Estimation of genetic parameters of reproductive traits in Zandi sheep using linear and threshold models

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ABSTRACT: Genetic parameters for reproductive traits in Zandi sheep were estimated from data records of 5025 lambs from 178 sires and 1967 dams collected between the years 1993 and 2010 using ASReml statistical package. Genetic parameters were estimated for four basic and two composite traits. Year of lambing and age of ewe were used as fixed effects. Due to repeated record of ewe animal direct genetic effects and permanent environmental effects were considered random. The heritability estimates for conception rate, number of lambs born, number of lambs born alive, number of lambs alive at weaning, number of lambs born per ewe exposed, and number of lambs weaned per ewe exposed were low with linear model – 0.05, 0.14, 0.12, 0.09, 0.05, and 0.04 respectively while the estimates resulting from threshold analysis were 0.11, 0.19, 0.14, 0.16, 0.12, and 0.11, respectively. Estimates of heritabilities for animal genetic and permanent environmental effects were low mainly due to the typical strong influence of environmental factors on reproductive traits. Estimates of repeatabilities for animal permanent environmental effects were low to medium by linear analysis, and medium by threshold analysis. These estimates of genetic parameters may provide a basis for deriving selection indexes for reproductive traits.

Keywords: reproductive traits; genetic parameters; linear model; threshold model; Zandi sheep

Two general classes of phenotypes are measured in animal breeding data: continuous and discrete. Many traits of importance, such as litter size, disease resistance, and livability are measured on a discrete scale that is categorical. Genetic evaluation for categorical traits is achieved through different methodology than evaluation of continuous traits (Abdel-Azim and Berger, 1999). In separate studies Gianola and Foulley (1983), Harville and Mee (1984), and Gilmour et al. (1985) have introduced threshold models (TM) for genetic evolution threshold traits. Threshold models methods are based on the assumption of an underlying unobservable continuous response variable that follows the assumptions of a mixed linear model (Gianola and Foulley, 1983; Harville and Mee, 1984). Categorical traits have generated extraordinary levels of interest in the field of animal breeding. The possible reasons are that many important economic traits such as reproductive traits or survival-related traits are categorical in nature, and some selection experiments in categorical were proven to have potential for genetic improvement.

Reproductive traits in sheep are the most important traits affecting profitability (Matos et al., 1997). These traits have categorical nature, but in practice the continuous distribution of traits is analyzed. In addition, to have true and accurate pedigree records, applying the appropriate model for analyzing the characteristics of high precision in the estimation of genetic parameters will be evaluated.

Vatankhah et al. (2008) reported the heritability of conception rate, number of lambs born, number of lambs at weaning, number of lambs born alive, number of lambs born per ewe joined and number of lambs weaning per ewe joined 0.01, 0.10, 0.08, 0.06, 0.05 and 0.03, respectively. Heritability of number of born lambs and number of weaned lambs in Turkish Sakiz sheep reported by Ceyhan et al. (2009) was 0.03 and 0.18. Also, Rashidi et al. (2011) reported the heritability of these traits in Moghani sheep 0.11 and 0.02, respectively. A number of researchers in separate studies (Matos, 1993; Rao, 1997; Brien et al., 2002; Casellas et al., 2007; Mekkawy et al., 2010) have compared estimates of genetic parameters in reproductive traits for different sheep breeds using real and simulated data. They have concluded that a threshold model with linear models estimating genetic parameters and genetic evaluation are preferred. Such estimates have been scarce for Iranian sheep breeds. Therefore, the main objective of this study was to obtain effects of genetic and non-genetic estimates of reproductive traits in Zandi sheep using repeatability linear and threshold models that are necessary to develop an efficient selection strategy for improvement of reproduction.

MATERIAL AND METHODS

Geographical location and flock management

Data were collected from the Zandi Sheep Breeding Station located in Khojir National Park between Tehran and Abali (1547 m above mean sea level and 35°45'E and 51°40'N with a moderate climate). The flock was established in 1991. The aim of the project was to establish a nucleus source to improve other flocks in the region. The starting animals were purchased from different sheep farms in the region. The flock is generally reared by following conventional industry practices. Controlled breeding is practiced. The mating season commences in August. Artificial insemination (AI) is run during the breeding season. Ewes on heat undergo AI with the restriction that mating between very closely related animals is avoided. The maximum number of ewes allocated to each AI ram is no more than 25 heads in each breeding year. Animals that do not conceive by AI are allocated to natural servicing. In this case, ewes are assigned to ram breeding groups with an average mating ratio of 10–15 ewes per ram. Lambings commence in January. At birth, each lamb is identified, and date of birth, sex, type of birth, and weight are recorded. Coat color is black in newborns but gradually changes with age in a way that adult animals are found in black, light brown, and gray. Weaning occurs on average 90 days after lambing. Ewes and weaned lambs are kept on natural pasture during the day and penned at night. Supplemental feeding comprising dried alfalfa and barely grain was offered during winter season and particularly prior to mating and at late pregnancy. Replacement males and females were selected mainly on their conformation and health, and also on milk yield of their dams.

Traits studied

The analyzed traits can be assigned in two main categories: basic and composite traits. Basic traits were conception rate (CR, with measure 1 or 0, meaning whether an ewe exposed to a ram lambed or not), number of lambs born (NLB, with measure 0, 1, or 2, which was the number of fully formed lambs born per ewe lambing), number of lambs born alive (NLBA, with measure 1 or 2, which was the number of lambs alive at 24 h of age), number of lambs alive at weaning (NLAW, with measure 1 or 2, which was the number of lambs alive

Table 1. Description of the data set used in the study

Trait	No. of records	No. of ewes	No. of ewes' sires	Mean	SE	CV (%)
CR	5025	1967	178	0.91	0.28	30.76
NLB	4464	1892	169	1.10	0.33	30.23
NLBA	4139	1708	147	1.07	0.35	32.59
NLAW	4139	1708	147	1.02	0.45	44.51
NLB/EE	5025	1967	178	1.01	0.51	50.94
NLW/EE	5025	1967	178	0.95	0.55	57.68

CR = conception rate, NLB = number of lambs born, NLBA = number of lambs born alive, NLAW = number of lambs alive at weaning, NLB/EE = number of lambs born per ewe exposed, NLW/EE = number of lambs weaned per ewe exposed at weaning). Conception rate is a binary random variable and all other traits have discrete numerical observation. The composite traits with discrete numerical observation were number of lambs born per ewe exposed (NLB/EE = CR × NLB) and number of lambs weaned per ewe exposed (NLW/EE = CR × NLAW). A summary of data structure and descriptive statistics of the considered traits are presented in Table 1.

Statistical analysis

Preliminary least squares analyses were performed for the traits applying the general linear model (GLM) procedure of SAS software package (SAS Institute, 2004) to determine fixed effects which should be included in the final models. The fixed effects included in the final statistical model were lambing year with 18 classes (1993–2010) and age of the ewe at lambing with 7 classes (2–8 years old). The interaction between lambing year and age of the ewe at lambing was not significant; therefore it was not included in the final model.

The variance components for the investigated traits were analysed with univariate repeatability linear model (e.g. Rosati et al., 2002; Afolayan et al., 2008; Vatankhah et al., 2008; Ceyhan et al., 2009; Rashidi et al., 2011) and univariate repeatability threshold model (e.g. Mekkawy et al., 2010) using the ASReml statistical package (Gilmour et al., 2006) fitting a repeatability model as follows:

$$y = \mathbf{X}b + \mathbf{Z}a + \mathbf{W}pe + e$$

where:

y = vector of observation
b = vector of fixed effects
a = vector of direct additive genetic effects
pe = vector of permanent environmental effects related to repeated records of ewes
e = vector of residual effects
$\mathbf{X}, \mathbf{Z}, \mathbf{W}$ = design matrices associating the corresponding effects with vector y

The (co)variance structure for the random effects was:

$$\mathrm{Var}\begin{bmatrix} \boldsymbol{a} \\ \boldsymbol{pe} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 \\ 0 & \mathbf{I_d}\sigma_{pe}^2 & 0 \\ 0 & 0 & \mathbf{I_n}\sigma_e^2 \end{bmatrix}$$

where:

$\boldsymbol{a}$ = direct additive genetic effects
$\boldsymbol{pe}$ = permanent environmental effects related to repeated records of ewes
$\boldsymbol{e}$ = residual effects (all effects assumed to be normally distributed with mean of zero and variances $\mathbf{A}\sigma_a^2$, $\mathbf{I_d}\sigma_{pe}^2$, and $\mathbf{I_n}\sigma_e^2$, respectively)
σ_a^2 = direct additive genetic variance
σ_{pe}^2 = permanent environmental variance related to repeated records of ewes
σ_e^2 = residual variance
$\mathbf{A}$ = additive numerator relationship matrix
$\mathbf{I_d}$, $\mathbf{I_n}$ = identity matrices with order equal to the number of ewes and records respectively

Also, repeatability was calculated using the following formula:

$$r = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_p^2}$$

where:

σ_a^2 = direct additive genetic variance
σ_{pe}^2 = permanent environmental variance related to repeated records of ewes
σ_p^2 = phenotypic variance

RESULTS AND DISCUSSION

Coefficient of variation for a particular trait is a criterion to determine the trait variation. Coefficient of variation for the studied traits ranged from 30.23% for number of lambs born to 57.68% for number of lambs weaned per ewe exposed. Matika et al. (2003) reported coefficients of determination in Sabi sheep for conception rate, number of lambs born, number of lambs at weaning, number of lambs born per ewe exposed, and number of lambs weaned per ewe exposed 35.9, 30.5, 48.9, 47.8, and 62.9%, respectively.

Effects of age of ewe at lambing and lambing year were statistically significant ($P < 0.01$) for all studied traits. Significant influence of lambing year on reproductive traits in the present study can be explained by variation in climatic conditions. Significant effect of lambing year on reproductive traits in different sheep breeds has been reported by several authors (Ekiz et al., 2005; Vatankhah et al., 2008; Ceyhan et al., 2009; Mokhtari et al., 2010). There was a general tendency for the improvement of traits with the increasing age of the ewe at lambing. Differences in maternal effects, nursing, and maternal behavior of ewe at different ages are reasons for the significant effects of age of the ewe at lambing. Significant effects of age of ewe at lambing on reproductive traits of sheep have been reported by Rosati et al. (2002), Ekiz et al. (2005), Afolayan et al. (2008), and Rashidi et al. (2011).

Estimates of variance components, heritability, permanent environmental variance to phenotypic variance, and repeatability for the studied traits with linear analysis are presented in Table 2. Heritability estimate for conception rate was 0.05 ± 0.02 in this study. The estimate of heritability for this trait in Dorset, Rambouillet, Finnsheep, Suffolk, and Targhee breeds and their composite lines was 0.06 (Rosati et al., 2002), which is consistent with the result of our study. Low estimate of heritability for conception rate can be due to the impact of environmental factors on the variability of this trait and it was attributed to discontinuance (Rosati et al., 2002). Also, Vatankhah et al. (2008) reported even lower heritability for this trait in Lori-Bakhtiari sheep (0.01 ± 0.01).

Estimates of heritability for number of lambs born and number of lambs born alive were 0.14 ± 0.02 and 0.12 ± 0.02, respectively. Estimates of direct heritability for number of lambs born are in general agreement with those reported by Rao and Notter (2000), Safari et al. (2005), Hanford et al. (2006), and Vatankhah et al. (2008), though lower (0.10, 0.05, 0.05, 0.06, 0.01, 0.11) estimates have been reported by Rosati et al. (2002), van Wyk et al. (2003), Ekiz et al. (2005), Maxa et al. (2007), Mokhtari et al. (2010), and Rashidi et al. (2011), respectively. Heritability for number of lambs born alive in Sabi sheep and Lori-Bakhtiari sheep reported by Matika et al. (2003) and Vatankhah et al. (2008) was 0.04 and 0.08, respectively.

Heritability estimate for number of lambs born per ewe exposed was 0.05 ± 0.02, i.e. lower than for number of lambs born, but it was in agreement with weighted mean reported for this trait (Fogarty, 1995; Safari et al., 2005). Rosati et al. (2002) reported the value of 0.09 for heritability of number of lambs born per ewe exposed in four sheep of the breed. Also, Matika et al. (2003) reported 0.02 for heritability of this trait in Sabi sheep.

The heritability estimates for number of lambs alive at weaning (0.09 ± 0.02) and number of lambs weaned per ewe exposed (0.04 ± 0.02) were higher than weighted mean of those in literature (Fogarty, 1995; Safari et al., 2005). Vatankhah et al. (2008)

Table 2. Estimates of variance components, genetic and phenotypic parameters for reproductive traits of Zandi ewes with linear and threshold analysis

Trait	σ_a^2	σ_{pe}^2	σ_e^2	σ_p^2	h_d^2 ± SE	p_e^2 ± SE	r
Linear analysis							
CR	0.0030	0.0050	0.078	0.078	0.05 ± 0.02	0.06 ± 0.02	0.10
NLB	0.0240	0.0210	0.174	0.174	0.14 ± 0.02	0.12 ± 0.02	0.25
NLBA	0.0165	0.0089	0.138	0.138	0.12 ± 0.02	0.06 ± 0.02	0.19
NLAW	0.0148	0.0030	0.160	0.160	0.09 ± 0.02	0.02 ± 0.02	0.11
NLB/EE	0.0140	0.0330	0.287	0.287	0.05 ± 0.02	0.12 ± 0.02	0.17
NLW/EE	0.0110	0.0260	0.245	0.283	0.04 ± 0.02	0.09 ± 0.02	0.13
Threshold analysis							
CR	0.0075	0.0161	0.040	0.0636	0.11 ± 0.01	0.25 ± 0.02	0.37
NLB	0.0330	0.0370	0.099	0.169	0.19 ± 0.01	0.21 ± 0.03	0.41
NLBA	0.0185	0.0102	0.097	0.126	0.14 ± 0.01	0.08 ± 0.01	0.22
NLAW	0.0169	0.0104	0.078	0.105	0.16 ± 0.01	0.09 ± 0.04	0.26
NLB/EE	0.0291	0.0487	0.164	0.241	0.12 ± 0.01	0.20 ± 0.03	0.32
NLW/EE	0.0180	0.0256	0.108	0.151	0.11 ± 0.01	0.16 ± 0.02	0.28

σ_a^2 = direct genetic variance, σ_{pe}^2 = permanent environmental variance, σ_e^2 = residual variance, σ_p^2 = phenotypic variance, h_d^2 = direct heritability, p_e^2 = ratio of permanent environmental variance on phenotypic variance, r = repeatability, SE = standard error
CR = conception rate, NLB = number of lambs born, NLBA = number of lambs born alive, NLAW = number of lambs alive at weaning, NLB/EE = number of lambs born per ewe exposed, NLW/EE = number of lambs weaned per ewe exposed

reported heritability of number of lambs weaned alive and number of lambs weaning per ewe joined in the order 0.06 ± 0.02 and 0.03 ± 0.02. Rosati el al. (2002) estimated heritability of these traits at 0.01 and 0.07, respectively.

Coefficient of repeatability ranged from 0.10 to 0.25, what is in agreement with results by Matika et al. (2003), Vanimisetti et al. (2007), Afolayan et al. (2008), and Mokhtari et al. (2010). The estimates show that the correlation between various records produced for reproductive traits obtained from the linear analysis is low, so that to increase production during the lifetime of the ewes, decision about culling on one record of reproductive traits attends with low accuracy.

Estimation of repeatability for reproductive traits with threshold analysis is shown in Table 2. Variance components estimated using threshold analyses were quite different from the linear analysis. Estimates of direct genetic variance and permanent environmental variance in the threshold analysis were higher than those for all traits in the linear analysis, but estimates for residual variance were lower in the linear threshold analysis than the corresponding values in the linear analysis.

The phenotypic variance estimate for all traits in threshold analysis was lower than corresponding values in linear analysis. The results of this study for different components of variance estimated by linear and threshold analysis have also been reported by other researchers (Brien et al., 2002; Poortahmasb et al., 2007). It is as though these traits have a set of polynomial distribution and variances are dependent on the means, because in this type of distribution, the variance depends on the frequency of observations in each of the categories (Quass et al., 1988; Berger, 1994).

The heritability and repeatability estimates for conception rate with threshold analysis were 0.11 and 0.37 respectively, i.e. the values were higher than the corresponding values in linear analysis. Coefficient of heritability of this trait in Rambouillet and Finnsheep breeds was 0.10 and 0.17, respectively (Matos et al., 1997). Also, Poortahmasb et al. (2007) in agreement with results of this study reported that heritability and repeatability of conception rate with threshold analysis in Lori-Bakhtiari sheep were 0.08 and 0.67 respectively. Heritability estimates for number of lambs born (0.19), number of lambs born alive (0.14), and number of lambs born per ewe exposed (0.12) were higher than corresponding values in linear analysis.

The heritability estimates in number of lambs born in Rambouillet and Finnsheep breeds were 0.25 and 0.13, respectively, i.e. higher than results of this study (Matos et al., 1997). Also, Matos et al. (1997) reported that the heritability estimate for number of lambs born in Finnsheep breed ranged from 0.26 to 0.76 with threshold analysis. In other study, the heritability estimates for number of lambs born alive and number of lambs born per ewe exposed in Lori-Bakhtiari sheep with threshold analysis were 0.10 and 0.08, respectively (Poortahmasb et al., 2007).

Heritability estimates for number of lambs alive at weaning (0.16) and number of lambs weaned per ewe exposed (0.11) were higher than corresponding values in linear analysis. Poortahmasb et al. (2007) showed that the heritability estimate for number of lambs weaned per ewe exposed was 0.10 with threshold analysis. This showed that the pattern changes in the process of changing the model used for analysis are similar to the results of this study.

Brien et al. (2002) used linear and threshold models to predict direct and maternal genetic effects on number of lambs alive at weaning in Australian West Merino sheep. The estimated heritability of this trait with linear and threshold analysis was 0.08 and 0.12, respectively. From this it implies that the univariate threshold animal model was better for genetic evaluation of reproductive traits than the univariate linear animal model. The superiority theory that univariate threshold models are better for estimating genetic parameters and breeding value predicts than the univariate linear models is in agreement with the results of this study (Schaeffer, 2004).

Heritabilities for number of lambs born in Mule sheep estimated by linear and threshold analyses of the real and simulated data were 0.08 and 0.12–0.18 (Mekkawy et al., 2010). Casellas et al. (2007) reported that heritability of number of lambs born in Ripollesa sheep estimated by linear and threshold analysis was 0.03 and 0.13, what is in agreement with the results of this study.

Estimates of coefficient of repeatability for reproductive traits with threshold analysis ranged from 0.22 to 0.44. These estimates show that, contrary to estimates from the linear analysis, correlation between various records for reproductive traits is medium to high, so that the decision about culling ewe according to one record from the ewe reproductive traits has to be careful enough. Estimates of direct genetic variance were higher with the threshold analysis for all traits than values estimated using a linear analysis. Also, values of residual variance were lower for all traits with the threshold analysis than values estimated using a linear analysis. The results of this study showed a threshold model with a higher power for expressing the variance and for accuracy of predictions than the linear model. Especially when coefficients of heritability traits are low, threshold model has more advantages (Janssens et al., 2004).

CONCLUSION

The results of the present study have shown that although heritability of reproductive traits with linear and threshold analysis was low, and response to selection for these traits slow, usage of the threshold analysis rather than the linear analysis would increase accuracy and eventually would speed up the response to selection. Also considering the precision of this genetic trait, a trait that is a function of the heritability coefficient, it seems that the estimates of genetic parameters from threshold analysis better correspond to the values obtained from the linear model, because they have higher heritability.

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