Small Ruminant Research 149 (2017) 1–5

Contents lists available at ScienceDirect

Small Ruminant Research

journal homepage: www.elsevier.com/locate/smallrumres

Estimates of variance components due to parent-of-origin effects for body weight in Iran-Black sheep

Mahmoud Amiri Roudbar[a], Mohammadreza Mohammadabadi[a], Ahmad Ayatollahi Mehrgardi[a], Rostam Abdollahi-Arpanahi[b,*]

[a] Department of Animal Science, College of Agriculture, Shahid Bahonar University of Kerman, P.O. Box 76169-133, Kerman, Iran
[b] Department of Animal and Poultry Science, College of Aburaihan, University of Tehran, P.O. Box 465, Pakdasht, Iran

ARTICLE INFO

Article history:
Received 20 December 2015
Received in revised form 3 January 2017
Accepted 4 January 2017
Available online 5 January 2017

Keywords:
Imprinting
Growth traits
Maternal effects
Heritability
Iran-Black sheep

ABSTRACT

In this study, variances due to differential expression of paternally and maternally imprinted genes for body weight of Iran Black sheep, a composite breed made by cross Chios rams with Iranian Baluchi ewes, were estimated. Data on body weight at birth (BW), weaning (WW), at the age of six months (W6), 9 months (W9) and one year (W12) were provided by the National Animal Breeding Center of Iran. Body weight records were obtained from a total of 5164 animals. The number of records used to estimate (co)variance components for BW, WW, W6, W9 and W12 were 4953, 3926, 3367, 2923 and 2704, respectively. Imprinting variances were estimated using the inverse of the gametic relationship matrix. Models were selected based on Bayesian information criterion. Estimates of variance for paternal imprinting effects, which induced changes in maternal gene expression, were approximately zero for all traits. Thus, adding paternal imprinting effects into model had no beneficial effects on our estimates. In contrast, maternal imprinting effects originating from paternal gene expression, had significant effects on body weight traits, and ranged from 12% (±6.6) to 23% (±5.2) of the total phenotypic variance. Interestingly, the best model for WW and W6 traits was achieved when maternal parent-of-origin effects were included in the model. Adding maternal parent-of-origin effects to the model resulted in a decrease in the estimates of heritability for all studied traits. Our results demonstrate the importance of including parent-of-origin effects into the model for the analysis of sheep body weight.

1. Introduction

Imprinting is a cis-acting mechanism that works on a single chromosome and depends on an epigenetic system to modify one of the two parental chromosomes. These changes alert the expression of the imprinted gene on one parental chromosome. So, the genotypic effect of the heterozygous individual depends on the parental origin of the alleles. Cytosine methylation, one of the most important epigenetic mechanisms, establishes the paternal and maternal imprinting in the gametic stage. Other epigenetic mechanisms, including histone modifications, histone variants, and non-coding RNAs confer differential expression of imprinted genes, according to parent-of-origin (Barlow and Bartolomei, 2014).

Recently, a study on detection of quantitative trait loci (QTL), which accounted for parent-of-origin effects on growth and carcass traits in beef cattle, identified 24 loci which can be imprinted parentally (Imumorin et al., 2011). To date, about 18 loci have been identified as imprinted genes in sheep (for complete list see http://igc.otago.ac.nz/home.html). These imprinted genes contribute to regulate growth and development. For instance, some genes that affect growth of the embryo, placenta, and neonate belong to imprinting regulation (Barlow and Bartolomei, 2014). Therefore, imprinted genes could significantly impact the estimation of genetic parameters, and the lack of parent-of-origin effects in the statistical models could bias the prediction of breeding values (Tier and Meyer, 2012).

In the last two decades, methods for estimation of imprinting effects were developed. These types of effects were first estimated by fitting a model that considers only effects of a single parent (de Vries et al., 1994). Thereafter, paternal and maternal effects were calculated separately in a model introduced by Essl and Voith (2002). Subsequently, a model was presented to detect imprinted quantitative trait loci (QTL) in outbred populations (de

* Corresponding author.
E-mail addresses: Mahmood.amiri225@gmail.com (M. Amiri Roudbar), mrm2005@gmail.com (M. Mohammadabadi), mehrgardi@uk.ac.ir (A.A. Mehrgardi), r.abdollahi@ut.ac.ir (R. Abdollahi-Arpanahi).

http://dx.doi.org/10.1016/j.smallrumres.2017.01.002
0921-4488/

Table 1
Descriptive statistics of birth (BW), weaning (WW), 6-month (W6), 9-month (W9) and yearling (W12) body weight traits.

Item	Trait				
	BW	WW	W3	W9	W12
Number of records	4953	3926	3367	2923	2704
Mean (kg)	3.65	20.82	30.23	33.31	39.25
Standard deviation (kg)	0.83	5.02	5.96	5.62	6.89
Minimum (kg)	1.4	6	14	18	20
Maximum (kg)	6.3	35	49	50	62
Number of sires	104	98	97	96	95
Number of dams	1227	1090	1025	981	964
Number of male lambs	2508	1993	1720	1468	1355

Koning et al., 2002). The correlation between sire and dam gametes has been used as an alternative to estimate imprinting variances (Neugebauer et al., 2010b). Recently, Tier and Meyer (2012) fitted a model in which the gametic relationship matrix was used simultaneously to estimate variances and covariance of sire and dam gametic effects. The pig is the most studied animal for parent-of-origin effects among livestock (de Vries et al., 1994; Holl et al., 2004; Neugebauer et al., 2010a). For instance, Neugebauer et al. (2010a) found that between five percent and 10 percent of the total additive genetic variance was explained by genomic imprinting. Despite of many studies on parent-of-origin effects in cattle and pig (Neugebauer et al., 2010a; Imumorin et al., 2011; Meyer and Tier, 2012), there have not been any studies on estimation of variance due to parent-of-origin effects in sheep. Therefore, the aim of this study was to estimate parent-of-origin effects for different growth traits in sheep.

2. Materials and methods

2.1. Data collection and structure

Data for many production traits of Iran-black sheep were collected from a single flock located in the Sheep Breeding Station of Abbasabad (Khorasa Razavi province, Iran) from 1984 to 2008. Birth weight (BW), weaning weight (WW), 6-month weight (W6), 9-month weight (W9) and yearling weight (W12) of Iran-Black sheep were retrieved from National Animal Breeding Center (ABC) database. The Iran-black breed is composed of half Baluchi and half Chios (Rashidi, 2013). The breeding project started in 1975, and the recording of performance data began in 1984. In this project, Chios rams were mated with Iranian Baluchi ewes to produce Iran-Black sheep. Lamb age ranged from 60 to 120, 150 to 210, 210 to 320 and 320 to 395 days for WW, W6, W9 and W12, respectively. The description and structure of aforementioned body weight traits are presented in Table 1.

The summary of the pedigree structure is shown in Table 2. The proportions of male and female consisted of 48.93% and 51.07% of the total lambs, respectively. Pedigree analyses were performed using ENDOG v4.8 program (Gutiérrez and Goyache, 2005). The effective population size (N_e) was estimated based on the change in inbreeding (ΔF_i) (Gutierrez et al., 2009) using the following formula:

$$\Delta F_i = 1 - \sqrt[t_i-1]{1 - F_i}$$

where t_i and F_i are the equivalent of the discrete generations and the inbreeding coefficient of individual i, respectively. After averaging of the coefficients of individual increase in inbreeding, N_e was estimated using following formula:

$$N_e = \frac{1}{2\Delta F}$$

Table 2
The results of pedigree analysis of data.

Item	Value
Total individuals	5164
Total sires	104
Total dams	1227
Individuals with progeny	1331
Individuals with no progeny	3833
Individuals with known sire and dam	4960
Individuals with unknown sire and dam	204
Individuals in reference population	204
Average inbreeding coefficients	0.037
Average family size	2.239
Average of relatedness	0.681
Number of founders	204
Number of ancestors	212
Effective population size (N_e)[a]	33.16
Effective number of founders for reference population	25
Effective number of ancestors for reference population	22
Effective population size of founders	26.47

[a] N_e was estimated based on the change in inbreeding (ΔF_i).

2.2. Statistical analysis

Initially, fixed effects were examined to determine their significance in the statistical model for each trait. Lamb gender, birth type, dam age in years, month of birth, and year of birth were used as fixed effects. Lamb age in days was considered as a covariate in the statistical models. Except month of birth, all fixed effects were significant ($P \leq 0.01$) and were included in the models. Any phenotypic record exceeding three standard deviations from the mean was removed. Animals of unknown sex were also eliminated.

Variance and covariance components were estimated in two steps. In the first step, six univariate mixed models with different combinations of random effects, including direct additive genetic, maternal genetic and maternal permanent as random effects; as well as covariance between maternal genetic and direct additive genetic effect; were evaluated in order to determine the most appropriate models for subsequent (imprinting) analysis. The six univariate models were:

Model A: $\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_1\boldsymbol{a} + \boldsymbol{e}$

Model P: $\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_1\boldsymbol{a} + \boldsymbol{Z}_2\boldsymbol{c} + \boldsymbol{e}$

Model M0: $\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_1\boldsymbol{a} + \boldsymbol{Z}_3\boldsymbol{m} + \boldsymbol{e}, \boldsymbol{cov}(\boldsymbol{a}, \boldsymbol{m}) = 0$

Model M1: $\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_1\boldsymbol{a} + \boldsymbol{Z}_3\boldsymbol{m} + \boldsymbol{e}, \boldsymbol{cov}(\boldsymbol{a}, \boldsymbol{m}) = \boldsymbol{A}\sigma_{\boldsymbol{a},\boldsymbol{m}}$

Model PM0: $\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_1\boldsymbol{a} + \boldsymbol{Z}_2\boldsymbol{c} + \boldsymbol{Z}_3\boldsymbol{m} + \boldsymbol{e}, \boldsymbol{cov}(\boldsymbol{a}, \boldsymbol{m}) = 0$

Model PM1: $\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_1\boldsymbol{a} + \boldsymbol{Z}_2\boldsymbol{c} + \boldsymbol{Z}_3\boldsymbol{m} + \boldsymbol{e}, \quad \boldsymbol{cov}(\boldsymbol{a}, \boldsymbol{m}) = \boldsymbol{A}\sigma_{\boldsymbol{a},\boldsymbol{m}}$

where **y** is a vector of observations (different body weights); **b, a, c, m** and **e** are vectors of fixed, direct additive genetic, maternal permanent, maternal genetic, and residual effects, respectively; **X**, $\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ are design matrices relating observations to the fixed, direct additive genetic, maternal permanent, and maternal additive genetic effects, respectively; **A** is the numerator relationship matrix; $\sigma_{a,m}$ is the covariance between direct and maternal