Genetic analysis of longevity and lamb survival from birth to yearling in Moghani sheep

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ABSTRACT
The objective of this study was to estimate genetic parameters for longevity and survival traits from birth to yearling in Moghani breed of sheep. The data set comprised of 4580 lamb survival records collected during 1994 to 2012 in the breeding station of Moghani sheep. Traits studied were cumulative lamb survival from birth up to 3 (S1), 6 (S2), 9 (S3) and 12 (S4) months of age, and corresponding longevity of lambs (L1, L2, L3 and L4, respectively). The linear and threshold animal model analyses were run using a restricted maximum likelihood method and average information algorithm (AIREML) of the WOMBAT software and MATVEC program, respectively. Also, cumulative survival traits were analysed using the sire model through the Weibull proportional hazard function of the MATVEC program. Direct heritability estimates obtained from different linear models varied from 0.004–0.021, 0.014–0.023, 0.058–0.069 and 0.006–0.061 for L1, L2, L3 and L4, respectively. Also, heritability estimates on the logarithmic scale for S1, S2, S3 and S4 obtained from the Weibull sire model were 0.57, 0.40, 0.08 and 0.03, respectively. Medium to high estimates of heritability for survival traits, employing proportional hazard models, suggest that lamb survival could be improved through direct selection within the flock.

1. Introduction
Survival of lambs is a compound character affected by many various effects connected to weather conditions, management, lamb and ewe behaviour, and other environmental factors (Smith 1977; Christley et al. 2003; Everett-Hincks et al. 2005; Tomaszyk et al. 2014; Aktay et al. 2015; Moraes et al. 2016). Increasing lamb numbers raised per ewe in a given year would result in improved productivity of ewes. Low survival rates of lambs may also perform as a hindrance to obtaining greater reproductive efficiencies because the profit of increasing the litter size at birth is frequently neutralized by lamb survival decreases related to an increase in multiple births (Slee et al. 1991). Therefore, breeding programmes with the objective of enhancing reproductive efficiency should be improved to keep the rate of alive births (increasing survival rate) (Brien et al. 2010). Many efforts have been conducted to recognize the key variables engaged in neonatal susceptibility at recent years (Hinch and Brien 2014; Abdelqader et al. 2017), but the outcomes are greatly affected by production and management systems and breed of lambs. Conducting survival analysis through the application of survival times makes possible the distinction between the early or late death of lambs in a given period. In addition, analysis of actual survival time permits for the application of records of lambs which were died or culled over the period considered because of reasons not associated with their survivability (Sawalha et al. 2007). It was reported that lamb survival from birth to yearling is generally as 20–40% in various sheep breeding systems and causes a negative effect on genetic progress and economic considerations of sheep breeding (Mukasa-Mugerwa et al. 2000; Tibbo 2006; Hatcher et al. 2010; Thomas 2010). Estimates of heritability for survival rate obtained by linear animal models are reported to be generally low, ranging from 0.00 to 0.11 (Safari et al. 2005), halting or slowing the genetic progress rate. Models of survival analysis have been applied to appraise the survival of many disparate farm animal species (Vukasinovic et al. 2001; Caraviello et al. 2004; Rogers et al. 2004; Serenius and Stalder 2004; Sewalem et al. 2005; Sawalha et al. 2007; Barazande et al. 2012). The distinction between models of survival analysis and other models used for conventional evaluation of survival is that time-dependent factors and censored records may be included into the models of survival analysis (Borg 2007). Lamb survival and ewe longevity would be improved by implementing genetic selection programmes and through improved management interventions. In this regard, understanding the genetic parameters of longevity and lamb survival is necessary to evaluate the possibility of including these traits into the selective breeding programmes within sheep populations. Therefore, the objective of current study was to estimate genetic parameters of the longevity and survival traits from birth to yearling in Moghani breed of sheep using proportional hazard models through the Weibull function, linear and threshold models of analysis.

2. Materials and methods
The data set used in this study comprised of 4580 lamb survival records collected during 1994 to 2012 from 1749 ewes and 350
rams in the breeding station of Moghani sheep (in Ardebil province, Iran). One of the main Iranian meat sheep breeds is Moghani which is prominent for its tolerance to harsh climatic conditions, ability to provide heavy lambs and large body size. The Moghani breed is fat-tailed and ewes and rams are polled. The coat colour is mostly white and the colour of the face, feet and legs are brown. The breeding station of Moghani sheep was founded in Ardebil province (northwest of Iran) in order to identify the best rams and dispense them to the commercial flocks to improve genetically the performance of animals. The Moghani sheep rear under a traditional migratory method and the flock kept in winter pastures from November to April and in summer ranges during May to October. The main feeding sources of animals are pasture grasses; however, some barley might be supplied for breeding animals nearly two weeks before the start of the mating period, over the final month of pregnancy and the first month of milking. Breeding period commenced from August and lasted to October. Lambing period occurred from January to February. The identity of the parents of each lamb was known because the controlled mating method was performed in the flock. The weaning age of lambs is 120 days old and male and female lambs were bred at 18 months of age. Ewes and rams were remained within the flock for up to 6 years and one year, respectively. Male and female lambs were reared in separate flocks from 6 months of age onwards (Ghavi Hossein-Zadeh and Ardalan 2010). The longevity of lambs (in days) was calculated from the date of death or the lamb being removed from the flock minus birth date as a continuous trait. Longevity traits were longevity of lambs from birth up to 3 (L1), 6 (L2), 9 (L3) and 12 (L4) months of age. Survival traits studied were cumulative lamb survival from birth up to 3 (S1), 6 (S2), 9 (S3) and 12 (S4) months of age. For each survival time or period, a lamb obtained a code of either 0 or 1 for lamb death or alive as a binary trait in the linear and threshold models and a censored code for the Weibull proportional hazards model (0 for right censored and 1 for death or removal from the flock). Censored records of lambs were considered in the data set because models used for survival analysis accounting for a known lamb survival time until censoring event or death. Lambs which remained in the flock up to the respective age were considered as censored, taking a code of 0. Live lambs which were removed from the flock before given age are censored at the removal day. Records for lambs which died because of accidental deaths or lambs removed from the flock for other unknown reasons, before the corresponding age were also considered as censored.

The generalized linear model (GLM) procedure of the SAS program (SAS Institute 2002) was used for the statistical analysis of longevity. Variables which were significant at \( P < .05 \) were included in the final models of analysis. The following model was used for the analysis:

\[
Y_{ijklno} = \mu + A_i + B_j + T_k + S_l + M_m + b_1(W_{ijklno} - \bar{W}) + b_2(W_{ijklno} - \bar{W})^2 + e_{ijklno},
\]

where \( Y_{ijklno} \) - longevity records, \( \mu \) - overall mean; \( A_i \) - fixed effect of \( i \)th dam age \( (i = 1, 2, \ldots, 7) \); \( B_j \) - fixed effect of \( j \)th birth year \( (j = 1, \ldots, 18) \); \( T_k \) - fixed effect of \( k \)th birth type \( (k = 1, 2) \); \( S_l \) - fixed effect of \( l \)th lamb sex \( (l = 1, 2) \); \( M_m \) - fixed effect of \( m \)th birth month \( (m = 1, \ldots, 5) \); \( W_{ijklno} \) - birth weight as covariate; \( \bar{W} \) - average birth weight; \( b_1 \) and \( b_2 \) - linear and quadratic regression coefficients of longevity on birth weight, respectively, and \( e_{ijklno} \) - random residual error.

Survival analysis was conducted using the Weibull proportional hazards models of the LIFEREG procedure in SAS (SAS Institute 2002). The following model was used to analyse the fixed effects on cumulative survival traits:

\[
(Y \times S)_{ijklno} = \mu + A_i + B_j + T_k + P_l + M_m + b_1(W_{ijklno} - \bar{W}) + b_2(W_{ijklno} - \bar{W})^2 + e_{ijklno},
\]

where \( Y_{ijklno} \) - age at failure (death or censoring); \( S_{ijklno} \) - censor code of 0 or 1; \( P_l \) - fixed effect of \( l \)th lamb sex \( (l = 1, 2) \) and other variables were defined earlier. Lamb sex, birth type, dam age, birth year and month, and linear and quadratic effects of birth weight had significant effects on all survival and longevity traits and included in the final models for genetic analysis.

The following linear models were used for genetic analysis of longevity and survival traits:

Model 1: \( y = Xb + Za + e \).
Model 2: \( y = Xb + Za + Zc + e \).
Model 3: \( y = Xb + Za + Zm + m + e \) with Cov\((a, m) = 0\).
Model 4: \( y = Xb + Za + Zm + m + e \) with Cov\((a, m) = A\sigma_{am}^2\).
Model 5: \( y = Xb + Za + Zm + Zc + e \) with Cov\((a, m) = A\sigma_{am}^2\).

Where \( y \) is a vector of observations, \( b \) is a vector of fixed effects with incidence matrix \( X \), and \( a \sim N(0, \sigma_a^2) \) and \( m \sim N(0, \sigma_m^2) \), are vectors of direct and maternal genetic effects with incidence matrices \( Z_a \) and \( Z_m \), respectively, \( c \sim N(0, I, \sigma_c^2) \) is a vector of random maternal permanent environmental effects with incidence matrix \( Z_c \) and \( e \sim N(0, I, \sigma_e^2) \) is a vector of random residual effects. Also, \( \sigma_a^2 \) is the direct genetic variance, \( \sigma_m^2 \) is the maternal genetic variance, \( \sigma_c^2 \) is the maternal permanent environmental variance, \( \sigma_e^2 \) is the residual variance, \( A \) the additive genetic relationship matrix, and \( I \) and \( I_n \) are the identity matrices of order equal to the number of maternal permanent environmental effects and the number of records, respectively. The most suitable model amongst all six models was determined based on Akaike's Information Criterion (AIC) (Akaike 1973):

\[
AIC_i = -2 \log L_i + 2 p_i,
\]

where \( \log L_i \) is the maximized log likelihood of model \( i \) at convergence and \( p_i \) is the number of parameters obtained from each model. The model with the lowest AIC is considered as the best model for genetic analysis of longevity.

The linear (for longevity and survival traits) and threshold (for survival traits) animal model analyses were run using a restricted maximum likelihood method and average information algorithm (AIRML) of the WOMBAT software (Meyer 2006) and MATVEC program (Wang et al. 2001), respectively. Cumulative survival traits were analysed using the Weibull proportional hazard function of the MATVEC program (Wang et al. 2001).
The hazard function (Ducrocq and Casella 1996; Casellas et al. 2007) was modelled as follows:

\[ h(t; x) = h_0(t) \times \exp(x' \beta + z' \gamma), \]

where \( h(t; x) \) is the instantaneous death rate at time \( t \) of a particular animal, \( h_0(t) \) is the baseline hazard function of the Weibull distribution with shape parameter \( \rho \) and scale parameter \( \lambda \) and \( x \) is vector of random additive genetic effect of sire with incidence vector \( z \). It was assumed that \( s \sim N(0, A \sigma_s^2) \). The average information (AI) REML algorithm was used to maximize the likelihood. The survival heritability on the logarithmic scale \( (h_s^\text{log}) \) for the Weibull sire model was estimated as follows:

\[ h_s^\text{log} = \frac{4 \sigma_s^2}{\left( \sigma_s^2 + \frac{\pi^2}{6} \right)}, \]

where \( \frac{\pi^2}{6} \) is a variance of the Weibull model. The effective heritability \( (h_e^\text{eff}) \), which is not dependent on the parameters of the Weibull model, was calculated as follows:

\[ h_e^\text{eff} = \frac{4 \sigma_s^2}{\left( \sigma_s^2 + 1 \right)}. \]

### 3. Results

Cumulative percent of culling cases from birth to yearling is shown in Figure 1. Cumulative percent of cullings were increased from the first months of age to yearling in a sigmoid pattern. This induced the lower survival rate of lambs until yearling age. Estimates of direct and maternal heritabilities, ratio of maternal permanent environmental variance to phenotypic variance, correlation between direct and maternal genetic effects and AIC values for longevity and survival traits from birth up to yearling obtained under different linear models are shown in Tables 1 and 2, respectively. Direct heritability estimates obtained from different models varied from 0.004 to 0.021, 0.014 to 0.023, 0.058 to 0.069 and 0.006 to 0.061 for L1, L2, L3 and L4, respectively. Estimates of direct heritabilities obtained from linear models ranged from 0.001 to 0.008, 0.000 to 0.004, 0.000 to 0.004 and 0.000 to 0.002 for S1, S2, S3 and S4, respectively.

Estimates of maternal heritabilities under different models were low and ranged from 0.000 to 0.026, 0.000 to 0.019, 0.000 to 0.019 and 0.000 to 0.048 for L1, L2, L3 and L4, respectively. Maternal heritability estimates for S1, S2, S3 and S4 obtained from linear animal models were 0.000 to 0.015, 0.004 to 0.009, 0.001 to 0.004 and 0.001 to 0.009, respectively. Fitting maternal permanent environmental effect (Model 2) into the model provided the lowest AIC values for all longevity traits compared with other models used for genetic analysis. Therefore, Model 2 was selected as the best model for estimating genetic parameters of all longevity traits. Model 3 which included direct and maternal genetic effects provided the lowest AIC values and selected as the best linear model for genetic analysis of S1 and S2, but Model 1 with only direct genetic effect selected as the best model of genetic analysis for S3 and S4 due to the lowest AIC values. Ratios of maternal permanent environmental variance to phenotypic variance for longevity traits obtained from model 2 varied from 0.008 (for L3) to 0.024 (for L4). Also, estimates of ratio of maternal permanent environmental variance to phenotypic variance for survival traits were low (0.001 to 0.012). Estimates of correlation between direct and maternal genetic effects for longevity and survival traits were low and ranged from −0.01 to −0.004 and −0.010 to 0.073, respectively. Although most direct-maternal correlation estimates obtained in this study were negatively low. Estimates of genetic parameters for survival traits obtained from threshold models are shown in Table 3. Heritability estimates for S1, S2, S3 and S4 were 0.0013, 0.0031, 0.145 and 0.147, respectively. Therefore, threshold estimates of heritability for survival traits increased from birth to yearling age. Threshold heritability estimates for survival traits, especially S3 and S4, were generally greater than linear estimates for these traits.

Estimates of genetic parameters for survival traits obtained from sire model using the Weibull proportional hazard function are shown in Table 4. The estimates of heritabilities on the logarithmic scale \( (h_s^\text{log}) \) for S1, S2, S3 and S4 obtained from the Weibull sire model were 0.57, 0.40, 0.08 and 0.03, respectively. Also, effective heritabilities for abovementioned survival traits were estimated to be 0.37, 0.28, 0.05 and 0.02, respectively. Therefore, heritabilities on the logarithmic scale and effective heritabilities decreased from birth to yearling age.

### 4. Discussion

Similar trend was reported for the pattern of cumulative culling by Vatankhah (2013) in Lori-Bakhtiar lambs and Getachew et al. (2015) in Menz sheep. Also, Barazandeh et al. (2012) observed that the cumulative survival of Kermani lambs declined with increasing age from birth to weaning.

Generally consistent with the results of this study, Nadaf Fahmideh et al. (2017), Vatankhah (2013), El-Saied et al. (2005) and...
Consistent with the current results, Southey and Leymaster (2008) reported low estimates of direct heritabilities for longevity in Guilan sheep (0.02–0.059), Lori-Bakhtiar sheep (0.01–0.08), Churra sheep (0.02–0.06) and UK hill sheep (0.08), respectively. Ramezani and Ghavi Hossein-Zadeh (2017) and Meekkawy et al. (2009) obtained greater estimates of direct heritability for longevity in Mehrraban sheep (0.16–0.22) and crossbred Mule ewes (0.27), respectively. Greater estimates of direct heritabilities for longevity compared with maternal heritability estimates obtained in this study were consistent with the results of Nadaf Fahmideh et al. (2017) in Guilan sheep and Bahri Binabaj (2014) in Karakul and Baluchi sheep. Consistent with the current results, Southey and Leymaster (2008), Vatankhah and Talebi (2009), Brien et al. (2010), Hatcher et al. (2010), Barazandeh et al. (2012), Vatankhah (2013) and Getachew et al. (2015) reported estimates of heritability for survival traits from birth to different ages using different linear animal models were low in USA sheep breeds (0.036–0.052), Lori-Bakhtiar sheep (0.00 to 0.13), Sheep CRC’s Information Nucleus (0.010–0.012), Australian Merino sheep (0.02–0.07), Kerman sheep (0.04–0.09), Lori-Bakhtiar sheep (0.00 to 0.09) and Menz sheep (0.02 to 0.10), respectively.

Consistent with the results of this study, Vatankhah (2013) reported low estimates of maternal heritabilities for longevity (0.00 to 0.04) and survival rate (0.00 to 0.03) from birth to yearling.

Table 1. Estimates of genetic parameters for longevity from birth up to yearling obtained from different linear models.

| Model | h² | L1 | L2 | L3 | L4 |
|-------|----|----|----|----|----|
| Model 1 | h² | 0.001 ± 0.001 | 0.002 ± 0.002 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 2 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 3 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 4 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 5 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 6 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |

Notes: h²: Direct heritability; h²m: Maternal heritability; C²m: Ratio of maternal permanent environmental variance to phenotypic variance; r(a,m): Correlation between direct and maternal genetic effects; AIC: Akaike’s Information Criterion; The best models indicated with bold-faced AIC values. S1: Longevity from birth up to 3-month of age; S2: Longevity from birth up to 6-month of age; S3: Longevity from birth up to 9-month of age; S4: Longevity from birth up to yearling.

Table 2. Estimates of genetic parameters for survival from birth up to yearling obtained from different linear models.

| Model | S1 | S2 | S3 | S4 |
|-------|----|----|----|----|
| Model 1 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 2 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 3 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 4 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 5 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
| Model 6 | h² | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 | 0.0001 ± 0.000 |
| AIC   | -12464.90 | -8644.42 | -7045.07 | -6968.88 |
different age periods in Lori-Bakhtiari sheep. Generally, estimates of direct heritability for longevity traits were greater than maternal ones. Similarly, ratios of maternal permanent environmental variance to phenotypic variance for longevity and survival traits were estimated to be from 0.00 to 0.03 and 0.01 to 0.02 in Lori-Bakhtiari sheep, respectively (Vatankhah 2013).

The negative correlations between direct and maternal effects proposes that selection for animals with greater survival to specific age has subordinate genes for the survival of their own offspring when they become mothers (Everett-Hincks et al. 2005). Estimates of heritability for a discrete character such as survival trait, when analysed with a linear model, rely on the trait frequency (Gianola 1982). Therefore, contrasting the estimates from various breeds or populations would not be straightforward (Ghavi Hossein-Zadeh 2014). Also, it was reported that conducting linear analysis approach for a binary discrete trait would result in biased estimates of genetic parameters because of various degrees of censoring within the explanatory variable levels (Southey et al. 2004). In general agreement with this statement, one simulation study indicated that the linear model analysis of binary data for a given trait has always underestimated true heritabilities (Ghavi Hossein-Zadeh et al. 2006, 2014). Therefore, the methodology used for genetic evaluation of categorical characters is different from that of continuous ones and a threshold model would be a more appropriate model for genetic analysis of categorical traits because it considers the categorical nature of these characters (Ghavi Hossein-Zadeh 2011).

There were generally low reports of threshold estimates of heritability for survival traits in the literature but the results of previous studies showed that direct heritability estimates for lamb survival obtained from a threshold animal model were 0.01 in Romney sheep (Lopez-Villalobos and Garrick 1999) and 0.14 in Coopworth sheep (Everett-Hincks et al. 2005). Sire variance estimates for survival traits from birth to yearling obtained in the current study were generally consistent with previous studies (Southey et al. 2001, 2003, 2004; Casellas et al. 2007; Sawalha et al. 2007; Vatankhah 2013). In general agreement with the results of this study, Southey et al. (2001), Barazandeh et al. (2012) and Vatankhah (2013) reported heritability estimates in logarithmic scale for survival traits were in the range from 0.12 to 0.21, 0.23 to 0.36 and 0.17–0.25 in terminal sire composite population of sheep, Kermani lambs and Lori-Bakhtiari sheep, respectively. Also, Sawalha et al. (2007) reported heritability estimates of survival rate from birth to yearling age obtained by the Weibull sire model were in the range of 0.18 to 0.33 in Scottish Blackface lambs. It should be noted that in sire models, only relationships among sires are considered, whereas in animal models, all relationships are considered. This provides some bias in estimates obtained from sire models. Therefore, if the intensity of selection is greater for males than for females, estimates from sire variances are expected to underestimate genetic variance (Ghavi Hossein-Zadeh 2011).

The perspectives for genetic improvement of survival rate within a breed of sheep would mostly be low to medium due to the low heritability estimates (both direct and maternal) for this trait (Safari et al. 2005; Brien et al. 2010; Matheson et al. 2012). But genetic progress is not exclusively depending on the estimate of heritability for a specific, and also reliant on generation interval, intensity of selection, and the genetic variance for a trait (Brien et al. 2010). Genetic progress for survival trait in sheep would be improved by possible methods, including the implementation of indirect selection through direct selection for more heritable trait which have high genetic correlation with survival traits, progeny testing of sires, selection on the basis of the total weaning weight of lambs and application of other relatives information in genetic evaluations (Snowder and Fogarty 2009; Brien et al. 2010). In addition, Hatcher et al. (2010) suggested that genetic gains would be possible for lamb survival through using repeated measurements. Also, Cloete et al. (2009) reported 0.5% realized genetic gain per year for lamb survival by implementing selection on the multiple-rearing ability of ewes. Low heritability estimates for longevity and survival traits would be assigned to small additive genetic variance for these traits and the influence of non-genetic effects on them (Pryce and Veerkamp 2001; Ghaderi-Zefreh et al. 2017). Also, low heritability estimates for traits in this study implied that improvement of longevity and survival traits could be attained by direct selection for one or more traits which have positive correlation with under study traits (Khan et al. 2017). The results of a previous study (Riggio et al. 2008) indicated that low heritability estimates for survival traits could be due to the composite nature of these traits with many variables causing death. Other possible reasons for this low heritability are the difficulties in careful registration of data and considering all the relevant variables (Miglior 1999; Ghavi Hossein-Zadeh 2014). Medium to high heritability estimates, employing proportional hazard models through Weibull function, imply that the survival rate could be improved through direct selection within the flock. The heritability estimates for survival traits showed that estimates obtained from sire model using the Weibull proportional hazard function were generally greater than those obtained using linear and threshold animal models. Previous studies stated that conducting survival analysis with proportional hazard models using Weibull function is helpful for non-normally distributed survival data.

### Table 3. Estimates of genetic parameters for survival traits obtained from threshold models.

| Trait | Additive variance | Residual variance | Heritability |
|-------|------------------|------------------|-------------|
| S1    | 0.00131          | 1                | 0.0013      |
| S2    | 0.0032           | 1                | 0.0031      |
| S3    | 0.169            | 1                | 0.145       |
| S4    | 0.173            | 1                | 0.147       |

Note: S1: Survival from birth up to 3-month of age; S2: Survival from birth up to 6-month of age; S3: Survival from birth up to 9-month of age; S4: Survival from birth up to yealing.

### Table 4. Estimates of genetic parameters for survival traits obtained from sire model using the Weibull proportional hazard function.

| Trait | $\sigma_s^2$ | $h_{\text{eff}}^2$ | $h_{\text{eff}}^2$ |
|-------|-------------|-------------------|-------------------|
| S1    | 0.167       | 0.57              | 0.37              |
| S2    | 0.165       | 0.40              | 0.28              |
| S3    | 0.02        | 0.08              | 0.05              |
| S4    | 0.0067      | 0.03              | 0.02              |

Note: $\sigma_s^2$: Sire additive genetic variance; $h_{\text{eff}}^2$: heritability on the logarithmic scale; $h_{\text{eff}}^2$: Effective heritability; S1: Survival from birth up to 3-month of age; S2: Survival from birth up to 6-month of age; S3: Survival from birth up to 9-month of age; S4: Survival from birth up to yealing.
data because this method of analysis apply all the censored records to consider the lower bound of survival at a specified censoring time (Allison 1995; Klein and Moeschberger 1997; Vatankhah 2013). Therefore, including censored records in a survival analysis is superior to evaluations that keep out these types of records (Klein and Moeschberger 1997; Borg 2007). But selective censoring possibly inserts bias into the evaluations. In lamb survival data, selective censoring takes place when breeders preferentially cull small and poor doing lambs and less vigorous lambs from large litters in the flock (Borg 2007).

5. Conclusion

The results of this study indicated that heritability estimates for survival traits obtained from sire model using the Weibull proportional hazard function were generally greater than those estimated using the Weibull proportional hazards model and a linear model for predicting the genetic merit of US Jersey sires for daughter longevity. J Dairy Sci. 87:1469–1476.

In lamb survival data, selective censoring takes place when breeders preferentially cull small and poor doing lambs and less vigorous lambs from large litters in the flock (Borg 2007).

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References

Abdelqader A, Idrish R, Tabbaj MA, Abujaamieh M, Titi H, Al-Fatafah AR. 2017. Factors influencing Awassi lambs survivorship under fields conditions. Livest Sci. 199:1–6.

Akaike H. 1973. Information theory and an extension of the maximum like-lihood principle. Proceedings of the 2nd International Symposium on Information Theory, Sep 2–8, Budapest, Hungary, pp. 267–281.

Aktas AH, Dursun Ş, Dogan Ş, Kiyrm Z, Demirci U, Halici I. 2015. Effects of ewe live weight and age on reproductive performance, lamb growth, and survival in central anatolian merino sheep. Arch Anim Breed. 58:451–459.

Allison PD. 1995. Survival analysis using the SAS system: A practical guide. Cary, NC: SAS Institute Inc.

Bahri Binabaj F. 2014. Genetic study of survival criteria at different ages and their relationship with reproductive traits in Karakul and Baluchi sheep [MSc thesis]. Ferdowsi University of Mashhad, Iran.

Barazande A, Molaei Moghbeli S, Vatankhah M, Ghavi Hossein-Zadeh N. 2012. Lamb survival analysis from birth to weaning in Iranian kermani sheep. Trop Anim Health Prod. 44:929–934.

Borg RC. 2007. Phenotypic and genetic evaluation of fitness characteristics in sheep under a range environment [Ph.D dissertation]. Blacksburg: Virginia Polytechnic Institute and State University.

Brien FD, Hebart ML, Smith DH, Hocking Edwards JE, Greeff JC, Hart KW, Refshauge G, Bird-Gardiner TL, Gaunt G, Behrendt R, et al. 2010. Opportunities for genetic improvement of lamb survival. Anim Prod Sci. 50:1017–1025.

Caravelli DZ, Weigel KA, Gianola D. 2004. Comparison between a Weibull proportional hazards model and a linear model for predicting the genetic merit of US Jersey sires for daughter longevity. J Dairy Sci. 87:1469–1476.

Casellas J, Caja G, Such X, Piedrafita J. 2007. Survival analysis from birth to slaughter of Ripollesa lambs under semi-intensive management. J Anim Sci. 85:S12–S17.

Christley RM, Morgan KL, Parkin TDH, Frnc NP. 2003. Factors related to the risk of neonatal mortality, birth-weight and serum immunoglobulin concentration in lambs in the UK. Prev Vet Med. 57:209–226.

Cloete SWP, Misztal I, Olivier JJ. 2009. Genetic parameters and trends for lamb survival and birth weight in a merino flock divergently selected for multiple rearing ability. J Anim Sci. 87:2196–2208.

Coningen J, Bishop SC, Grundy B, Waterhouse A, Simm G. 2001. Multitrait selection indexes for sustainable UK hill sheep. Anim Sci. 73:413–423.

Ducrocq V, Casella G. 1996. A Bayesian analysis of mixed survival models. Genet Sel Evol. 28:505–529.

El-Sayed UM, De La Fuente LF, Carriedo JA, San Primitivo F. 2005. Genetic and phenotypic parameter estimates of total and partial lifetime traits for dairy ewes. J Dairy Sci. 88:3265–3272.

Everett-Hincks JM, Lopez-Villalobos N, Blair HT, Stafford KJ. 2005. The effect of ewe maternal behavior score on lamb and litter survival. Livest Prod Sci. 93:51–61.

Getachew T, Gizaw S, Wurzinger M, Haile A, Rischkowsky B, Okeyo AM, Sölkner J, Mézàros G. 2015. Survival analysis of genetic and non-genetic factors influencing ewe longevity and lamb survival of Ethiopian sheep breeds. Livest Sci. 176:22–32.

Ghaderi-Zefrehemi M, Rabbanikhah E, Baneh H, Peters SO, Imumorin IG. 2017. Factors influencing Awassi lambs survivorship under field conditions.Livest Sci. 199:1–6.

Hatcher S, Atkins KD, Safari E. 2010. Lamb survival in Australian merino sheep: A genetic analysis. J Anim Sci. 88:3198–3205.

Hatcher S, Atkins KD, Safari E. 2010. Lamb survival in Australian merino sheep: A genetic analysis. J Anim Sci. 88:3198–3205.

Hinch GN, Brien FD. 2014. Lamb survival in Australian flocks: A review. Anim Prod Sci. 54(6):656–666.

Khan PK, Blair HT, Lopez-Villalobos N. 2017. Modelling genetic improvement of pabna cattle in Bangladesh. J Appl Anim Res. 45(1):524–528.

Ghavi Hossein-Zadeh N. 2011. Estimation of genetic parameters and genetic change for stillbirth in Iranian Holstein cows: a comparison between linear and threshold models. Agric Food Sci. 20:287–297.

Ghavi Hossein-Zadeh N. 2014. Linear and threshold analysis of direct and maternal genetic effects for secondary sex ratio in Iranian buffaloes. J Appl Genet. 55:365–372.

Ghavi Hossein-Zadeh N, Ardalan M. 2010. Estimation of genetic parameters for body weight traits and litter size of Moghani sheep, using a Bayesian approach via Gibbs sampling. J Agr Sci. 148:363–370.

Ghavi Hossein-Zadeh N, Nejati-Javaremi A, Miraei-Ashtiani SR, Mehrabani-Yeganeh H. 2006. Effect of threshold nature of traits on heritability esti-mates obtained by linear model. 8th WCALGP, Aug 13–18, Belo Horizonte, MG, Brasil.

Gianola D. 1982. Theory and analysis of threshold characters. J Anim Sci. 54:1079–1096.

Hatcher S, Atkins KD, Safari E. 2010. Lamb survival in Australian merino sheep: A genetic analysis. J Anim Sci. 88:3198–3205.

Hinch GN, Brien FD. 2014. Lamb survival in Australian flocks: A review. Anim Prod Sci. 54(6):656–666.

Khan MKI, Blair HT, Lopez-Villalobos N. 2017. Modelling genetic improvement of pabna cattle in Bangladesh. J Appl Anim Res. 45(1):239–246.

Klein JP, Moeschberger ML. 1997. Survival analysis: techniques for censored and truncated data. New York: Springer-Verlag.

Klein JP, Moeschberger ML. 1997. Survival analysis: techniques for censored and truncated data. New York: Springer-Verlag.

Lopez-Villalobos N, Garrick DJ. 1999. Genetic parameter estimates for lamb survival in Romney sheep. Proc New Zeal Soc Anim Prod. 59:121–126.

Matheson SM, Bünker L, Dwyer CM. 2012. Genetic parameters for fitness and neonatal behaviour traits in sheep. Behav Genet. 42:899–911.

Mekkawy W, Roehe R, Lewis RM, Davies MH, Bünger L, Simm G, Haresign W. 2015. Survival analysis of genetic and non-genetic factors influencing ewe longevity and lamb survival of Iranian Holstein dairy cattle. J Appl Anim Res. 45(1):524–528.

Mekkawy W, Roehe R, Lewis RM, Davies MH, Bünger L, Simm G, Haresign W. 2015. Survival analysis of genetic and non-genetic factors influencing ewe longevity and lamb survival of Iranian Holstein dairy cattle. J Appl Anim Res. 45(1):524–528.

Meyers K. 2006. WOMBAT – A program for mixed model analyses by restricted maximum likelihood. Armidale, Australia: User notes. Animal Genetics and Breeding Unit, University of New England.
Miglior F. 1999. Selection for fertility traits. Proceedings of the 24th EHFC Meeting 110–114.

Moraes ABD, Poli Cesar HEC, Fischer V, Fajardo NM, Alfa MF, Porciuncula GCD. 2016. Ewe maternal behavior score to estimate lamb survival and performance during lactation. Acta Scient Anim Sci. 38(3):327–332.

Mukasa-Mugerwa E, Lahlou-Kassi A, Anindo D, Rege JEO, Tembely S, Tobbo M, Baker RL. 2000. Between and within breed variation in lamb survival and the risk factors associated with major causes of mortality in indigenous Horro and Menze sheep in Ethiopia. Small Rumin Res. 37:1–12.

Nadaf Fahmideh M, Ghavi Hossein-Zadeh N, Golshani M. 2017. Study of genetic relationship between longevity and body weights in guian province native sheep. Anim Sci J. (Pajouhesh & Sazandegi. 30(115):93–102. (In Persian with English abstract).

Pryce JE, Veerkamp RF. 2001. The incorporation of fertility indices in genetic improvement programmes. In: Diskin MG, editor. Fertility in the high-producing dairy cow. Galway, Ireland: British Society of Animal Science. Occasional Publication. 26:237–250.

Ramezani S, Ghavi Hossein-Zadeh N. 2017. Genetic and non-genetic factors affecting longevity of Mehraban sheep. Res Anim Prod. 8(17):157–165. (In Persian with English abstract).

Riggio V, Finocchiaro R, Bishop SC. 2008. Genetic parameters for early lamb survival and growth in scottish blackface sheep. J Anim Sci. 86:1758–1764.

Rogers PL, Gaskins CT, Johnson KA, MacNeil MD. 2004. Evaluating longevity of composite beef females using survival analysis techniques. J Anim Sci. 82:860–866.

Safari E, Fogarty NM, Gilmour AR. 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Livest Prod Sci. 92:271–289.

SAS. 2002. SAS user’s guide v. 9.1: statistics. Cary, NC: SAS Institute, Inc.

Sewalem A, Kistemaker GJ, Ducrocq V, Van Doormaal BJ. 2005. Genetic analysis of herd life in Canadian dairy cattle on a lactation basis using a Weibull proportional hazards model. J Dairy Sci. 88:368–375.

Slee J, Alexander G, Bradley LR, Jackson N, Stevens D. 1991. Genetic aspects of cold resistance and related characters in newborn merino lambs. Aust J Exp Agric. 31:175–182.

Southey BR, Rodriguez-Zas SL, Leymaster KA. 2003. Discrete time survival analysis of lamb mortality in a terminal sire composite population. J Anim Sci. 81:1399–1405.

Southey BR, Rodriguez-Zas SL, Leymaster KA. 2004. Competing risks analysis of lamb mortality in a terminal sire composite population. Anim Sci. 82:2892–2899.

Thomas DL. 2010. Performance and utilization of northern european short-tailed breeds of sheep and their crosses in North America: a review. Animal. 4:1283–1296.

Tibbo M. 2006. Productivity and health of indigenous sheep breeds and crossesbreds in the central Ethiopian highlands. Doctoral Thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Vukasinovic N, Moll J, Casanova L. 2001. Implementation of a routine genetic evaluation for longevity based on survival analysis techniques in dairy cattle populations in Switzerland. J Dairy Sci. 84:2073–2080.

Wang T, Fernando RL, Kachman DS. 2001. MATVEC user’s guide. Lincoln: Department of Biometry, University of Nebraska.