9960	10.9801	0.0191	0.0620	-0.3709	0.3000
9 mo	3.6125	7.6173	-36.1396	24.6285	0.0412	0.1340	-0.8009	0.6721
12 mo	6.6690	12.9021	-71.4093	44.9950	0.3545	1.1589	-6.9247	5.8336

SD: standard deviation.

This implies that without any direct selection for lamb longevity during the last years, genetic progress has been made through indirect selection. The mean and standard deviation of autosomal breeding values were higher than sex-linked in all of considered traits. There is significant variation in autosomal and sex-linked breeding values for lamb longevity at all ages in the population (Table 4). The correlation coefficients between breeding values of autosomal (A) and sex-linked (S) are shown in Table 5. Correlation coefficients for A-S, was low to medium. In general, the Spearman correlations were lower than Pearson procedure for all ages and breeding values types.

The overall mean of lamb longevity up to yearling recorded in this study was in range in the literature for different breeds of sheep (Yapi *et al.* 1990; Green and Morgan, 1993; Nash *et al.* 1996; Mukasa-Mugerwa *et al.* 2000; Mandal *et al.* 2007; Sawalha *et al.* 2007). The lamb longevity was higher when compared to values obtained for some sheep breeds such as Menz and Horro (Mukasa-Mugerwa *et al.* 2000).

The highest decrease in lamb longevity occurred during after weaning period (65.74 days), which is in accordance with values reported for Menz and Horro sheep (Mukasa-Mugerwa *et al.* 2000), but higher than values reported for some breeds of sheep such as Scottish Blackface and Muzaffarnagari (Sawalha *et al.* 2007; Mandal *et al.* 2007). This is due to extreme environmental changes in this period. Lambs were weaned at 90 ± 5 days of age and kept on a pasture of cultivated alfalfa which may not cover the lamb's requirements. The significant variations in lamb longevity from birth up to 12 months of age in different years may be attributed to variation in the environmental conditions, feed availability and other management factors. Similarly, Berhan and Van Arendonk (2006) and Mandal *et al.* (2007), observed significant effects of year of birth for lamb mortality rates. The changes in longevity of lamb with age of dam obtained in this study were similar to Smith (1977), who reported that yearling ewes had lambs with smaller birth weight, lower vigor, and higher mortality rates than lambs from older ewes.

Ewe age effects on lamb mortality have been shown to reduce lamb mortality with increasing ewe age (Southey *et al.* 2001; Sawalha *et al.* 2007), although Morris *et al.* (2000), in accordance with the results of this study showed slight decreases in longevity of lambs born to ewes greater than 5 years of age.

Table 5 Correlation coefficients between autosomal (A) and sex-linked (S) breeding values of longevity in Lori-Bakhtiari lambs

Stay to	Pearson correlation	Spearman correlation
1 mo	0.46	0.43
2 mo	0.37	0.37
3 mo	0.36	0.35
6 mo	0.08	0.11
9 mo	0.15	0.20
12 mo	0.17	0.23

The non-significant effect of dam age in lamb longevity up to 6 months of ages could be attributed to the existence of the mother's body weight as a covariate in the model, because some differences are corrected by this covariate. The non-significant effect of the birth type on lamb longevity obtained in this study could be attributed to correction for lamb's birth weight, which included in the model to analysis. The birth weights are normally lower for lambs born in larger litters (Smith, 1977; Morris *et al.* 2000; Sawalha *et al.* 2007) and therefore these lambs may be at greater risk of illnesses. Lambs born in multiple litters may also have higher mortality due to limitation in milk production by the dam, either as a result of low genetic potential for milk production or restricted nutrient intake in limiting environments (Snowder and Knight, 1995). The higher lamb longevity in female lambs compared to males is in agreement with other findings (Nash *et al.* 1996; Mukasa-Mugerwa *et al.* 2000; Mandal *et al.* 2007; Sawalha *et al.* 2007; Vatankhah and Talebi, 2009). Lower longevity in male lambs may be due to sex-linked determinants which have not yet been identified (Mandal *et al.* 2007), but is the main objective in this study. The intermediate optimum range for birth weight obtained in this study has been presented in many evaluations of lamb survival or longevity (Smith, 1977; Lopez-Villalobos and Garrick, 1999; Morris *et al.* 2000; Sawalha *et al.* 2007). Smith (1977) concluded that birth weight had a large influence with most early life mortality occurring in lambs with birth weights below the mean. Morris *et al.* (2000) found similar results with a larger proportion of dead lambs with light birth weights. One possible explanation for the elevated mean mortality rate at birth for lambs with the smallest birth weight is hypothermia, whilst dystocia can be a cause of mortality for lambs with the heaviest birth weights (Sawalha *et al.* 2007). Consequently, selection for optimal birth weight, rather than maximum birth weight, should be practiced when viability and birth weight are to be improved simultaneously.

Autosomal and maternal heritability estimates obtained in this study are in the range of values reported in the literature for direct and maternal heritability. For example, the weighted average heritability of survival rate and longevity to weaning in a review of 24 studies was 0.04 (Fogarty, 1995). Safari *et al.* (2005) in a review of 16 studies reported the range of direct and maternal heritability estimates in lamb survival rate were from zero to 0.11 and zero to 0.19, respectively. Vatankhah (2013) reported low estimates of direct heritabilities (0.01 to 0.09) for survival rate from different linear models, maternal heritabilities ranged from 0.00 to 0.04 and decreased as the age of lambs increased. The sex-linked heritabilities for lamb longevity were similar to the corresponding values of autosomal heritability up to 3 months of age obtained in this study. This implies that the genetic importance of sex-linked effects on longevity of lamb is equal to the genetic autosomal effects. In review the literature, there was not any report on the heritability of sex-linked for traits associated with longevity in sheep. Low estimates of the direct (autosomal and sex-linked) heritability for lamb longevity (<0.10) could be attributed to small additive genetic variance of viability and the impact of non-genetic factors on this trait. According to Riggio *et al.* (2008), one explanation for low heritability for lamb survival or longevity is that it is a composite trait and many factors may lead to death. As improving lamb longevity has a great economic importance, the potential for genetic improvement by within flock selection would be less effective due to low heritability estimates by linear animal models.

According to the estimates of autosomal, sex-linked and maternal genetic correlations, between longevity of lambs before and after weaning, genetic selection on lamb's longevity up to weaning age could improve the longevity after weaning ages.

Due to the lack of direct genetic selection for longevity of lamb and average breeding values greater than zero for autosomal and sex-linked effects obtained in this study, the genetic progress already obtained in this flock can be attributed to indirect selection for traits such as total weight of litter weaned (TWW) per ewe joined and correlated responses. One indirect selection method to improve lamb's longevity is to use composite traits. Selection could be performed on a composite trait that incorporates lamb's longevity or survival rate and is likely to be part of an overall breeding objective, i.e. it has intrinsic economic value to the breeder, as it affects either returns or costs or both. Examples are number of lambs weaned (NLW) or TWW per ewe joined, both relying on a favorable correlated response in lamb's longevity or survival (Brien *et al.* 2014). This seems a reasonable expectation as, for example, favorable genetic correlations of 0.76 (Swan *et al.* 2001) and 0.55

(Hebart *et al.* 2010) have been estimated between NLW and lamb survival from two large Merino flock studies in Australia. A similar, strong genetic correlation of 0.73 has also been reported between TWW and lamb survival (Afolayan *et al.* 2008).

The low to medium estimates of Pearson correlation coefficients and lower estimates of rank correlation coefficients between A-S breeding values of lamb's longevity at all ages indicated that genetic selection on autosomal breeding values solely, cannot choose animals with high breeding values for sex-linked effects.

CONCLUSION

The present investigation revealed that, although the overall lamb's longevity up to yearling observed in this study is not low, but the mortality rate distribution is not suitable, because the highest mortality rate occurred after weaning period (6 to 12 months of age). With regard to non-genetic factors on the longevity of lambs from birth to the yearling age, it could be concluded that in order to improve the longevity of lambs focus should be on improve non-genetic factors and management conditions. Breaking up direct additive genetic variance of lamb's longevity in to autosomal and sex-linked in this study showed that the proportion of the variance related to the sex-linked effects was similar to the proportion of variance attributed to autosomal effects up to weaning. Although, response to selection of lamb's longevity is low due to low estimates of heritability, genetic analysis of longevity using animal models which able to partition total additive genetic variation in to autosomal, sex-linked and maternal effects could make a more effective genetic selection. Thus, genetic selection based on a combination of three sources of BVs with suitable relative economic weights is recommended to improve genetically lamb's longevity.

ACKNOWLEDGEMENT

We are grateful to the head and all of the coworker in Sholi station to collect the data and allowed to use them.

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