



IJABBR- 2014- eISSN: 2322-4827

International Journal of Advanced Biological and Biomedical Research

Journal homepage: www.ijabbr.com



Original Article

Estimation of Genetic Parameters for Kleiber Ratio and Trends for Weight at Birth and Weaning in Arabi Sheep

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ARTICLE INFO

Article history:

Received: 09 Sep, 2014

Revised: 20 Sep, 2014

Accepted: 18 Oct, 2014

ePublished: 30 Nov, 2014

Key words:

Kleiber ratio

Direct heritability

Direct genetic trend

Arabi sheep

ABSTRACT

Objective: Estimation of genetic parameters for Kleiber ratio (KR) and genetic trends for pre-weaning weights of Arabi sheep has not been previously conducted. **Methods:** Data and pedigree information were collected at the Khuzestan Ramin Agricultural and Natural Resources University, Animal Science Research Station, located in southwest Iran, from 2001 to 2008. (Co)variance components and corresponding genetic parameters were estimated using the restricted maximum likelihood procedure by excluding or including maternal genetic or maternal permanent environmental effects. Six animal models were fitted to optimise the model KR from birth to weaning, which is defined as the ratio of growth rate and metabolic rate and can be utilized as an indirect selection for feed conversion. Moreover, three-trait analyses were performed using the most appropriate models obtained in single-trait analyses on the basis of Akaike's information criterion. **Results:** Direct heritability (h^2_d) estimate of 0.11 was obtained and maternal permanent environmental effects (pe^2) contributed 10% of the total phenotypic variation for KR. Genetic trends for weight at birth and weaning were obtained by regression of average breeding values, on birth year. Direct genetic trends were positive and significant ($p < 0.05$) for weight at birth and weaning (6 and 24 g per year, respectively). Genetic correlations among traits ranged from -0.52 to 0.89 and phenotypic correlations from -0.21 to 0.71. **Conclusions:** Results showed the importance of inclusion of maternal permanent environmental effects in designing appropriate breeding programs to obtain accurate estimates of genetic parameters, and it is sounded that KR is a recommended option in selection program.

1.INTRODUCTION

Sheep population in Iran is composed of 27 breeds and their crosses, with more than 50 million heads (Vatankhah et al., 2004). In Iran, native forages are the main source of feed in sheep production. Arabi sheep is one of the most important dual-purpose (meat and wool) native sheep breeds of Iran. Most of these sheep are raised in Khuzestan province (more than 1.8 million animals), and are well adapted to humid-tropical

environmental conditions (Shokrollahi and Baneh, 2012). Arabi sheep breed is characterised as white, cream, black and dark/bright brown colour, horned rams and polled ewes, fat-tailed, and medium-sized (ewe and ram adult weight are approximately 48 and 63 kg, respectively). Accurate prediction of breeding value of animals is one of the best tools available to maximise response to selection programme. Success of a breeding programme can be assessed by actual change in breeding value, expressed as the proportion of expected theoretical change of the

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breeding value mean for the trait under selection (Jurado et al., 1994). Estimation of genetic trend is important to assess the efficiency of applied breeding schemes and to provide breeders with information to develop more efficient selection programmes. In any selection programme aimed to increase growth performance, improving the efficiency of feed conversion is necessary in order to achieve maximum output. An indirect criterion to evaluate feed conversion is applying the Kleiber ratio (KR), which is defined as growth rate/body weight^{0.75} (Kleiber, 1947; Scholtz et al., 1990), since a great correlation between KR and feed efficiency is observed (Scholtz and Roux, 1988). In fact, animals with greater KR require less maintenance energy.

There is no published research regarding estimates of phenotype and genetic parameters for KR and genetic trends of weight at birth and weaning in Arabi sheep. Thus, our objective was to estimate these parameters. Furthermore, the correlations among traits were estimated to improve the efficiency of genetic selection.

2. MATERIALS AND METHODS

2.1. Data and management

Data and pedigree information were collected at the Khuzestan Ramin Agricultural and Natural Resources University, Animal Science Research Station, located in Khuzestan province, southwest Iran, from 2001 to 2008. Analysed traits were KR from birth to weaning, weight at birth and weaning. Animals were raised on pasture during the spring and summer seasons, and had access to farm residual feeds during autumn, and housed at night. Maiden ewes were exposed to rams at approximately 1.5 years of age and kept in the flock until death or apparent infertility. Breeding season started early August and ended early October. The corresponding lambing season was from early January to early February. Lambs were weighed, ear-tagged and their parents identified within 24 h of birth. Birth date, sex and type of birth were also recorded. After lambing, lambs were kept with their dams for 2 weeks. During this time, lambs were kept indoors and allowed to be nursed twice a day. Lambs were weaned at an average age of 4 months. The data structure and descriptive statistics are summarised in Table 1.

2.2. Statistical analyses

Initially, least square means were performed using the GLM procedure of SAS (SAS Institute Inc., Cary, NC, USA) to identify fixed effects to be included in the model. A linear model was used to identify fixed effects on variation of KR:

$$Y_{ijklmn} = \mu + Y_i + A_j + S_k + T_l + e_{ijklmn}$$

Where y is records of traits, μ = mean, Y_i = effect of birth year ($i = 8$; 2001-2008), A_j = effect of age of dam at lambing ($j = 6$; 2- to 7-year olds), S_k = effect of lamb's sex ($k = 2$; male and female), T_l = effect of birth type ($l = 2$; single and twin) and e_{ijklmn} is residual effects. Least squares means and standard error for KR are depicted in Table 2.

Six different animal models were fitted to estimate (co)variance components and corresponding genetic parameters by using the Wombat (Meyer, 2007) software. Additive direct effects were included in Model 1, whereas maternal permanent environmental effects were included in Model 2, which is fitted as additional random effect, un-correlated with all other effects in the model. Model 3 had additive maternal effects included, which is fitted as the second random effect. Model 4 was the same as Model 3, but it was allowed for a direct-maternal genetic covariance [$Cov(a, m)$]. Model 5 and Model 6 had maternal genetic and maternal permanent environmental effects included, ignoring and including direct-maternal genetic covariance, respectively. The models are as follows:

$$y = Xb + Z_1a + e \quad \text{Model 1}$$

$$y = Xb + Z_1a + Z_3pe + e \quad \text{Model 2}$$

$$y = Xb + Z_1a + Z_2m + e \quad \text{Cov}(a, m) = 0 \quad \text{Model 3}$$

$$y = Xb + Z_1a + Z_2m + e \quad \text{Cov}(a, m) = A\sigma_{am} \quad \text{Model 4}$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + e \quad \text{Cov}(a, m) = 0 \quad \text{Model 5}$$

$$y = Xb + Z_1a + Z_2m + Z_3pe + e \quad \text{Cov}(a, m) = A\sigma_{am} \quad \text{Model 6}$$

Where y , b , a , m , pe , and e are vectors of observations, fixed effects, direct genetic effects, maternal genetic effects, maternal permanent environmental effects, and residual effects, respectively. X , Z_a , Z_m , and Z_{pe} are the incidence matrices regarding observations to the respective fixed and random effects. It was assumed that:

$$E(y) = x\beta, \quad E \begin{bmatrix} a \\ m \\ pe \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix},$$

$$\text{Var} \begin{bmatrix} a \\ m \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_d\sigma_{pe}^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

Where β is the vector of fixed effects, A is the additive numerator relationship matrix, σ^2_a is the direct genetic variance, σ^2_m is the maternal genetic variance, σ_{am} is the direct-maternal genetic covariance, σ^2_{pe} is the maternal permanent environmental variance, σ^2_e is the residual variance, and I_d and I_n are identity matrices with orders equal to number of dams and records, respectively. In order to determine the most apposite model, Akaike's information criterion (AIC) was used (Akaike, 1974):

$$AIC_i = -2 \log L_i + 2p_i$$

Where $\log L_i$ is the maximised 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 was chosen as the most suitable model. Genetic analyses

of early growth traits revealed the importance of maternal additive genetic effects for weight at birth and weaning in previous study (Mohammadi et al., 2010a). Thus, the most appropriate model for BW and WW was included direct additive genetic effects as well as maternal genetic effects (Model 3). Subsequently, breeding values of individual animals were predicted with the best linear unbiased prediction (BLUP) methodology. In order to estimate genetic trends, means of predicted genetic values for lambs were calculated in year of birth. Genetic trends were obtained by regressing means of predicted genetic values on year of birth for each trait. Genetic, phenotypic and environmental correlations were estimated using three-trait analysis with the same fixed effects as single-trait models.

Table 1.

Description of data set with some pedigree information regarding studied traits in Arabi sheep

Character	Traits		
	Weight at birth	Weight at weaning	KR
Number of records	2445	2237	2098
Number of sire	139	127	115
Number of dam	804	784	739
No. of dams with own records	398	336	322
No. of progenies/sire	17.59	17.61	18.24
No. of progenies/dam	3.04	2.85	2.84
Overall means \pm SE	4.18 \pm 0.02	20.06 \pm 0.14	14.42 \pm 0.09
C.V (%)	18.87	14.98	19.37

C.V.: coefficient of variation.

3. RESULTS AND DISCUSSION

3.1. Heritability estimates

Least squares means (\pm SE) for KR are shown in Table 2. Fixed effects of year of birth, sex of lamb, type of birth, and age of dam were significant for KR ($p < 0.01$). Heritability estimates fitting different models and AIC values for KR are shown in Table 3. *Note.* σ^2_a : direct additive genetic variance; σ^2_m : maternal additive genetic variance; σ^2_c : maternal permanent environmental variance; σ_{am} : direct-maternal genetic covariance; σ^2_e : residual variance; σ^2_p : phenotypic variance; h^2_d : direct heritability; h^2_m : maternal heritability; c^2 : ratio of maternal permanent environmental effect; r_{am} : direct-maternal genetic correlation

Kleiber ratio has great phenotypic correlation with feed efficiency; thus, selection for Kleiber ratio led to indirect selection for feed efficiency and improvement of feed efficiency and growth traits under extensive breeding systems (Abegaz et al., 2005). For KR, when maternal effects were ignored (Model 1), direct heritability was 0.12. Fitting permanent environmental maternal effects

(Model 2) slightly reduced the direct variance and AIC value indicating important maternal effects that represent 10% of the phenotypic variance. Fitting maternal genetic (Model 3) rather than permanent environmental maternal effects also decreased AIC value over Model 1, but less than that of Model 2. The estimates of direct and maternal heritability from Model 3 were 0.11 and 0.05, respectively. The declination of direct heritability when maternal genetic effects are included indicates that these effects are important for KR. This is in agreement with Savar-Sofla et al. (2010) indicated maternal effects constitute a considerable part of the phenotype variance for Kleiber ratio in Moghani sheep. In Model 4, the estimate of direct-maternal genetic covariance was -0.81, leading to a correlation between direct and maternal effects of -0.68. However, direct heritability estimate slightly increased as compared to Models 1, 2 and 3 to 0.13. In this model, AIC value was similar to that in Model 3. Fitting both maternal genetic and permanent environmental maternal effects excluding correlation between direct and maternal effects (Model 5) and including (Model 6) were significantly not different from decrease in AIC value as compared to Model 2. Based on the AIC values and the number of parameters included in the models, Model 2 was

determined to be the most appropriate model for KR. Estimation of h^2_d for KR (0.11) in the optimum model was in agreement with estimate by Eskandarinasab et al. (2010) and Ghafouri-Kesbi et al. (2011) in Afshari and Zandi sheep, respectively. Nevertheless, higher and lower values were reported by Mohammadi et al. (2011) and Ved Prakash et al. (2012) in Zandi sheep and Malpura

sheep, respectively. The maternal permanent environmental effects can be associated with influences of uterine environment, multiple birth effects on milk production of dam, feeding at late stages of gestation and mothering behaviour of dam (Maria et al., 1993). The pe^2 for KR (0.10) was lower than the finding of Mohammadi et al. (2010b) for Sanjabi sheep (0.21).

Table 2.

Least squares means and standard error of KR from birth to weaning in Arabi sheep

Fix effects	Trait
	KR
	LSM \pm SE
Sex of lamb	**
Male	14.90 ^a \pm 0.16
Female	14.04 ^b \pm 0.13
Type of birth	**
Single	14.68 ^a \pm 0.11
Twin	13.43 ^b \pm 0.14
Age of dam (Year)	**
2	13.64 ^d \pm 0.21
3	14.16 ^c \pm 0.20
4	14.29 ^{bc} \pm 0.26
5	14.71 ^b \pm 0.22
6	14.94 ^b \pm 0.24
7	15.48 ^a \pm 0.28
Year of birth (1993-2008)	**

** Significant effect at $P < 0.01$

Table 3.

Estimations of (co)variance components, genetic parameters and AIC values with best model highlighted in bold for KR with different animal models

Model	σ^2_a	σ^2_c	σ^2_m	σ_{am}	σ^2_s	σ^2_p	h^2_d	c^2	h^2_m	r_{am}	AIC
1	2.30	--	--	--	16.81	19.11	0.12 \pm 0.03	--	--	--	708.4
2	2.10	1.91	--	--	16.01	19.11	0.11\pm0.03	0.10\pm0.02	--	--	706.0
3	2.10	--	0.96	--	16.05	19.11	0.11 \pm 0.02	--	0.05 \pm 0.02	--	706.4
4	2.49	--	0.57	-0.81	16.91	19.16	0.13 \pm 0.03	--	0.03 \pm 0.02	-0.68	706.4
5	2.10	0.96	0.76	--	15.29	19.11	0.11 \pm 0.03	0.05 \pm 0.02	0.04 \pm 0.03	--	706.6
6	2.30	1.15	1.15	-1.19	15.73	19.14	0.12 \pm 0.03	0.06 \pm 0.02	0.06 \pm 0.02	-0.73	706.7

3.2. Genetic trends

Genetic improvement of small ruminants needs a suitable selection program and also a breeding strategy, which having knowledge of genetic trend as a beacon light is necessary to perform so. Direct and maternal genetic trends (g per year) for pre weaning traits are demonstrated in Table 4. The genetic trend of weight at birth shows a mild ascending change that had ascending and descending fluctuations over an 8-year period.

However, there was overall increase in the magnitude, irrespective of the ups and downs in different years in weight at birth, as illustrated in Fig. 1. Our obtained value for direct genetic trend of weight at birth (6 g per year) was in accordance with the findings of Klerk and Heydenrych (1990), evaluating Dohne Merino in South Africa. However, estimates reported by Gizaw et al. (2007) in Menz sheep was greater than our estimate, but values reported by Mokhtari and Rashidi (2010) was lesser. Maternal genetic trend estimate for weight at

birth (5 g per year) was closer to the value obtained for direct, but lesser than the finding of Lotfi Farokhad et al. (2011) in Arman sheep. Generally, it seems that selection of sires was based on phenotypic characteristics.

Means of predicted breeding values of weight at weaning in each year of birth are illustrated in Fig. 2. The genetic improvement was non-significant for weight at weaning until 2002. The reason is possibly due to unselecting of lambs birthed in 2001 (owing to non-reaching to mature age). A decline in genetic trends was observed between 2005 and 2006. The reason of this decrease could be due to culling of many superior ewes in previous years because of elderly, unfavorable environmental conditions, and inclusion of many new ewes with less genetic value in flock. The direct genetic trend estimate of WW was 24 g per year. Shaat et al. (2004) evaluating worked on Ossimi sheep in Egypt, reported 1970-1999 was 20 g per year for weight at weaning; which is in agreement with the estimate encountered in our study. Greater estimated value was obtained by others (Lax et al., 1979; Shaat et

al., 2004; Mokhtari and Rashidi, 2010). Maternal genetic trend estimate for weight at weaning (15 g per year) was greater than the value obtained by Lotfi Farokhad et al. (2011). Annual fluctuations of weight at birth and weaning probably results from sudden climate changes, feeding level and hygiene of flock, so in performing animal breeding programs before any carrying out, optimal environmental conditions should be provided to obtaining more genetic potential. Usually, the cause of low-genetic improvement is due to more use of rams with low genetic value, lack of breeding objectives, non-use of appropriate selection criteria, inaccuracy in traits recording and non-execution of predicted programs in the aspect of flock size and replacement (Vatankhah et al., 2004). In general, these genetic trend estimates provide a good picture of the selection program for Arabi sheep although unfavorable environmental conditions affected upon genetic values prediction and caused decreased genetic improvement of traits in selected programs.

Table 4.

Estimates of correlations between studied traits in Arabi sheep

Trait 1	Trait 2	r_{a12}	r_{e12}	r_{p12}
Weight at birth	Weight at weaning	0.80 ± 0.05	0.44 ± 0.04	0.58 ± 0.04
Weight at birth	KR	-0.52 ± 0.04	0.16 ± 0.06	-0.21 ± 0.02
Weight at weaning	KR	0.89 ± 0.08	0.55 ± 0.01	0.71 ± 0.01

r_{a12} : genetic correlation between trait 1 and 2; r_{e12} : environmental correlation between traits 1 and 2; r_{p12} : phenotypic correlations between traits 1 and 2.

3.3. Correlation

The correlation components between the traits are presented in Table 4. Estimation of positively and highly genetic correlation between weight at birth and weaning (0.80) indicates the presence of common favor direct genes for both traits. Therefore, breeders could improve weight at weaning by selecting high weight at birth animals. Similarly, Kamjoo et al. (2014) found similar genetic correlation for these traits in Iran-Black sheep. Negatively genetic correlations between weight at birth and KR (-0.52) imply that different mechanism is involved in expressing of these traits at different stages of growth (Ved Prakash et al., 2012). Positively and highly genetic correlation between weight at weaning and KR (0.89) indicate that lambs with weaning weight are supposed to be more efficient users of feed, efficiency of the animals will be improved by selecting them. On the other hand, it appears that selection for KR can result in desirable genetic responses in weight at weaning. The negatively phenotypic correlation between weight at birth and KR (-0.21) may be considered as a consequence of negative values of KR for some animals. Phenotypic

correlation were 0.58 and 0.71 for weight at birth with weaning and weight at weaning with KR; respectively. Our findings were generally in the range of estimates of Mohammadi et al. (2011), Kamjoo et al. (2014) and Mohammadi et al. (2013).

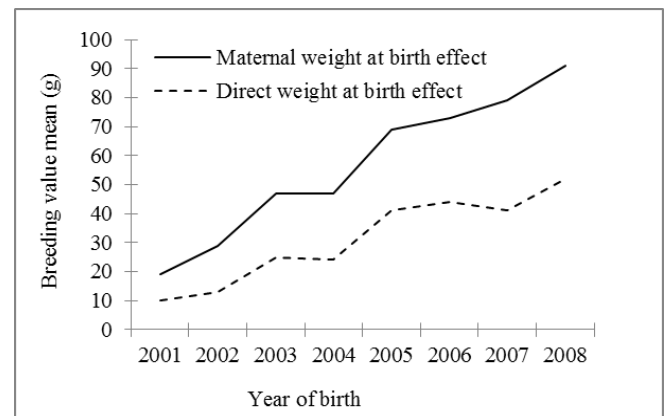


Fig. 1: Means of predicted breeding value of weight at birth in each year of birth

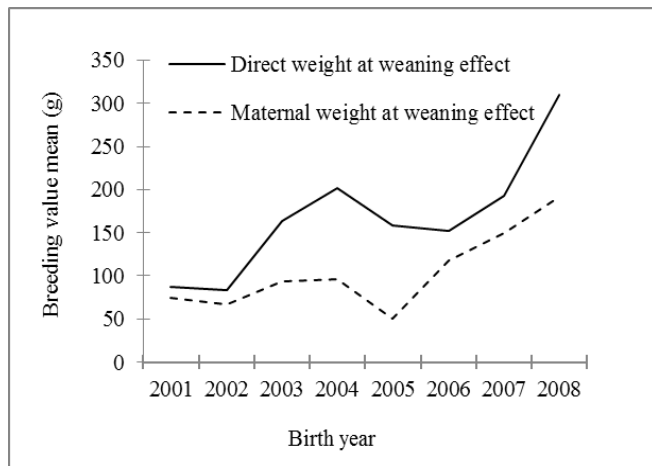


Fig. 2: Means of predicted breeding value of weight at weaning in each year of birth

CONCLUSION

Current results indicate that permanent environmental effects of dam are important for KR and ignoring these effects would cause inaccurate genetic evaluation. Given the above estimations, it seems that growth efficiency in terms of the KR could be applied in selection to increase the efficiency of growth. In addition, results showed the utilisation of KR in order to improve the efficiency of feed conversion and decrease in the costs of production system. The genetic progress estimations were low, reflecting the actual lack of consistent directional selection for clear selection purposes.

ACKNOWLEDGEMENT

I would like to appreciate all Animal Science Research Station staff of Khuzestan Ramin Agricultural and Natural Resources University, for farm managing and on farm data collecting.

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