



Estimation of the variance due to parent-of-origin effects for productive and reproductive traits in Lori-Bakhtiari sheep[☆]

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ABSTRACT

Parent-of-origin effects are often excluded from models used for estimating of additive and non-additive genetic variances. Omission of parentally-linked genetic factors, such as imprinting, from statistical models has potential to induce profound bias during the estimation. In this study, parent of origin variance for productive and reproductive traits in Lori-Bakhtiari sheep was estimated using a gametic relationship matrix approach. The data set were obtained from a total of 7568 animals, collected from 1994 to 2012 from the Lori-Bakhtiari research flock at Shooli station in Shahrekord, Iran. Growth traits were included birth weight (BWT), weaning weight (WWT), 6-month weight (WT6), 9-month weight (WT9), yearling weight (WT12), average daily gain from birth to weaning (ADGa), and from weaning to 6-month (ADGb). In addition, litter size at birth (LSB), litter size at weaning (LSW), litter mean weight per lamb born (LMWLB), and litter mean weight per lamb weaned (LMWLW) were analyzed as basic reproductive traits, and total litter weight at birth per ewe lambing (TLWB) and total litter weight at weaning per ewe lambing (TLWW) as composite reproductive traits. Models including or excluding maternal and paternal imprinting effects were compared using the ayesian information criterion (BIC). For all growth traits, except WT6 and WT12, adding maternal imprinting effects into the models decreased BIC, with estimates ranging from 10.5% (WWT) to 23.3% (BWT) of the total phenotypic variance. Paternal imprinting effects, in the other hand, was estimated as 6.9% of the total phenotypic variance for ADGb. For reproductive traits, maternal imprinting effects explained up to 6% of total phenotypic variance for TLWW. Adding paternal or maternal imprinting to the models decreased the direct additive genetic, maternal additive genetic and maternal permanent environmental variance for the growth traits.

1. Introduction

Genomic imprinting is an important epigenetic regulation mechanism in diploid organisms, in which a monoallelic with parental specific expression pattern occurs for a subset of genes (Barlow and Bartolomei, 2014). As such, it makes distinction between heterozygous individuals depending on the parental origin of the alleles in imprinted loci.

Since 1971, the first time that the importance of imprinting genes was found for normal mouse development (Searle and Beechey, 1978), less than 100 loci have been detected so far as imprinted genes in mammals (for a complete list see <http://igc.otago.ac.nz/home.html>).

These genes have essential roles on development and growth in mammals (Barlow and Bartolomei, 2014). Earlier studies detected some imprinted loci which have major effects on complex traits. For instance, a sheep with heterozygous genotype in the DLK1-GTL2 domain carrying a paternally inherited mutation has a muscular hypertrophy phenotype which is entirely distinct from the normal phenotype (Georges et al., 2003). So far, the exact number of imprinted loci has been remained unknown, but some studies showed that it could be more than one thousand (Gregg et al., 2010). Therefore, this large number of imprinted loci can make a significant contribution to quantitative traits variation (Neugebauer et al., 2010a; Meyer and Tier, 2012; Tier and Meyer, 2012). For example, Hu et al. (2015) showed that imprinting

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Table 1
The structure and descriptive statistics for growth traits in Lori-Bakhtiari sheep.

Traits ^a	No. of records	No. of ewes	No. of sires	No. of dams	No. of dams with own records and progeny	No. of service sires	Mean	C.V. (%)
BWT (kg)	6388	–	287	1 961	1356	–	4.99	15.56
WWT (kg)	5922	–	285	1 906	1325	–	28.86	19.36
WT6 (kg)	4632	–	273	1 743	1150	–	41.31	20.77
WT9 (kg)	2805	–	271	1 471	952	–	51.74	16.96
WT12 (kg)	2582	–	269	1 433	909	–	56.79	18.68
ADGa (g/d)	5778	–	285	1 902	1275	–	320.67	19.05
ADGb (g/d)	4578	–	273	1 742	1141	–	66.51	48.28
LSB	5034	1858	249	1 102	930	258	1.16	31.74
LSW	5034	1858	249	1 102	930	258	0.93	13.58
LMWLB (kg)	5046	1855	249	1 102	931	258	5.12	13.95
LMWLW (kg)	4673	1790	249	1 102	898	254	29.55	16.73
TLWB (kg)	5046	1855	249	1 102	931	258	5.87	26.71
TLWW (kg)	4673	1790	249	1 102	898	254	33.49	27.87

^a BWT: Birth weight; WWT: weaning weight; WT6: 6-month weight; WT9: 9-month weight; WT12: yearling weight; ADGa: average daily gain from birth to weaning; ADGb: average daily gain from weaning to 6-month weight; LSB: litter size at birth; LSW: litter size at weaning; LMWLB: litter mean weight per lambing; LMWLW: litter mean weight per lamb weaned; TLWB: total litter weight at birth per ewe lambing; TLWW: total litter weight at weaning per ewe lambing.

can have non-negligible contribution to the variation of body mass index in mice.

Initially the importance of imprinting regulations was showed in the early embryo development stage through the use of mouse mutants carrying chromosomal translocations (Searle and Beechey, 1978). After that many study have been done to determine the importance of imprinting mechanisms on economical traits in livestock (de Vries et al., 1994; Essl and Voith, 2002). Several methods have been used to estimate parent-of-origin effects in livestock species. Many of them attempted to estimate imprinting effects without using a gametic relationship matrix, in which the paternal and maternal imprinting could be calculated separately (de Vries et al., 1994; Essl and Voith, 2002) or simultaneously (Neugebauer et al., 2010b). Recently, Tier and Meyer (2012) used a method in which a gametic relationship matrix was used to estimate parent-of-origin effects, which seems to be a more sensible and powerful approach. The gametic relationship matrix can be calculated from the gametic pedigree which can be built from the animals' pedigree. In the gametic pedigree any animal has two probability elements including the maternal and paternal scores of genes being identical by descent (Schaeffer et al., 1989). Estimates of parent-of-origin effects in farm animals have been reported for pig (de Vries et al., 1994; Neugebauer et al., 2010a), cattle (Meyer and Tier, 2012; Tier and Meyer, 2012) and sheep (Amiri Roudbar et al., 2017). So far, parent-of-origin effects have been investigated for production traits, with no reports available for reproductive traits. Holl et al. (2004) showed that reproductive traits can be also affected by imprinted loci. Therefore, the aim of the present study was to estimate parent of origin variance, as well as genetic parameters, for productive and reproductive traits in Lori-Bakhteiari sheep, using a gametic relationship matrix.

2. Materials and methods

2.1. Animal and data collection

Lori-Bakhtiari sheep are primarily valued and raised for their meat production, and they have high-yield carcass yield. This breed is well adapted to pasture on mountains and cold weather conditions in the south western part of Iran. This breed has the largest fat-tail size among the other Iranian sheep breeds. To evaluate and increase the genetic and economic values of important traits in this breed, the Lori-Bakhtiari research flock, has been founded in 1989 under semi-migratory or village system, at Shooli station in Shahrekord, Iran. Ewes were randomly mated for the first time approximately at 18 months old to the rams more than 2 years old. From late August to late October, all sheep were grouped to single-sire pens with 20–25 ewes per ram, with lambing started in late January. Lambs were weighted and ear-tagged

within their first 24 h. During cold seasons, winter and spring, animals were kept in the Breeding Station, but in warm seasons, fall and summer, they were transferred to natural pasture (Vatankhah et al., 2008). Data and pedigree information for growth and reproduction traits used in this study were retrieved from National Animal Breeding Center (ABC) database in Iran, during a period of 18 years (1994–2012).

In this study, birth weight (BWT), weaning weight (WWT), 6-month weight (WT6), 9-month weight (WT9), yearling weight (WT12), average daily gain from birth to weaning (ADGa) and from weaning to 6-month (ADGb) were regarded as productive traits. Lamb age for WWT, WT6, WT9 and WT12 ranged from 60 to 120, 150 to 210, 210 to 320 and 320 to 395 days, respectively. Reproductive traits were classified under basic and composite groups. Litter size at birth (LSB, the total number of lambs born alive within a year per ewe lambing, coded as 1, 2 or 3), litter size at weaning (LSW, the total number of lambs weaned within a year per ewe lambing, coded as 0, 1 or 2), litter mean weight per lamb born (LMWLB, the average birth weight of lambs per ewe lambing) and litter mean weight per lamb weaned (LMWLW, the average weaning weight of lambs per ewe lambing) were analyzed as basic reproductive traits. Total litter weight at birth per ewe lambing (TLWB) and total litter weight at weaning per ewe lambing (TLWW) were also analyzed as composite reproductive traits. The structure and descriptive statistics of the data are summarized in Table 1. The population structure and inbreeding of our data were evaluated using ENDOG v4.8 program (Gutiérrez and Goyache, 2005). The summary of pedigree structure is shown in Table 2.

Table 2
The results of pedigree analysis of data.

Item	Value
Total individuals	7568
Average of inbreeding	0.53%
Mean of average relatedness	1.31%
Percentage of animals with known sire	87.59%
Percentage of animals with known dam	93.34%
Percentage of animals with known sire and dam	87.12%
Mean of maximum generations	4.67
Mean of complete generations	1.64
Mean of equivalent generations	2.86
Increase in inbreeding by maximum generation (ΔF)	0.14%
Effective population size (N_e) ^a	366.56
Effective number of founders for reference population	120
Effective number of ancestors for reference population	105
Effective population size of founders	144.97

^a N_e was estimated based on the change in inbreeding by maximum generation ($N_e = \frac{1}{2\Delta F}$).

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