Genetic analysis of growth traits in Iranian Makuie sheep breed

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Abstract

The Makuie sheep is a fat-tailed sheep breed which can be found in the Azerbaijan province of Iran. In 1986, a Makuie sheep breeding station was established in the city of Maku in order to breed, protect and purify this breed. The genetic parameters for birth weight, weaning weight (3 months), 6-month, 9-month and yearling weight, and average daily gain from birth to weaning traits were estimated based on 25 years of data using DFREML software. Six different models were applied and a likelihood ratio test (LRT) was used to select the appropriate model. Bivariate analysis was used to define the genetic correlation between studied traits. Based on the LRT, model II was selected as an appropriate model for all studied traits. Direct heritability estimates of birth weight, weaning weight, 6-month, 9-month and yearling weights and average daily gain from birth to weaning traits were estimated at approximately 0.63, 0.41, 0.48, 0.42, 0.36 and 0.37, respectively. Estimates of direct genetic correlation between birth and weaning weight, birth and 6-month weights, birth and 9-month weights, as well as between birth and yearling weights were 0.57, 0.49, 0.46 and 0.32, respectively. The results suggest there is a substantial additive genetic variability for studied traits in the Makuie sheep breed population, and the direct additive effect and maternal permanent environment variance are the main source of phenotypic variance.

Introduction

The Makuie sheep is a native breed of Iran and can also be found in Turkey (called as Ak Karaman). Its total population is estimated at approximately 2.7 millions (Abbasi and Ghafoori, 2011). It has been adapted to cold and highland environments (Safari, 1986). They are fat-tailed sheep with a medium-sized body, white in color with black rings around the eyes, nose and feet (Saadatnoori and Siahmansoor, 1986). They are kept in the Eastern and Western provinces Azerbaijan and their main products are meat, wool and milk (Saadatnoori and Siahmansoor, 1986). The rearing system is mostly extensive-migratory from April to September (on natural pastures in spring and summer), and semi-intensive from October to March (on stations and fed in barns during autumn and winter). Alfalfa, barley, corn silage, concentrates and grass are the main feedstuffs used in the semi-intensive rearing period.

Breeding with a superior breeding value in growth rate, egg, meat, milk, or wool production, has revolutionized agricultural livestock production throughout the world. The scientific theory of animal breeding is based on population and quantitative genetics. Population-based genetic parameters, especially heritabilities and correlation between traits, make up the most important information required to improve selection objectives, and determine the selection gain of current selection schema.

In 1986, the Makuie Sheep Breeding Station (MSBS) was established in the city of Maku, Western Azerbaijan, Iran by the Jihad Sazandegi Ministry (Safari, 1986) in order to protect, purify and improve this sheep breed (Safari, 1986). The breeding season starts late in the summer (in September) and early in the autumn (in October). It ends by the middle of autumn (early in November). Estrus synchronization is carried out in the flock with a progesterone-releasing intravaginal (CIDR). Ewes are then bred either by artificially insemination (in the first cycle of estrus) or with controlled rams. Flushing and equine chorion gonadotrophin (ECG) injection at CIDR removal are applied to increase the litter size. Ewes are kept in the flock for a maximum of 7 parities and rams for 5 breeding seasons. Lambing occurs once a year and it starts early in the second month of winter (late January). Lambs receive creep feeding during the first two weeks of age.

Although the population has been under selection for at least 25 years, to our knowledge there has been no report that has estimated genetic parameters in this sheep breed. The objectives of the present study were to estimate genetic parameters of growth traits as well as to reveal any association between traits by using genetic correlation analysis.

Materials and methods

In this study, data of the growth traits 5,212 lambs from 130 sires and 1,320 dams recorded during the period 1989 to 2010 at the Makuie Sheep Breeding Station (MSBS). Traits were birth weight (BW), weaning weight (WW), 6-month weight (6MW), 9-month weight (9MW), yearling weight (YW) and average daily gain from birth to weaning (ADG).

Statistical analysis

In model I, the direct additive genetic was considered as random effect. In model II, the direct additive genetic and maternal permanent environment was included as random effects. In the present model, genetic parameters were estimated according to genetics of the animals themselves and their permanent environment as uterine environment. It is clear that, in this model, the estimated $h^2$ was lower than those estimated by model I, because her-
Genetic analysis of growth in Makuei sheep

Results and discussion

Descriptive statistics

Descriptive statistics of measured traits based on age, sex and birth type (single or twin) are presented in Table 2. Male lambs were heavier than females at all ages and these differences were significant (P<0.01). The effect of lamb sex on body weight traits at different ages has been reported in various sheep breeds (Mokhtari et al., 2006; Miraei-Ashtiani et al., 2003). It could be due to differences in management, food availability, disease, and climatic conditions (rate of rainfall, humidity and temperature) that affect the quality and quantity of pasture forage and rearing systems in different years. The age of the dam was significant on birth weight (BW) (P<0.001), weaning weight (YW) (P<0.01), 6-month weight (6MW) and yearling weight (YW) (P<0.05) traits. Young ewes tend to produce smaller lambs. Primiparous ewes are not at their mature weight and complement their growth in addition to fetal growth. This could affect the lamb weight. It is well known that mothering ability, such as milk yield, increases with parity, as older ewes are usually larger and produce more milk (Dass and Acharya, 1970). However, the age of the dam did not have significant effect on 9MW trait. The same results were reported by El Fadili et al. (2000) on the Moroccan Timahdit sheep.

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Table 1. The six models and their fixed and random effects.

| Model | YR | SX | BT | AD | AN | M | PE | E | rAM |
|-------|----|----|----|----|----|---|----|---|-----|
| I     | *  | *  | *  | *  | *  | - | -  | * | -   |
| II    | *  | *  | *  | *  | *  | - | -  | * | -   |
| III   | *  | *  | *  | *  | *  | - | -  | - | -   |
| IV    | *  | *  | *  | *  | *  | - | -  | - | -   |
| V     | *  | *  | *  | *  | *  | - | -  | - | =0  |
| VI    | *  | *  | *  | *  | *  | - | -  | - | =0  |

YR, year; SX, sex; BT, birth type; AD, age of dam; AN, animal direct additive genetic; M, maternal genetic effect; PE, maternal permanent; E, error or residual effect; rAM, genetic correlation between direct additive genetic and maternal genetic.
Physiological characteristics and endocrinial system (type and quantity of hormone secretion, especially sex hormones) can explain the significant influences of gender (Aghaali-Gamasae et al., 2010).

The effect of birth type was significant on all studied traits. The frequency of single birth type was high compared to other types. A low number of triple birth types was seen so it was not included in the models. The significant effect of birth type on body weight can be due to limited uterine space during pregnancy, nutrition of the dam, especially during late pregnancy (regardless of twin or triple pregnant dams), and competition for milk sucking between multiple birth lambs during the birth to weaning period. Similar results have been reported in other breeds, such as the Hungarian Merino sheep (Komlosi, 2008).

The high value of PE2 for weaning weight suggests the importance of the permanent maternal environment. Including direct maternal genetic correlation in model VI yielded a large negative estimate for this parameter in all studied traits while $h^2_m$ and $h^2_a$ values were dramatically increased. This has also been reported in Australian Charolais Cattle (Meyer, 1992).

Negative correlations between direct and maternal effect for early growth traits are common but are not biologically possible (Mantiatis and Pollot, 2003). According to previous researchers (Meyer 1992), the possible reasons for the negative correlation may be environmental stresses (such as udder problems, and non-sufficient nutrition), different methods of animal management, different methods of data collection, size of data set, and data structure (from field condition or experimental condition). The experimental flocks due to standardized management are much less subject to having negative correlation between direct and maternal effects. Another reason for this negative correlation may arise from the number of offspring recorded per mother as a low number of offspring produce high negative correlation (Mantiatis and Pollot, 2003). It has been proved that the relative values of $h^2_a$ and $h^2_m$ were greatly influenced by the model used in the analysis of data.

Model selection

According to the equation $R^2 = \frac{SS_{\text{model}}}{SS_{\text{total}}}$, 16-40% of traits’ phenotypic variances were explained by the established factors (Table 3) and the effects of sex and birth type were the most important of the traits studied (P<0.001).

Table 2. Descriptive statistics of the growth traits in Iranian Makuie sheep.

| Trait   | Sex   | Birth type | No. of records | Mean, kg | SD  | CV, % |
|---------|-------|------------|----------------|----------|-----|-------|
| BW      | Male  | Single     | 1992           | 4.52     | 0.54| 11.91 |
|         | Male  | Twin       | 358            | 3.88     | 0.61| 15.65 |
|         | Female| Single     | 2015           | 4.27     | 0.50| 11.69 |
|         | Female| Twin       | 373            | 3.59     | 0.51| 14.08 |
| Overall |       |            | 4738           | 4.30     | 0.59| 13.78 |
| WW      | Male  | Single     | 1821           | 21.26    | 3.36| 15.80 |
|         | Male  | Twin       | 346            | 17.10    | 5.36| 31.34 |
|         | Female| Single     | 1955           | 19.70    | 2.94| 14.95 |
|         | Female| Twin       | 361            | 16.10    | 5.18| 32.16 |
| Overall |       |            | 4483           | 19.84    | 3.91| 19.68 |
| 6MW     | Male  | Single     | 1358           | 29.22    | 5.10| 17.44 |
|         | Male  | Twin       | 228            | 25.48    | 4.55| 17.86 |
|         | Female| Single     | 1673           | 26.46    | 4.03| 15.22 |
|         | Female| Twin       | 272            | 23.65    | 3.55| 15.00 |
| Overall |       |            | 3531           | 27.24    | 4.79| 17.59 |
| 9MW     | Male  | Single     | 1002           | 30.75    | 4.72| 15.34 |
|         | Male  | Twin       | 143            | 27.49    | 5.04| 18.34 |
|         | Female| Single     | 1411           | 27.40    | 3.96| 14.46 |
|         | Female| Twin       | 204            | 25.65    | 3.49| 13.60 |
| Overall |       |            | 2760           | 28.49    | 4.63| 16.24 |
| YW      | Male  | Single     | 382            | 40.00    | 5.68| 14.21 |
|         | Male  | Twin       | 45             | 37.62    | 5.88| 15.62 |
|         | Female| Single     | 1327           | 31.30    | 4.16| 13.30 |
|         | Female| Twin       | 191            | 30.04    | 3.73| 12.40 |
| Overall |       |            | 1945           | 33.03    | 5.76| 17.45 |
| ADG     | Male  | Single     | 1820           | 0.19     | 0.04| 21.47 |
|         | Male  | Twin       | 346            | 0.14     | 0.04| 24.93 |
|         | Female| Single     | 1955           | 0.17     | 0.03| 18.20 |
|         | Female| Twin       | 361            | 0.14     | 0.03| 24.18 |
| Overall |       |            | 4482           | 0.17     | 0.04| 21.47 |

BW, birth weight; WW, weaning weight; 6MW, 6-month weight; 9MW, 9-month weight; YW, yearling weight; ADG, average daily gain from birth to weaning; CV, coefficient of variation.

Heritability and (co)variance components for the traits

Birth weight

Direct heritability was estimated for birth weight (BW) using model I. It was 0.36 and was higher than that estimated for other breeds such as Dorper (Neser et al., 2001). However, using model II and introducing maternal permanent environment to the model, the direct heritability decreased to 0.27. The maternal permanent environment effect was 0.1. This indicates that the 10% of BW variation was explained by maternal permanent environment which was lower than that reported by other researchers (Neser et al., 2001). This suggested we should not use direct heritability as the only criteria for breeding programs.

Weaning weight

The estimates of $h^2_a$ and PE2 by using model II for weaning weight (WW) were 0.20 and 0.17, respectively; this was in agreement with other researchers such as Mandal et al. (2006). The high value of PE2 for weaning weight suggests the importance of the permanent maternal environment. Including direct maternal genetic correlation in model VI yielded a large negative estimate for this parameter in all studied traits while $h^2_a$ and $h^2_m$ values were dramatically increased. This has also been reported in Australian Charolais Cattle (Meyer, 1992).
(Koyuncu and Duru, 2009). From a developmental perspective, some negative correlations provide checks and balances between direct and maternal effects for growth traits. Whereas this condition could be involved in preventing the species from becoming much larger or producing more and more milk (Cundiff, 1972).

Six-month weight

The highest \( h_2^a \) for this trait were achieved by using models I and II, 0.48 and 0.42, respectively. For 6-month weight (6MW), 9-month weight (9MW) and yearling weight (YW) permanent maternal environment had less effect while the animal effect and maternal genetic played an essential role. In a previous study on the Sangsari breed, another Iranian fat-tailed sheep breed, the estimates of \( h_2^a \) and PE\(^2\) for 6-month weight (6MW) were higher than our estimates (Miraei-Ashtiani et al., 2007). According to the results obtained by Mantiatis and Pollott (2003), parameter estimates in different populations were strongly influenced by the number of progeny per dam and the proportion of mothers with recorded performance.

Nine-month weight

Our estimates based on models II were 0.37 and 0.05 for \( h_2^a \) and PE\(^2\), respectively, which were between the ranges of values estimated for the Kermani breed, another Iranian fat-tailed sheep breed (Mokhtaria et al., 2008). The maternal permanent environment, like 6-month weight (6MW) declined, whereas maternal genetic proved to be more dominant than direct genetic and permanent maternal environment.

Yearling weight

The estimates of \( h_2^a \) and PE\(^2\) for YW trait by using model II were 0.31 and 0.06, respectively. These results were in the range of other reports (Komlosi, 2008). The negative correlation between direct and maternal genetic in yearling weight (YW) trait as in Komlosi’s (2008) studies in Hungarian merino and meat sheep breeds may be due to fewer progeny recorded per dam (Mantiatis and Pollott, 2003).

Average daily gain from birth to weaning

Average daily gain from birth to weaning (ADG) is the important factor in sheep breeding systems, especially in mutton systems; therefore, it could be included in the selection index as a selection criterion. The average daily gain of the \textit{Makuie} breed was 170 g in this study. Using model II, direct heritability and heritability due to maternal permanent environment were estimated to be 0.17. Estimated values agreed with the value estimated for the Arabi sheep breed (another Iranian fat-tailed sheep) using the same model (Mohammadi et al., 2010).

Correlation study

A bivariate model was used to define the cor-

### Table 3. Analysis of variance for birth weight, weaning weight, 6-month weight, 9-month weight, yearling weight and average daily gain from birth to weaning traits in \textit{Iranian Makuie} sheep.

| Fixed effects | BW    | WW    | 6MW   | 9MW   | YW    | ADG   |
|---------------|-------|-------|-------|-------|-------|-------|
| Year          | ***   | ***   | ***   | ***   | *     |       |
| Age of dam    | ***   | *     | ***   | ***   | ***   | ***   |
| Sex           | ***   | ***   | ***   | ***   | ***   | ***   |
| Birth type    | ***   | ***   | ***   | ***   | ***   | ***   |
| R²            | 0.34  | 0.30  | 0.24  | 0.16  | 0.17  | 0.40  |

| **BW, birth weight; WW, weaning weight; 6MW, 6-month weight; 9WM, 9-month weight; YW, yearling weight; ADG, average daily gain from birth to weaning. *Significant at 0.05 probability level; **significant at 0.01 probability level; ***significant at 0.001 probability level; ns, not significant at 0.05 probability level.** |

### Table 4. Variance components and genetic parameters of different traits in \textit{Iranian Makuie} sheep breed.

| Trait          | MF | \( h_2^a \) | PE\(^2\) | \( h_2^m \) | \( \sigma_{AM} \) | \( \sigma_{AM} \) | Log-likelihood |
|----------------|----|------------|---------|------------|----------------|----------------|---------------|
| BW             | I  | 0.36       | 0.10    |            |                |                | 1281.3028     |
|                | II | 0.27       | 0.16    | 0.04       | 0.26           |                | 1304.1027     |
|                | III| 0.20       | 0.10    | 0.07       |                |                | 1304.1028     |
|                | IV | 0.20       | 0.10    | 0.11       | -0.005         | -0.16          | 1304.1028     |
|                | V  | 0.20       | 0.10    | 0.11       | -0.005         | -0.16          | 1304.1028     |
|                | VI | 0.20       | 0.10    | 0.11       | -0.005         | -0.16          | 1304.1028     |
| WW             | I  | 0.41       | 0.17    |            |                |                | -6733.6159    |
|                | II | 0.20       | 0.20    |            |                |                | -6673.8374    |
|                | III| 0.20       | 0.10    | 0.39       | 0.35           |                | -6733.8619    |
|                | IV | 0.20       | 0.17    | 0.00       |                |                | -6673.8375    |
|                | V  | 0.20       | 0.17    | 0.11       | -0.53          | -0.42          | -6673.8375    |
|                | VI | 0.20       | 0.17    | 0.11       | -0.53          | -0.42          | -6673.8375    |
| 6MW            | I  | 0.48       | 0.08    |            |                |                | -6086.6756    |
|                | II | 0.20       | 0.28    |            |                |                | -6072.7768    |
|                | III| 0.20       | 0.25    | 0.22       | 0.08           |                | -6086.6756    |
|                | IV | 0.20       | 0.20    | 0.22       | 0.08           |                | -6072.7768    |
|                | V  | 0.20       | 0.08    | 0.31       | -0.81          | -0.24          | -6072.7766    |
|                | VI | 0.20       | 0.08    | 0.31       | -0.81          | -0.24          | -6072.7766    |
| 9MW            | I  | 0.42       | 0.05    |            |                |                | -4666.9063    |
|                | II | 0.37       | 0.22    |            |                |                | -4666.9063    |
|                | III| 0.20       | 0.31    | -0.76      | -0.24          |                | -4666.9062    |
|                | IV | 0.20       | 0.05    | 0.17       |                |                | -4666.9063    |
|                | V  | 0.20       | 0.05    | 0.10       | 0.49           | 0.30           | -4666.9063    |
|                | VI | 0.20       | 0.05    | 0.29       | -2.02          | -0.45          | -3634.4798    |
| YW             | I  | 0.36       | 0.15    |            |                |                | -3636.6781    |
|                | II | 0.31       | 0.15    |            |                |                | -3634.4796    |
|                | III| 0.20       | 0.25    | -0.97      | -0.25          |                | -3636.6781    |
|                | IV | 0.20       | 0.06    | 0.11       |                |                | -3634.4796    |
|                | V  | 0.20       | 0.05    | 0.29       | -2.02          | -0.45          | -3634.4798    |
|                | VI | 0.20       | 0.15    | 0.10       | -7×10\(^{-4}\)  | -0.51          | -3635.2322    |

\( h_2^a \), direct heritability; \( h_2^m \), maternal heritability; \( \sigma_{AM} \), co-variance between direct additive and maternal additive genetic effects; \( \sigma_{AM} \), correlation between direct and maternal additive effects; PE\(^2\), heritability due to permanent environment; MF, fitted model; BW, birth weight; WW, weaning weight; 6MW, 6-month weight; 9WM, 9-month weight; YW, yearling weight; ADG, average daily gain from birth to weaning. 

[Ital J Anim Sci vol.11:e18, 2012] [page 101]
Table 5. Correlation between traits in Iranian *Makuie* sheep breed from bivariate DFREML analysis (based on model II).

| Trait 1 | Trait 2 | \(r_{p12}\) | \(r_{a12}\) | \(r_{pe12}\) | \(r_{e12}\) |
|---------|---------|-------------|-------------|-------------|-------------|
| BW      | BW      | 0.31        | 0.57        | 0.44        | 0.18        |
| BW      | 6MW     | 0.25        | 0.49        | 0.41        | 0.08        |
| BW      | 9MW     | 0.22        | 0.46        | 0.04        | 0.12        |
| BW      | YW      | 0.23        | 0.32        | 0.22        | 0.20        |
| BW      | ADG     | 0.15        | 0.33        | 0.31        | 0.02        |
| WW      | 6MW     | 0.68        | 0.94        | 0.09        | 0.49        |
| WW      | 9MW     | 0.63        | 0.83        | 0.57        | 0.45        |
| WW      | YW      | 0.50        | 0.84        | 0.57        | 0.30        |
| WW      | ADG     | 0.96        | 0.92        | 0.95        | 0.98        |
| GMW     | 9MW     | 0.75        | 0.93        | 0.91        | 0.62        |
| GMW     | YW      | 0.59        | 0.80        | 0.76        | 0.43        |
| GMW     | YW      | 0.73        | 0.87        | 0.78        | 0.64        |

\(r_{p12}\), phenotypic correlation between trait 1 and trait 2; \(r_{a12}\), direct additive genetic correlation between trait 1 and trait 2; \(r_{pe12}\), maternal permanent environmental correlation between trait 1 and trait 2; \(r_{e12}\), residual correlation between trait 1 and trait 2; BW, birth weight; WW, weaning weight; 6MW, 6-month weight; 9WM, 9-month weight; YW, yearling weight; ADG, average daily gain from birth to weaning.

Conclusions

Estimates of genetic parameters from the present study suggest that there is substantial additive genetic variability in the population for all studied traits. The high genetic correlation between weaning weight and yearling weight indicates that breeders’ rams could be selected at an earlier age. According to the LRT test we used, model II is the best model. This indicates that we need to include maternal permanent variance as an important proportion of phenotypic variance in breeding objectives.

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