Iranian Society of Animal Science

Journal of Livestock Science and Technologies

Shahid Bahonar University of Kerman

ISSN: 2322-3553 (Print) ISSN: 2322-374X (Online)

Paper type: Original Research

Genetic correlations between ewe reproductive and lamb weight traits in D’man sheep

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Received: 24 Jul 2021,
Accepted: 29 Oct 2021,
Published online: 22 Nov 2021,

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Abstract The objective of this study was to estimate genetic, phenotypic and residual correlations between ewe reproductive and lamb weight traits in D’man sheep. The data set consisted of 1804 reproductive and weight records collected between 1988 and 2015 from 530 replacement females, born from 82 sires and 298 dams. The ewe reproductive traits included litter size and litter weight at birth (LSB and LWB) and at 90 days (LSW and LWW) per ewe lambing and mating weight (MW), while the lamb weight traits investigated were weights at birth (BW), 90 (WW) and 135 (W135) days. Covariance components between the reproductive traits on the one hand and the weight traits on the other hand were estimated using bivariate analyses by employing the animal model that was deemed to be most appropriate from the univariate analyses for each trait. The genetic correlations between litter traits and body weights were low and in general not significantly different from zero ranging from -0.12 to 0.11, whereas those between ewe MW and lamb weights were positive and moderate varying from 0.16 to 0.51. The corresponding phenotypic correlations were slightly lower and varied from -0.04 between LSW and WW to 0.12 between LWW and BW and between LSW and W135. The residual correlations were in general similar to genetic correlations, except those between MW and body weights that were lower. It was concluded that selection for genetic improvement in either the reproductive and weight traits would have little effect on genetic response in the other trait.

Keywords: reproduction, growth, genetic parameter, covariance, phenotypic correlation

Introduction

The D’man breed is one of the most important local sheep -- breeds in Morocco. Its number is around 450000 sheep. It is raised in oases of Ziz and Draa valleys in Southeast of the country. The D’man is known for its exceptional reproductive -- traits (high prolificacy, precocious puberty, long sexual season…). As a matter of fact, its litter size at birth varied from 1 to 7 lambs with an average of 1.90 lambs (Boujenane, 1996). However, the D’man sheep have generally a slow growth rate (135 g/day for average daily gain between birth and days) and low body weights (2.14 kg and 14.5 kg at birth and 90 days, respectively) (Boujenane, 2006). Studies carried out reported low heritability estimates for ewe litter traits (Boujenane et al., 1991; Boujenane et al., 2013)- and, low to medium for lamb weight traits (Boujenane and Kerfal 1990; Boujenane et al., 2015). They also repo-

2021, 9 (2): 41-49 DOI: 10.22103/jlst.2021.17958.1376 http://lst.uk.ac.ir

rted positive genetic correlations among litter traits and among weight traits that ranged from 0.63 to 0.93 and from 0.66 to 1.00, respectively.

Genetic improvement of either ewe reproductive or lamb growth traits could be realized by direct selection for these traits. However, the possible presence of negative genetic correlations between reproductive and growth traits can undermine single-trait selection since direct selection for increasing one trait may lead to undesirable correlated responses in the other traits. Hence, to improve one group of traits without altering traits of the other group, the genetic and phenotypic correlations between ewe reproductive and lamb weight traits should be estimated in order to set up an optimal selection program and to predict the correlated responses from selection for particular traits.

Numerous studies have evaluated correlations between reproductive and growth traits in sheep. Notter et al. (2018) estimated the genetic correlations to range from 0.07 to 0.20 between lamb body weight and subsequent ewe number of lambs born and weaned per ewe lambing in Katahdin sheep. Bromley et al. (2001) studied Columbia, Polypay, Rambouillet, and Targhee sheep breeds and found that estimates of genetic correlations of birth weight with litter weight weaned ranged from -0.22 to 0.28. They concluded that if selection were practiced on litter weight weaned, the correlated responses would be expected to be favorable or neutral for prolificacy and growth traits. Snyman et al. (1998) observed in Afrino sheep high positive genetic correlations of 0.75, 0.77 and 0.89 between total weight of lambs weaned per ewe joined and weaning weight, weight at 9 and 18 months, respectively. The corresponding phenotypic correlations were low positive (0.13, 0.24 and 0.26, respectively). Hanford et al. (2003) reported estimates of genetic correlations near zero between weight at birth and litter size traits and small and positive between weaning weight and litter size traits in Targhee sheep. Mohammadi et al. (2013) found that genetic correlations between birth weight and ewe's reproductive traits in Makooei sheep varied from small to moderate, ranging between -0.14 and 0.22, and those between ewe reproduction traits and weaning weight varied from moderate to high, positively ranging between 0.36 and 0.67. They indicated that weaning weight could be considered as a selection criterion in indirectly improving the ewe's reproductive traits. In Zandi sheep, the genetic correlations between reproductive traits and birth weight varied from 0.10 to 0.86, with weaning weight from 0.37 to 0.96 and with weight at 6 months from 0.19 to 0.95 (Mohammadi et al., 2014). The authors suggested that selection to improve weaning weight would have high effect on genetic response in total litter weight at weaning, and all of the reproductive traits in Zandi sheep. Unfortunately, there are no such correlation estimates between ewe reproductive and lamb weight traits in D'man sheep.

Therefore, the aim of the present study was to estimate genetic, phenotypic and residual correlations -- between ewe reproductive and lamb weight traits in D'man sheep that are necessary to develop efficient selection strategies for improving the mentioned important traits.

Materials and methods

Study site and flock management

The data used in the present study were collected from the D'man sheep station located at 62° 54′ W longitude and 40° 39′ S latitude. In this station, the flock was managed under an accelerated reproduction system of three lambing in 2 years and was kept indoors during all year; no grazing being allowed. Ewe lambs were first mated at about 12 months of age. Depending on the lactation stage and number of suckled lambs, lactating ewes were provided with 0.8 to 1.2 kg concentrate containing wheat bran, barley, sugar beet pulp, date residue and vitamin and mineral mix, and 1 to 3 kg of alfalfa. Pregnant ewes were fed 0.6 to 0.8 kg concentrate and 1 to 2 kg of alfalfa. At lambing, ewes' udders were inspected to assess the milk yield. Excess lambs from multiple births were artificially reared, as were lambs that could not be reared by their own dam. After lambing, lambs and their mothers were individually penned for 1 to 3 days, according to the size of the litter. Lambs were kept with their mothers until weaning at about 90 days. After weaning, lambs were placed in separate sex groups and were offered about 500 g/day of the same feed for the first 2 months after weaning. Ewes were vaccinated against enterotoxemia and treated against internal and external parasites. At 1 month of age, lambs were vaccinated against enterotoxemia with a booster 1 month later. They were also treated against internal parasites at weaning. More details regarding the flock management can be found in Boujenane et al. (2015).

Data recorded and traits analyzed

Data were collected for lambing years 1988 to 2015. Newborn lambs were identified individually by an ear tag, and dam identification number, birth date, sex and type of birth were recorded within 18 hours of birth. The lambs were weighed at birth (BW) and every 3 weeks until weaning. The weights at 90 days (WW) and 135 days (W135) were obtained by linear interpolation using the appropriate weightings. The reproductive traits analyzed were litter size at birth (LSB) defined as the number of lambs born alive or dead per ewe lambing; it had seven categories, litter size at 90 days (LSW) was the number of lambs present at 90 days per ewe lambing; it had five categories, litter weight at birth (LWB) was the sum of birth weights of lambs born for each ewe lambing and litter weight at 90 days (LWW) was the sum of individual weights at 90 days of all lambs naturally weaned per ewe lambing. Before calculating litter weight at birth and at 90 days, individual lamb weights at birth and at 90 days were adjusted for differences due to sex of lamb by adding to females' weights 0.18 kg and 3.3 kg, respectively. Also, mating weight (MW) represents the ewe's live weight recorded at mating.

Statistical analyses

The dataset for all traits included 1804 reproductive and weight records from 530 replacement females, born from 82 sires and 298 dams. Descriptive statistics for studied traits are shown in Table 1. For each ewe, there are as many records as there are lambing. Each record of this dataset commonly included lamb weight traits of the ewe and reproductive traits recorded at one of its lambing. Progeny records of sires with fewer than 5 progeny in the dataset were omitted. The least squares analyses of variance using the GLM procedure of SAS (2002) was applied to identify important fixed effects to be considered in the final model. The statistical model for reproductive traits included fixed effects for age at lambing (5 levels: age ≤1.5, 1.5 < age≤2, 2 < age≤2.5, 2.5 < age≤3 and age >3 years), parity (5 levels: 1, 2, …, 5 or greater) and period of lambing (41 levels: autumn-1988, …, autumn-2015), which is a combination of season of lambing (spring, summer and autumn) and year of lambing (1988-2015). The one for weight traits included fixed effects for age of dam (5 levels: age ≤1.5, >1.5 to ≤2, >2 to ≤2.5, >2.5 to ≤3 and >3 years), type of birth (4 levels: single, twin, triplet, and quadruplet or greater) and period of birth (35 levels), which is a combination of season of birth (3 levels: spring, summer and autumn) and year of birth (1988-2015). Sex was excluded for weight traits because only the weights of the ewes with reproduction records were included in this dataset. Interactions between fixed effects were not tested for all traits and hence were assumed to be negligible. Effects found to be significant (P<0.05) in these analyses were included in subsequent analyses.

Table 1. Summary statistics of the traits studied

Trait[a]	Number of records	Arithmetic mean	Standard deviation	Coefficient of variation (%)	Minimum	Maximum
Ewe						
LSB	1804	2.36	0.95	40.2	1	7
LSW	1804	2.01	0.95	47.3	0	5
LWB (kg)	1804	6.18	1.99	32.2	1.00	14.0
LWW (kg)	1804	38.4	17.3	45.0	0.00	87.0
MW (kg)	1804	45.6	7.93	17.4	23.0	85.0
Lamb						
BW (kg)	1804	2.69	0.60	22.3	1.00	4.00
WW (kg)	1804	19.0	2.80	14.7	9.00	26.5
W135 (kg)	1804	27.0	3.46	12.8	13.0	40.7

[a] BW: birth weight, WW: weight at 90 days, W135: weight at 135 days, LSB: litter size at birth, LSW: litter size at 90 days, LWB: litter weight at birth, LWW: litter weight at 90 days, MW: mating weight

For the estimation of genetic parameters, single-trait analyses were initially implemented with derivative-free restricted maximum likelihood procedures using the MTDFREML program of Boldman et al. (1995). For each weight trait, 12 different animal models were fitted by ignoring or including maternal additive genetic effect, maternal permanent environmental effect, maternal temporary environmental effect (i.e. litter) and covariance between direct and maternal additive genetic effects.

$$y = Xb + Z_a a + e \tag{1}$$

$$y = Xb + Z_a a + W_{pe} pe + e \tag{2}$$

$$y = Xb + Z_a a + Z_m m + e \quad \text{with} \quad Cov(a,m) = 0 \tag{3}$$

$$y = Xb + Z_a a + Z_m m + e \quad \text{with} \quad Cov(a,m) = A\,\sigma_{am} \tag{4}$$

$$y = Xb + Z_a a + Z_m m + W_{pe} pe + e \quad \text{with} \quad Cov(a,m) = 0 \tag{5}$$

$$y = Xb + Z_a a + Z_m m + W_{pe} pe + e \quad \text{with} \quad Cov(a,m) = A\,\sigma_{am} \tag{6}$$

$$y = Xb + Z_a a + W_c c + e \tag{7}$$

$$y = Xb + Z_a a + Z_m m + W_c c + e \quad \text{with} \quad Cov(a,m) = 0 \tag{8}$$

$$y = Xb + Z_a a + Z_m m + W_c c + e \quad \text{with} \quad Cov(a,m) = A\,\sigma_{am} \tag{9}$$

$$y = Xb + Z_a a + W_{pe} pe + W_c c + e \tag{10}$$

$$y = Xb + Z_a a + Z_m m + W_{pe} pe + W_c c + e \quad \text{with} \quad Cov(a,m) = 0 \tag{11}$$

$$y = Xb + Z_a a + Z_m m + W_{pe} pe + W_c c + e \quad \text{with} \quad Cov(a,m) = A\,\sigma_{am} \tag{12}$$

where **y** is a vector of observations, **b** is a vector of fixed effects with incidence matrix **X**, **a** $\sim N(0, \mathbf{A}\sigma^2_a)$ and **m** $\sim N(0, \mathbf{A}\sigma^2_m)$ are vectors of direct and maternal additive genetic effects with incidence matrices $\mathbf{Z_a}$ and $\mathbf{Z_m}$, respectively, **pe** ~N(0, $\mathbf{I_d}\,\sigma^2_{pe}$) is a vector of random maternal permanent environmental effects with incidence matrix $\mathbf{W_{pe}}$, **c** ~N(0, $\mathbf{I_c}\,\sigma^2_{c}$) is a vector of random maternal temporary environmental effects with incidence matrix $\mathbf{W_c}$, and **e** ~N(0, $\mathbf{I_n}\,\sigma^2_{e}$) is a vector of random residual effects. Also, σ^2_a is the direct additive genetic variance, σ^2_m is the maternal additive genetic variance, σ_{am} is the covariance between direct and maternal additive genetic effects, σ^2_{pe} is the maternal permanent environmental variance, σ^2_c is the maternal temporary environmental variance, σ^2_e is the residual variance, **A** is the additive genetic relationship matrix, and $\mathbf{I_d}$, $\mathbf{I_c}$ and $\mathbf{I_n}$ are identity matrices of order equal to the number of dams, the number of litters and the number of records, respectively.

Similarly, for each reproductive trait, two animal models were fitted by ignoring or including permanent environmental effect due to repeated records. For all traits, convergence was considered reached when the variance of function values (-2 log L) in the simplex was less than 10^{-8}. To ensure that a global maximum was reached, several other rounds of iterations were used using results from the previous round as starting values. When estimates did not change at the second decimal, convergence was confirmed. The likelihood ratio test was used in order to select the most appropriate model for each trait. For two models with the same number of different random effects, and assuming identical fixed effect modelling, the model with the higher value for the log-likelihood fits the data best. The model with the fewest random effects was selected when differences between log likelihoods were not significant.

Covariance components between the ewe reproductive traits on the one hand and the lamb weight traits on the other hand were estimated using bivariate analyses by employing the model that was deemed to be most appropriate from the univariate analyses for each trait. The following bivariate animal models were fitted for the estimation of covariance components between reproductive traits and weight at birth and 90 days:

$y = Xb + Za + e$

$y = Xb + Z_a a + Z_m m + e$ with $\mathrm{Cov}(a,m) = A\sigma_{am}$

For reproductive traits and weight at 135 days, the following bivariate animal models were fitted:

$y = Xb + Za + e$

$y = Xb + Z_a a + Z_m m + Wpe + e$ with $\mathrm{Cov}(a,m) = A\sigma_{am}$

where **y**, **b**, **a**, **m**, **pe**, and **e** are the vectors of observations, fixed effects, direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects and residual random effects for the trait, respectively. Also, **X**, $\mathbf{Z_a}$, $\mathbf{Z_m}$ and **W** are incidence matrices relating the observations of the trait to fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects, respectively, σ_{am} is the covariance between direct and maternal additive genetic effects and **A** is the additive genetic relationship matrix. (Co)variance components from single-trait analyses were used to obtain starting values. Iterations were stopped when the variance of function values (-2 log L) in successive iterations changed less than 10^{-4} and then less than 10^{-6}, and analyses were repeated with converged estimates as priors to ensure global convergence.

Results and discussion

Estimates of genetic, phenotypic and residual correlations from bivariate analyses between ewe reproductive and lamb weight traits are presented in Table 2.

Table 2. Genetic, phenotypic and residual correlations between ewe reproductive (LSB, LSW, LWB, LWW and MW) and lamb weight (BW, WW and W135) traits[a]

	LSB	LSW	LWB	LWW	MW
			Genetic correlations		
BW	0.01±0.09	0.01±0.10	0.11±0.09	0.04±0.10	0.16±0.05
WW	-0.03±0.09	-0.10±0.10	0.11±0.09	-0.12±0.10	0.50±0.04
W135	0.00±0.10	-0.04±0.11	0.10±0.09	-0.08±0.12	0.51±0.09
			Phenotypic correlations		
BW	0.01	0.00	0.05	0.12	0.13
WW	-0.01	-0.04	0.04	-0.05	0.41
W135	0.00	0.01	0.04	-0.04	0.42
			Residual correlations		
BW	0.02±0.03	0.02±0.03	0.02±0.03	-0.01±0.03	-0.08±0.03
WW	-0.01±0.03	-0.03±0.03	-0.02±0.03	-0.05±0.03	0.01±0.03
W135	-0.04±0.04	0.04±0.04	-0.05±0.03	-0.07±0.02	0.04±0.02

[a] BW: birth weight, WW: weight at 90 days, W135: weight at 135 days, LSB: litter size at birth, LSW: litter size at 90 days, LWB: litter weight at birth, LWW: litter weight at 90 days and MW: mating weight

Correlations between birth weight and reproductive traits

The BW had positive and low genetic correlations with high standard errors with subsequent litter traits ranging from 0.01 with LSB and LSW to 0.11 with LWB, while its genetic correlation with MW was 0.16. The standard errors for the genetic correlations between BW and litter traits ranged from 0.09 to 0.12. Composite reproductive traits are expected to have high genetic correlation with each component trait. Thus, the relatively higher correlation between BW and LWB would be expected because BW is a component of LWB of the ewe. The low positive correlations between BW and reproductive traits might indicate that additive genetic effects on BW were essentially independent or only slightly genetically correlated to additive genetic effects on subsequent reproductive traits, suggesting that selection to improve genetic merit of BW would have a favorable or neutral impact on genetic responses in subsequent ewe reproductive traits. The findings of this study generally agree with most published estimates. Bromley et al. (2000) reported low to moderate genetic correlation between BW and LSB (from -0.01 to 0.26) and between BW and LSW (from -0.37 to 0.01) for Columbia, Polypay, Rambouillet and Targhee sheep breeds. Estimates of the genetic correlation between BW and LSB and between BW and LSW were 0.10 and 0.00, respectively in Columbia (Hanford et al., 2002), 0.00 and 0.00, respectively in Targhee (Hanford et al., 2003), 0.24 and 0.00, respectively in Rambouillet (Hanford et al., 2005) and 0.10 and 0.00, respectively in Polypay (Hanford et al., 2006) sheep breeds. Moreover, Mohammadi et al. (2013) found estimates of genetic correlation between BW and LSB, LSW, LWB and LWW of -0.07, -0.14, 0.22 and -0.03, respectively in Makooei sheep, and Safari et al. (2005) reported averages of 0.12, -0.09 and 0.12 between BW and LSB, LSW and LWW, respectively. Maxa et al. (2007) observed similar genetic correlations between BW and LSB in Texel (0.04) and Suffolk (0.02) breeds. These results, like those of the current study, indicate that selection to improve BW would have little influence on genetic response in reproductive traits. Contradictory to the results of the present study, Vatankhah and Talebi (2008) found high genetic correlation between BW and LWB (0.98) and between BW and LWW (0.75) in Lori-Bakhtiari sheep breed, and Mohammadi et al. (2014) reported comparable genetic correlations between BW and LSB (0.10), LSW (0.14), LSB (0.86) and LWW (0.72) in Zandi sheep. The genetic correlation between lamb BW and ewe MW reported in the current study is in the same line with those reported by Borg et al. (2009) between lamb BW and ewe adult weight at weaning (0.36), early lactation (0.21) and late gestation (0.40) in Western Range sheep.

The phenotypic correlations between BW and studied reproductive traits were positive, but slightly lower than their corresponding genetic ones. Estimates were 0.01, 0.00, 0.05, 0.12 and 0.13 between BW and LSB, LSW, -LWB, LWW and MW, respectively. Mohammadi et al. (2013) reported closer phenotypic correlations to those of this study between BW and litter traits (-0.08, -0.02, 0.02 and 0.02) and Notter et al. (2018) found -0.04 for BW-LSB and 0.001 for BW-LSW. Moreover, the results of this study are in part consistent with those of Vatankhah and Talebi (2008) and Mohammadi et al. (2014) between BW and LSB (0.05 and 0.03), LSW (0.02 and 0.01), LWB (0.20 and 0.28) and LWW (0.11 and 0.17) in two Iranian sheep breeds.

The residual correlations were positive and low between BW and LSB, LSW and LWB (0.02) and negative and low for BW-LWW (-0.01) and BW-MW (-0.08). Positive correlations indicate that an environment that is favorable to improvement of lamb birth weight will have a simultaneous improvement in ewe reproductive traits. Mohammadi et al. (2014) reported positive residual correlations varying from 0.02 to 0.09 between BW and litter traits for Zandi sheep and Bromley et al. (2000) found estimates ranging from 0.00 to 0.04 between BW and LSB and from 0.00 and 0.01 between BW and LSW for Columbia, Polypay, Rambouillet and Targhee sheep breeds. Contradictory to the negative residual correlation between lamb BW and ewe MW found in the present study, Borg et al. (2009) reported values of 0.27, 0.24 and 0.05 between lamb BW and ewe adult weight at weaning, early lactation and late gestation, respectively in western range sheep.

Correlations between lamb weight at 90 days and ewe reproductive traits

Estimates of genetic correlation were negative and low between WW and LSB (-0.03), LSW (-0.10) and LWW (-0.12), indicating that these measures of litter traits and WW are unrelated traits, positive and low between WW and LWB (0.11) and positive and moderate between WW and MW (0.49). Thus, selection to increase WW would have little or no influence on genetic merit for the reproductive trait. LWW is a composite trait of LSB, WW and survival of lambs in the litter. The negative correlation between WW and LWW is a misleading result because it was expected to find a positive correlation since WW is a multiplicative component of LWW. This result might indicate that the main component of LWW is LSB. Therefore, to improve LWW, selection should primary increase LSB of ewes rather than WW of lambs. Numerous genetic correlations between lamb weaning weight and ewe reproductive traits were reported in literature, and the majority of them indicated positive genetic correlations, so that selection for either one of these two traits might result in some increase in genetic merit for the other trait. Some of these findings are: WW-LSB (0.23), WW-LSW (0.14), WW-LWB (0.78) and WW-LWW (0.98) (Vatankhah and Talebi, 2008), WW-LSB (0.36), WW-LSW (0.43), WW-LWB (0.37) and WW-LWW

(0.67) (Mohammadi et al., 2013), WW-LSB (0.37), WW-LSW (0.52), WW-LWB (0.81) and WW-LWW (0.72) (Mohammadi et al., 2014), and WW-LSB (0.18) and WW-LSW (0.07) (Notter et al., 2018). Likewise, Rao and Notter (2000) observed that genetic correlations between WW and LSB were positive and often significant in Targhee and Suffolk sheep, but did not differ from zero in Polypay sheep. Furthermore, Borg et al. (2009) reported similar genetic correlation to that of this study between lamb WW and ewe adult weight at weaning, early lactation and late gestation of 0.36, 0.21 and 0.40, respectively.

The WW had negative phenotypic correlations varying from -0.05 to -0.01 with LSB, LSW and LWW, and it was phenotypically positively correlated with LWB (0.04) and MW (0.41). Our results were generally consistent with estimates of phenotypic correlations in literature that varied from 0.02 to 0.10 between WW and LSB (Safari et al., 2005; Vatankhah and Talebi, 2008; Afolayan et al., 2009; Mohammadi et al., 2013; Mohammadi et al., 2014; Notter et al., 2018), from 0.02 to 0.05 between WW and LSW (Vatankhah and Talebi, 2008; Mohammadi et al., 2013; Mohammadi et al., 2014; Notter et al., 2018), from 0.04 to 0.14 between WW and LWB and from 0.04 to 0.22 between WW and LWW (Vatankhah and Talebi, 2008; Mohammadi et al., 2013; Mohammadi et al., 2014).

Bivariate analyses of lamb WW and ewe reproductive traits yielded almost similar residual correlations ranging from -0.05 with LWW to 0.01 with MW. Few studies have shown estimates of residual correlation between lamb WW and ewe reproductive traits. Mohammadi et al. (2014) reported values ranging from 0.10 to 0.16 between WW and litter traits. Also, residual correlations between WW and LSB and LSW varying from 0.03 and 0.07 and from -0.01 and 0.04, respectively, were reported for Columbia (Hanford et al., 2002), Targhee (Hanford et al., 2003), Rambouillet (Hanford et al., 2005) and Polypay (Hanford et al., 2006) dual purpose sheep breeds.

Correlations between lamb weight at 135 days and ewe reproductive traits

The lamb post-weaning W135 was negatively genetically correlated to LSW and LWW, positively correlated to LWB and MW, and uncorrelated with LSB. Estimates were -0.04, -0.08, 0.00, 0.10 and 0.51 with LSW, LWW, LSB, LWB and MW, respectively. Estimates of genetic correlation between lamb post-weaning weight and ewe's reproductive traits in literature are scarce. They ranged from 0.10 to 0.92 (Vatankhah and Talebi, 2008) and from 0.19 to 0.95 (Mohammadi et al., 2014) between weight at 6 months and litter traits. Zishiri et al. (2013) found a high and positive genetic correlations (0.72) between post-weaning weight and LWW in the South African Dorper sheep breed, and Notter et al. (2018) reported low to moderate genetic correlations between -post-weaning weight and LSB (0.20) and between post-weaning weight and LSW (0.11) for Katahdin sheep breed. Likewise, Safari et al. (2005) reported averages of 0.17 and 0.06 between post-weaning weight and LSB and between post-weaning weight and LSW, respectively. In crossbred ewes, Afolayan et al. (2009) found a genetic correlation between post-weaning weight and LSB of 0.32. Borg et al. (2009) observed genetic correlations of 0.31 and -0.53 between weights at 120 and 365 days and LSB, respectively. They argued that the negative correlation between W365 and LSB might reflect an inverse relationship between body size and age at maturity, with larger animals reaching physiological maturity at older ages, thereby influencing lambing rates in younger ewes.

The phenotypic correlations for W135 and the various reproductive traits were negative with LWW (-0.04), nil with LSB and positive with LSW (0.01), LWB (0.04) and MW (0.42). The estimates of phenotypic correlation between post-weaning weight and LSB and between post-weaning weight and LSW were -0.06 and -0.06 for the Katahdin breed (Notter et al., 2018). Positive and low average phenotypic correlation was estimated between post-weaning weight and LSB (0.01) by Safari et al. (2005). Vatankhah and Talebi (2008) and Mohammadi et al. (2014) reported positive and low phenotypic correlations between weight at 6 months and litter traits that ranged from 0.01 to 0.14 and from 0.02 to 0.11, respectively.

The residual correlations were negative and ranged from -0.07 (W135-LWW) to -0.04 (W135- LSB), but positive between W135 and LSW as well as between W135 and MW (0.04). A different pattern of residual correlations found by Mohammadi et al. (2014) between weight at 6 months and litter traits ranged from 0.07 to 0.13.

Correlation between the maternal additive genetic effect for weight traits and the direct additive genetic effect for reproductive traits

All the correlations between maternal additive effect for lamb weight traits and direct additive effect for ewe reproductive traits did not differ from zero, and were smaller than their standard errors. The absence of correlations might indicate that there is no connection between maternal genes affecting weight traits and direct genes affecting reproductive traits. Estimates obtained in the current study were in agreement with those for WW and LSB that did not differ from zero for Targhee and Polypay sheep (Rao and Notter, 2000), and for BW, WW and post WW on one hand and LSB and LSW on the other hand that were negative and not significant except for that between BW and LSB (Notter et al., 2018). The latter workers explained their result by the adjustment of lamb BW for effects of litter size and rearing type in bivariate models that potentially removed transmitted additive effects of genes from the dam with additive effects on both BW and LSB or LSW. However, our results are conflicting with the positive correlations that ranged from moderate for Rambouillet and Targhee (0.43 and0.35) to large (0.70 and 0.71) for Columbia and Polypay breeds for LWW and BW (Bromley et al., 2001). The authors argued that such positive correlations would be expected because birth weight is a component of LWW of the ewe and a positive maternal effect on individual lamb BW would be expressed in LWW as a trait of the ewe. Likewise, estimates of correlations between direct genetic effects for LSB or LSW and maternal genetic effects for BW or WW varied from 0.21 to 0.66 in Columbia (Hanford et al., 2002), from 0.18 to 0.58 in Targhee (Hanford et al., 2003), from 0.06 to 0.70 in Rambouillet (Hanford et al., 2005) and from -0.03 to 0.73 in Polypay (Hanford et al., 2006) sheep breeds. Heydarpour et al. (2008) suggested that complete datasets with more links between dam performance records and offspring records, as well as more progeny per dam are required for reliable estimates of maternal genetic parameters for the single- and multiple trait situations.

General

Genetic, phenotypic and residual correlations observed in the present study between the ewe reproductive and lamb weight traits are in line with those reported by most other researchers (Hanford et al., 2002; Hanford et al., 2006; Notter et al., 2018), with the genetic correlations being generally smaller than their standard errors. The differences between results obtained in this study and the literature could be attributed mainly to the structure of data analyzed and the animal models applied. Researchers have analyzed datasets with different numbers of observations, individuals, sires, dams with and without records and number of progeny per sire and per dam. Maniatis and Plott (2003) suggested that data structure and the number of dams and grand-dams with records are important determinants of estimated direct and maternal effects in early growth traits. Moreover, reproductive and weight traits of replacement females only were used in this study, while in some other studies (Vatankhah and Talebi, 2008; Mohammadi et al., 2013, 2014) weight traits of males and females not retained as replacement, *i.e.* without reproductive traits, were included in the analyses. Also, most studies (Vatankhah and Talebi, 2008; Mohammadi et al., 2013, 2014; Zishiri et al., 2013) have used for bivariate analyses animal models that were deemed to be most appropriate from the univariate analyses for each trait. Thus, these models incorporated combinations of direct additive genetic, maternal additive genetic, maternal permanent environmental and maternal temporary environmental effects, with and without covariance between direct and maternal additive genetic effects. Also, residual effects on lamb BW were assumed independent of future permanent environmental and residual effects on LSB and LSW in retained replacement females (Notter et al., 2018), resulting in direct additive correlations between LSB and LSW and lamb BW that were consistently positive. Likewise, Hanford et al. (2002, 2003, 2005, 2006) included a permanent environmental effect in the model for weight traits that were measured only once for each animal. This assignment of a permanent environmental effect to those traits had forced the covariance between environmental effects into the covariance between permanent environmental effects rather than to the covariance between residual effects when one of the traits was measured more than once, hence allowing to estimate environmental correlations between an animal's own traits. Additionally, Notter et al. (2018) noted that excluding records of yearling ewes reduced estimates of direct additive correlations between lamb BW and ewe LSB and LSW by approximately 50%, suggesting that there may have been a small positive phenotypic carryover effect of lamb BW on reproductive performance in yearling ewes.

Furthermore, the differences between results could be also ascribed to the rate of twinning in different breeds of sheep (Vatankhah and Talebi, 2008). Some breeds studied by different researchers had a low twinning rate. Therefore, LWW was correlated to lamb WW, unlike that in prolific breeds such as the breed of the current study. Likewise, Hanford et al. (2006) explained the small estimate of genetic correlation between LSW and WW by the imposed restriction on the number of lambs that a ewe was allowed to rear.

Early weight traits in ewes were not positively and favorably genetically correlated with reproductive traits as it was expected. Afolayan et al. (2009) reported that the genetic relationships were generally slightly stronger for growth traits at later ages and the ewe productivity traits, suggesting that selection to increase any of the early growth traits for the ewes would result in a moderate increase in subsequent ewe reproduction as well as some improvement in the growth of their lambs.

Conclusion

Genetic correlations between lamb weight and ewe reproductive traits in D'man sheep breed were generally low and close to zero. These findings suggested that early selection based on increasing body weights will unlikely result in improvement in subsequent ewe reproductive traits, and vice-versa. Also, they indicated that selection for increased body weight may not have an undesirable genetic effect on the litter traits, chiefly the litter size at birth that is actually considered as optimum by D'man breeders.

Conflict of interest

The authors declare that there is no conflict of interest regarding this manuscript.

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