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Evaluating maternal imprinting effects for growth and reproductive traits in Murciano-Granadina goats

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Abstract This research aimed to conduct a genetic analysis of maternal imprinting effects on growth and reproductive characteristics in the Murciano-Granadina goats. Data for the present study were recorded between 2016 and 2022 on a farm in the Kerman province, Iran. Traits studied were body weight at birth (WB) and weaning (WW), pre-weaning average daily gain (ADG), Kleiber ratio (KR) and growth efficiency (GE). Reproduction traits were litter size at birth (LSB), litter size at weaning (LSW), total litter size at birth (TLWB) and total litter size at weaning (TLWW). An animal model was used to analyze the data. Comparison of the models with and without maternal imprinting effects was performed using Akaike's information criterion (AIC). Maternal imprinting had a significant impact on WB and LSW. The heritability estimates for maternal imprinting ($\mathrm{h}^2_{\mathrm{mi}}$) were 0.07±0.07 for WB and 0.07±0.02 for LSW. Accounting for maternal imprinting effects into the model resulted in a reduction of 2% and 56% in the direct heritability of WB and LSW, respectively. In addition, the value of $\mathrm{h}^2_{\mathrm{m}}$ for WB was reduced by approximately 75%. The results implied that there are maternal imprinting effects on the WB and LSW of Murciano-Granadina goats. Hence, the genetic evaluation models for these traits should consider the effect of maternal imprinting effect.

Keywords: body weight, goats, heritability, maternal imprinting effect, variance components

Introduction

Genomic imprinting, an epigenetic modification on a parental chromosome in the gamete or zygote, resulted in differential gene expression in the offspring (Neugebauer et al., 2010). Parent-of-origin effects are primarily attributed to genomic imprinting, a mechanism that involves parent-specific DNA methylation, known as imprints, which silences one copy of a gene inherited from a parent (Hu et al., 2016; Triantaphyllopoulos et al., 2016; Hofmeister et al., 2022). Imprinting effects modify gene expression based on the parental origin of alleles, a phenomenon known as the parent-of-origin effects (Blunk et al., 2017; Laurin et al., 2018; Okamoto et al., 2019). These effects become apparent only when the alleles from the parents are dissimilar (Guilmatre and Sharp, 2012; Lawson, 2013). In maternal imprinting, the mother's alleles are silenced in the offspring, either partially or completely (Neugebauer et al., 2010; Macias-Velasco et al., 2022). Imprinting plays a crucial role in animal breeding programs, as neglecting it may lead to biased estimates of the breeding values and genetic parameters (Tier and Meyer, 2012). Recent studies have shown the significant contribution of maternally imprinted genes on complex traits in pigs (Neugebauer et al., 2010), beef cattle (Meyer and Tier, (2012), chickens (Karami et al., 2019), and sheep (Ghafouri-Kesbi et al., 2022a, 2022b).

To promote rural development, governmental and private organizations suggest using highly productive exotic dairy goat breeds (Mokhtari et al., 2024b). Murciano-Granadina goats are renowned worldwide their dairy characteristics, ease of breeding, and tolerance to adverse environmental conditions (Martinez et al., 2011; Leon et al., 2012; Delgado et al., 2017). These characteristics have led to the decision to import approximately 3,000 Murciano-Granadina goats to the Iran since 2015 (Kaveh Baghbadorani et al., 2024; Mokhtari et al., 2024a). Purebred does and bucks were provided to local herds, or crossed with local goat breeds to attain this objective. The goal of this plan is to improve the efficiency of small-scale goat breeding farms that operate with minimal inputs, as well as to enhance the overall welfare of rural goat keepers in the southern Iran (Mokhtari et al., 2024a). While Murciano-Granadina goat breeding primarily emphasizes dairy production, it is crucial to consider the genetic and phenotypic characteristics associated with growth and reproduction to establish an effective breeding plan for Murciano-Granadina breed and local goats.

Although numerous imprinted genes, including IGF2–H19, CDKN1C–KCNQ1, and DLK1–GTL2 have been detected in livestock species which significant effects on muscle and growth performance (Hubert et al., 2024), due to a lack of suitable software, quantifying their contribution to the phenotypic variation of economic traits in livestock was delayed until recent years. Applying efficient softwares, several studies estimated the parent-of-origin effects on growth and reproductive traits in sheep and goats (Amiri Roudbar et al., 2018; Ghafouri-Kesbi et al., 2022a; Mokhtari et al., 2022a). These studies showed that separating imprinting genetic effects from additive genetic effects enhance the accuracy of genetic parameters and breeding values. However, as far as we know, there have been no previous reports on the maternal imprinting effects on the economic traits in Murciano-Granadina goats. Hence, this research quantified the maternal imprinting effects on growth and reproductive traits in Murciano-Granadina goats.

Materials and methods

Data and herd management

In this study, we used the data from Mokhtari et al. (2024a; 2024b) recorded over six years (2016-2022) at a private dairy goat flock in Chah-Shahi village, Ghaleh-Ganj city, Kerman province, Iran. This region has a hot, semi-arid and desert-like climate, 409 m above mean sea level and with average annual rainfall of 166 mm (Kaveh Baghbadorani et al., 2024). The goats, managed under intensive conditions, were grouped based on their sex, age, and health status. The health status of the goats was evaluated based on their body condition score, appetite, and mobility. Alfalfa hay, wheat straw, corn silage, sugar beet pulp, and concentrates were fed based on the age and production level. The concentrate mixture contained (per kg) 210 g barley, 400 g corn, 225 g soybean and rapeseed meals, 85 g meat and fat powder, 77 g vitamin and mineral mixture, and 3 g common salt. Water was available freely and the animals were treated with antiparasitic drugs (Ivermectin and Paranil) and vaccinated against enterotoxaemia, foot-and-mouth disease, and brucellosis. The breed does not exhibit seasonal reproductive behavior, and bucks are typically housed together with does for an unspecified period. The kids were ear-tagged at birth, and their parents, date of birth, gender, type of birth, and birth weight were recorded. The kids were kept with their dams for approximately ten days, after which they were separated by their gender. Kids were weaned at around 80 days of age. At approximately nine months' of age and 25 kg weight, the does were mated with bucks at 15:1 ratio.

Evaluated traits

The evaluated traits were the weight of kids at birth (WB) and weaning (WW), pre-weaning average daily gain (ADG), and pre-weaning efficiency-related traits such as the Kleiber ratio (KR; Kleiber, 1947) and growth efficiency (GE; Dass et al., 2004). The ADG, KR, and GE were computed as ([WW-WB]/weaning age) × 1000, ADG/WW$^{0.75}$ and ([WW-WB]/WB) × 100, respectively. The reproductive traits analyzed included the litter size at birth (LSB), litter size at weaning (LSW), total litter weight at birth (TLWB), and total litter weight at weaning (TLWW). The TLWB and TLWW were computed after adjusting the birth weight and weaning weights for the gender by applying the multiplicative adjustment factors. The least squares analysis was used to determine the adjustment factors.

Statistical analysis

The GLM procedure of SAS software (SAS, 2004) was applied to identify the environmental factors that should be included in the animal model. Year of kidding (7 classes), month of kidding (12 classes), age of dam at kidding (6 classes), gender of kids (2 classes), and birth type (3 classes) were considered as the fixed effects for growth and efficiency-related traits (KR and GE). The year-month interaction was also significant for WB and GE and, therefore, was included in the fixed part of the model. The kidding year (6 classes) and doe age (6 classes) were the fixed effects for reproductive traits. For WW and TLWW, the kids' age at weaning (in days) was used as a linear covariate.

Growth and efficiency-related traits

A two-step procedure was employed to study the influence of maternal imprinting effects on the traits of interest. The first stage involved the analysis of growth and efficiency-related traits using six univariate animal models, ignoring maternal imprinting effects (models 1-6). Various random effects were included in models, such as direct additive genetic, maternal additive genetic, and maternal permanent environmental effects. The univariate models were as follows:

y=Xβ+Z₁a+e		Model 1
y=Xβ+Z₁a+Z₂c+e		Model 2
y=Xβ+Z₁a+Z₃m+e	Cov(a,m)=0	Model 3
y=Xβ+Z₁a+Z₃m+e	Cov(a,m)=Aσam	Model 4
y=Xβ+Z₁a+Z₃m+Z₂c+e	Cov(a,m)=0	Model 5
y=Xβ+Z₁a+Z₃m+Z₂c+e	Cov(a,m)=Aσam	Model 6

where, **y** is a vector of records for the studied traits; **β**, **a**, **c**, **m**, and **e** represent the vectors of fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental, and residual effects, respectively. Incidence matrices **X**, $\mathbf{Z_1}$, $\mathbf{Z_2}$, and $\mathbf{Z_3}$ relate the records to the corresponding effects. The (co)variance structure of the random effects for the full model was as follows:

$$\mathrm{Var}\begin{bmatrix}\mathbf{a}\\ \mathbf{m}\\ \mathbf{c}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{a,m} & 0 & 0\\ \mathbf{A}\sigma_{a,m} & \mathbf{A}\sigma_m^2 & 0 & 0\\ 0 & 0 & \mathbf{I}_c\sigma_c^2 & 0\\ 0 & 0 & 0 & \mathbf{I}_n\sigma_e^2\end{bmatrix}$$

where, the σ_a^2, σ_m^2, σ_c^2, and σ_e^2 are variances for direct additive genetic, maternal additive genetic, maternal permanent environmental, and residual factors, respectively. $\mathbf{I}_c$ and $\mathbf{I}_e$ are identity matrices, with their dimensions corresponding to the number of does and records, respectively. The matrix **A** captures the additive genetic relationships. Moreover, σ_{am} signifies the covariance between direct and maternal genetic effects. The best model for each trait (Model **M**) was selected based on the Akaike's information criterion (AIC) (Akaike, 1974):

AIC= -2LogL+2p

in which, Log L corresponds to the maximum Log likelihood, and p represents the number of parameters to be estimated. The model deemed the best had the lowest AIC.

In the second step maternal imprinting effect was added to Model M and changes in AIC values were monitored. Paternal imprinting effect was not considered because of computational problems which prevent the analyses to be converged. The animal model that included the maternal imprinting effects was as follows:

Model 7: **y=M+Z₄gₘ+e**

where, **M** represents the fixed and random effects selected in the initial step; $\mathbf{Z_4}$ is the incidence matrix relating observations to the maternally imprinted effects, and $\mathbf{g_m}$ represents the vector of maternally imprinted effects. The random effect covariance structure for Model 7 was as follows:

$$\mathrm{Var}\begin{bmatrix}\mathbf{l}\\ \mathbf{g_m}\end{bmatrix} = \begin{bmatrix}\mathbf{\Sigma} & 0\\ 0 & \mathbf{G}\sigma_{gm}^2\end{bmatrix}$$

in which, **l** represents the vectors of random effects in the selected model's first step for each trait; **Σ** denotes the covariance matrix structure of the chosen model. It was assumed that $\mathbf{g_m}$ ~ *N* (0, $\mathbf{G}\sigma_{gm}^2$) in which **G** is the gametic relationship matrix and σ_{gm}^2 is the variance of maternal parent-of-origin effects. The inverse of the gametic relationship matrix (G^{-1}) was used as the provided covariance matrix. The calculation of matrix G used the algorithm created by Tier and Meyer (2012). The diagonal elements of the gametic relationship matrix (g_{ii}) equaled 1, while the off-diagonal elements (g_{ij}) were computed using the algorithm suggested by Meyer and Tier (2012):

$g_{ij} = (g_{im} + g_{ip})/2$

where, m and p represent the maternal and paternal gametes of gamete j, respectively.

Reproductive traits

Similar to the growth traits, a two-step method was employed to calculate the (co)variance components and genetic parameters for the reproductive traits. The analysis of reproductive traits initially involved a repeatability animal model in the following way:

y=X*β*+Z₁a+Z₂pe+e

Next, the model incorporated the maternal imprinting to examine its impact on the genetic parameters of reproductive traits as outlined:

y=X*β*+Z₁a+Z₂pe+Z₃g*ₘ*+e

Except for the vector pe, which represents the permanent environmental effects of repeated records for animals and is assumed pe~ N(0, $\mathbf{I}_d\sigma_{pe}^2$), all other terms align with the models used for growth traits. The design matrix $\mathbf{Z_2}$ and $\mathbf{Z_3}$ connect observations to the animal permanent environmental and maternal imprinting effects. The identity matrix, I_d, has an order that corresponds to the number of animals. The Wombat software (Meyer, 2020) was used to conduct genetic analysis of the studied traits, employing the AI-REML algorithm.

Results

Pedigree information and descriptive statistics

A summary of the pedigree structure is presented in Table 1. The pedigree comprised of 21,785 individuals, the offspring of 448 sires and 6,398 dams. The recorded pedigree included 19,211 individuals with known parents, 2,288 with one known parent, and 2,860 with both parents unknown. Only 31.43% of animals in the pedigree had offspring. Table 2 displays the descriptive statistics for the traits being studied. The mean values for growth traits were 2.44 kg (WB), 10.30 kg (WW), and 100.93 gr (ADG). For efficiency-related traits the values were 17.60 for KR and 331.04% for GE. The means values for reproductive traits were 1.40 (LSB), 1.55 (LSW), 3.29 kg (TLWB), and 12.93 kg (TLWW). The average gain of 100.93 g/day led to a 76.38% increase in the body weight from birth to weaning. The coefficient of variation varied from 16.80% for WB to 42.70% for TLWB.

Table 1. Pedigree structure of Murciano-Granadina goats

Parameter	N
No. of generations	5
No. of individuals in the pedigree file	21785
No. of inbreds	813
No. of sire	448
No. of dam	6398
No. of individuals with progeny	6846
No. of individuals with no progeny	14939
No. of founders	2288
No. of individuals with both parents known	19211
No. of individuals with both parents unknown	2288
No. of individuals with one parent unknown	286
Average family size	2.07
Average inbreeding coefficients (%)	0.30
Average inbreeding coefficients in the inbred (%)	6.8
Maximum inbreeding coefficients (%)	31.25
Minimum inbreeding coefficients (%)	0.39

Model comparisons

The AIC values for the different models are given in Table 3. Model 5, which accounted for the direct additive genetic, maternal additive genetic, and maternal permanent environmental effects without considering covariance between direct and maternal additive genetic effects was identified as the best model for WB. The model that best fit WW, ADG, KR, and GE included both direct additive genetic and maternal additive genetic effects without considering covariance between direct and maternal additive genetic effects (Model 3). Integrating the maternal parent-of-origin effect into the model **M** during the second step enhanced the model's general properties, evidenced by a reduction in AIC value. Therefore, model 7 was the best for WB. For WW, ADG, KR, and GE, introducing maternal parent-of-origin effects to the model **M** did not improve the AIC value. Hence, model **M** was chosen as the final best model for these characteristics. For all reproductive traits, except for LSW, the model without maternal imprinting effects was found to be the best model. For LSW, the model with maternal imprinting effects was the best model.

Table 2. Descriptive statistics of analyzed traits in Murciano-Granadina goats

	Traits[a]								
Item	WB (kg)	WW (kg)	ADG (g/d)	KR	GE (%)	LSB	LSW	TTLWB (kg)	TLWW (kg)
No. of records	15043	7301	7301	7301	7301	10546	6108	10546	6108
No. of sires with progeny	341	306	306	306	306	151	132	151	132
Average number of progenies per sire	44.00	23.86	23.86	23.86	23.86	69.38	45.92	69.25	46.27
No. of dams with progeny	4192	3036	3037	3037	3037	482	343	482	343
Average number of progenies per dam	3.59	2.40	2.40	2.40	2.40	21.88	17.81	21.88	17.81
No. of service sires	-	-	-	-	-	340	310	339	309
Min	1.10	5.20	32.6	8.50	105.71	1.00	0.00	1.10	5.20
Max	4.20	23.00	331.97	31.60	983.33	3.00	3.00	11.85	59.50
Mean	2.44	10.30	100.93	17.60	331.04	1.40	1.55	3.29	12.93
SD[b]	0.41	1.35	20.90	3.06	88.25	0.53	0.56	1.38	5.28
CV[b] (%)	16.80	20.70	20.71	17.40	26.66	37.80	36.20	42.07	40.80

[a]WB: weight at birth; WW: weight at weaning; ADG: average daily gain from birth to weaning; KR: Kleiber ratio at weaning; GE: growth efficiency during birth to weaning; LSB: litter size at birth; LSW: litter size at weaning; TLWB, total litter weight at birth; TLWW, total litter weight at weaning.
[b]SD: standard deviation; CV: coefficient of variation.

Table 3. AIC values for the univariate analyses of the growth traits in Murciano-Granadina goats

Models	Traits[a]				
	WB	WW	ADG	KR	GE
1	-12598.300	10837.32	51302.91	23311.54	72428.29
2	-12764.77	10833.28	51664.25	23287.21	72418.6
3	-12742.96	**10825.89**	**51283.71**	**23284.58**	**72391.64**
4	-12750.62	10843.13	51287.86	23294.14	72399.53
5	**-12778.102**	10859.7	51284.46	23288.59	72410.93
6	-12775.12	10850.19	512887.5	23296.64	72401.33

[a]WB: weight at birth; WW: weight at weaning; ADG: average daily gain from birth to weaning; KR: Kleiber ratio at weaning; GE: growth efficiency from birth to weaning.

Genetic parameters

Table 4 provides the estimated variances and heritabilities for growth traits. Only birth weight was influenced by maternal imprinting effects among growth and efficiency-related traits. When the effect of maternal imprinting was included in the model **M**, the value of δ_a^2 for WB decreased by approximately 6.29%. Also, there was a drastic reduction of 85.71% in the estimate of δ_m^2 for this trait. The estimated maternal imprinting heritability (h_{mi}^2) for WB was 0.07±0.07. Other growth traits showed a minimal contribution of maternal imprinting to phenotypic variance. The estimated h_a^2 values for WB, WW, ADG, KR, and GE were 0.10±0.02, 0.09±0.03, 0.06±0.02, 0.05±0.02, and 0.11±0.03, respectively. The estimates for variance components, genetic parameters, and maternal imprinting effects for reproductive traits are provided in Table 5. The maternal imprinting effect explained 1.20, 7.26, 1.45, and 0.95% of the phenotypic variance for LSB, LSW, TLWW, and

TLWB, respectively. A significant effect of the maternal imprinting effects was found only for LSW. By adding the maternal imprinting effects to model 1 for LSW, the additive genetic variance significantly decreased by 55.56%. The estimated value of $\mathrm{h}^2_{\mathrm{mi}}$ for LSW was 0.07±0.02. The repeatability of reproductive traits ranged from 0.02 for LSB to 0.09 for LSW. The value of $\mathrm{h}^2_{\mathrm{a}}$ for reproductive traits ranged from 0.01±0.01 (LSB) to 0.04±0.02 (LSW).

Table 4. Model comparison with and without maternal imprinting effects and (co) variance components of growth and efficiency related traits (final best model in bold) in Murciano-Granadina goats

Trait[a]-Model	AIC	δ^2_a	δ^2_c	δ^2_m	δ^2_{mi}	δ^2_e	δ^2_p	h^2_a	h^2_c	h^2_m	h^2_{mi}
WB											
M (Model 5)	-12778.10	0.0159	0.0145	0.0070		0.128	0.165	0.10±0.02	0.09±0.01	0.04±0.01	
7	**-12781.12**	**0.0149**	**0.0149**	**0.0010**	**0.0120**	**0.122**	**0.165**	**0.09±0.02**	**0.09±0.01**	**0.01±0.01**	**0.07±0.07**
WW											
M (Model 3)	**10825.88**	**0.158**		**0.121**		**1.376**	**1.655**	**0.10±0.02**		**0.07±0.01**	
7	10827.90	0.158		0.121	0.001	1.376	1.656	0.10±0.02		0.07±0.01	0.001±0.14
ADG											
M (Model 3)	**51283.72**	**28.880**		**23.928**		**368.51**	**421.318**	**0.07±0.02**		**0.06±0.01**	
7	51285.66	28.871		23.903	0.009	368.53	421.313	0.07±0.02		0.06±0.01	0.00±0.14
KR											
M (Model 3)	**23284.58**	**0.508**		**0.625**		**7.947**	**9.080**	**0.06±0.02**		**0.07±0.01**	
7	23286.58	0.507		0.624	0.001	7.948	9.081	0.05±0.02		0.07±0.01	0.00±0.13
GE											
M (Model 3)	**72391.64**	**875.25**		**689.90**		**6202.65**	**7767.80**	**0.11±0.03**		**0.09±0.02**	
7	72393.64	875.92		690.82		6202.93	7770.10	0.11±0.03		0.09±0.05	0.00±0.13

δ^2_a: additive genetic variance; δ^2_c: maternal permanent environmental variance; δ^2_m: maternal genetic variance; δ^2_{mi}: maternal imprinting variance; δ^2_e: residual variance; δ^2_p: phenotypic variance; h^2_a: direct heritability; h^2_m: maternal heritability; h^2_c: maternal permanent environmental effect; h^2_{mi}: maternal imprinting heritability; M: best model selected in the step one; AIC: Akaike information criterion.
[a]WB: weight at birth; WW: weight at weaning; ADG: average daily gain from birth to weaning; KR: Kleiber ratio at weaning; GE: growth efficiency during birth to weaning.

Table 5. Model comparison with and without maternal imprinting effects and (co) variance components of reproductive traits (final best model in bold) in Murciano-Granadina goats

Trait[a]-Model	AIC	δ^2_a	δ^2_{pe}	δ^2_{mi}	δ^2_e	δ^2_p	h^2_a	r	h^2_{mi}
LSB									
1	**-1967.43**	**0.002**	**0.004**		**0.245**	**0.251**	**0.01±0.01**	**0.02**	
2	-1966.92	0.002	0.001	0.003	0.245	0.251	0.01±0.01	0.02	0.01±0.01
LSW									
1	-611.391	0.028	0.001		0.282	0.312	0.09±0.02	0.09	
2	**-612.330**	**0.013**	**0.001**	**0.023**	**0.280**	**0.317**	**0.04±0.02**	**0.05**	**0.07±0.02**
TLWB									
1	**6653.45**	**0.018**	**0.024**		**1.268**	**1.311**	**0.02±0.01**	**0.03**	
2	6653.79	0.017	0.006	0.019	1.268	1.311	0.01±0.01	0.02	0.02±0.01
TLWW									
1	**12719.71**	**0.799**	**0.001**		**7.887**	**23.958**	**0.03±0.01**	**0.04**	
2	12720.46	0.702	0.001	0.228	7.888	23.958	0.03±0.01	0.03	0.01±0.02

[a]δ^2_a: additive genetic variance; δ^2_{pe}: individual permanent environmental variance; δ^2_{mi}: maternal imprinting variance; δ^2_e: residual variance; δ^2_p: phenotypic variance; h^2_a: direct heritability; r: repeatability; h^2_{mi}: maternal imprinting heritability; AIC: Akaike information criterion.
[a]LSB: litter size at birth; LSW: litter size at weaning; TLWB, total litter weight at birth; TLWW, total litter weight at weaning.

Discussion

Growth and efficiency-related traits

Recent studies suggest that genomic imprinting significantly contributes to the genetic architecture of complex traits, potentially accounting for a substantial portion of phenotypic variance (Hu et al., 2016; Okamoto et al., 2019). Previous studies (Mokhtari et al., 2022b; Kheirabadi et al., 2024) have investigated the effect of maternal imprinting on WB and WW in goats. Our study revealed that imprinted loci handled 7% of the overall phenotypic variance in the WB of Murciano-Granadina kids. In a study on Baluchi sheep, Ghafouri-Kesbi (2022a) found significant maternal imprinting effects on WB, explaining 12% of the phenotypic variation. In Kermani sheep, Mokhtari et al. (2022a) reported that maternal imprinting explained 14% of the phenotypic variation in WB. Amiri Roudbar et al. (2018) investigated the impact of maternal imprinting effects on WB in Zandi sheep. They found that maternal parent-of-origin contributed approximately 23.30% to the phenotypic variance. In Markhoz goats, maternal imprinting effects had a similar effect on WB, accounting for 10% total phenotypic variance (Kheirabadi, 2024). These findings emphasize the importance of considering maternal parent-of-origin effects in the genetic evaluations for growth traits. In contrast to our findings, Amiri Roudbar et al. (2017) and Mokhtari et al. (2022b) concluded that maternal imprinting effects did not play a significant role in body weight variation for Iran Black sheep and Raeini Cashmere goats, respectively. Furthermore, Ghafouri-Kesbi et al. (2022a) found that WB was not influenced by the effects of maternal imprinting in Makuie sheep. It is intriguing how different sheep and goat breeds exhibit varying patterns of imprinting effects. Maternal imprinting did not significantly contribute to the phenotypic variation of WW, ADG, KR, and GE. Consistent with this study, Kheirabadi (2024) found that maternal imprinting had no effect on pre-weaning ADG in Markhoz goats. Thus, there is no need to consider maternal imprinting effects when estimating variance components for these traits. This outcome is in line with the findings of Ghafouri-Kesbi et al. (2022a) who analyzed the same trait in Baluchi and Makuie sheep. However, Kheirabadi (2024) concluded that maternal imprinting effects are necessary for the estimation of variance components of pre-weaning KR in Markhoz goats. The variation in the impact of imprinting effects on growth traits may be because of differences in the imprinting patterns observed across various tissues, as suggested by Barlow and Bartolomei (2014). The estimation of maternal imprinting variance has also been documented in other livestock species (Neugebauer et al., 2010; Okamoto et al., 2019; Perdomo-González et al., 2023).

It is notable that for WB, although model 7 which included maternal imprinting effects substantially fitted the data better than the models without this effect, estimated value of $\mathrm{h}_{\mathrm{mi}}^2$ had high standard errors (SE), which shows the lower reliability of the estimate. In animal models, SE is an indicator of data size, data structure, and deep and quality of pedigree used. Shallow pedigree, small data size, the low proportion of recorded dams, as well as fewer numbers of progeny per dam, negatively affects the precision of the maternal components estimation which is reflected in $\mathrm{h}_{\mathrm{mi}}^2$ with high SE. Therefore, estimated value of $\mathrm{h}_{\mathrm{mi}}^2$ should be treated with caution (Ghafouri-Kesbi et al., 2022a). By adding the maternal imprinting effects to the model, the values of $\mathrm{h}_{\mathrm{m}}^2$ and $\mathrm{h}_{\mathrm{a}}^2$ decreased for WB. Our findings align with those of Mokhtari et al. (2022a) and Ghafouri-Kesbi et al. (2022a), who also reported a decrease in $\mathrm{h}_{\mathrm{m}}^2$ and $\mathrm{h}_{\mathrm{a}}^2$ for the same trait when they incorporated maternal imprinting effects into the genetic models for Kermani and Baluchi sheep, respectively. Contrary to our findings, Mokhtari et al. (2022b) demonstrated that the estimates of $\mathrm{h}_{\mathrm{a}}^2$ for WB in Raeini Cashmere goat remained consistent when maternal imprinting effects were included in the model. Ghafouri-Kesbi et al. (2022a) found similar results for estimates of $\mathrm{h}_{\mathrm{mi}}^2$ values as 0.07 and 0.02 for weight at birth and weaning in Iranian Makuie sheep. Moreover, Mokhtari et al. (2022b) reported $\mathrm{h}_{\mathrm{mi}}^2$ values of 0.00 and 0.09 for birth and weaning weights, respectively, in Raeini Cashmere goats.

Other studies (Amiri Roudbar et al., 2018; Ghafouri-Kesbi et al., 2022a, 2022b; Mokhtari et al., 2022a) reported higher $\mathrm{h}_{\mathrm{mi}}^2$ values for ADG and GE (0.02 and 0.06) compared to the current study. However, their KR results were in line with our estimate of 0.00 for $\mathrm{h}_{\mathrm{mi}}^2$. According to Ghafouri-Kesbi et al. (2022b), the maternally imprinting heritability for ADG and KR was 0.03 and 0.01 in Baluchi sheep and 0.11 and 0.14 in Makuie sheep. The $\mathrm{h}_{\mathrm{mi}}^2$ value for ADG in the study of Mokhtari et al. (2022a) on Kermani sheep was 0.05. The activity of imprinted genes is limited to particular tissues during specific developmental stages, resulting in diverse impacts on traits (Mokhtari et al., 2022b).

For WB, including the maternal imprinting effects in the model that contained the additive genetic effect, led to a reduction in the additive genetic variance, a finding which has also been reported by other authors (Tier and Meyer, 2012; Amiri Roudbar et al., 2018). By incorporating the maternal imprinting effects in the analysis, the estimates of δ_{a}^2 decreased by 29%, 10%, 12%, and 20% for WB, WW, ADG, and KR in Baluchi sheep (Ghafouri-Kesbi et al., 2022a); it was suggested that maternally imprinted genes were a significant source of genetic variation for growth and efficiency-related traits and should be incorporated into models for the genetic evaluation of Baluchi lambs. If an animal model ignores the maternal imprinting effects, it may lead to overestimation of the additive genetic variance, because imprinting effects will be masked by the additive genetic effects. Some research has explored the potential confounding effects between the maternal genetic and maternal imprinting effects (Hager et al., 2008). It was stated that maternal parent-of-origin effects can mimic their impacts, so maternal imprinting effects are likely to be confounded with maternal genetic effects.

Including the maternal imprinting as a random effect led to a significant decrease in maternal genetic variance for WB. The value of $\mathrm{h}_{\mathrm{m}}^2$ for WB decreased in Lori-Bakhtiari sheep (Amiri Roudbmar et al., 2018) and Raeini Cashmere goat (Mokhtari et al., 2022b) after including maternal imprinting effects in the model. However, no changes were detected in the estimated $\mathrm{h}_{\mathrm{c}}^2$ for this trait. In a study on Australian beef cattle (Meyer and Tier, 2012), including the maternal imprinting in the model, did not impact on the maternal permanent environment in agreement with the current findings. Ghafouri-Kesbi et al. (2022a) reported that by including the maternal imprinting effects, the value of $\mathrm{h}_{\mathrm{c}}^2$ for WB increased from 0.36 to 0.39. Overall, the confounding effect appears to be specific to maternal genetic effects and maternal imprinting. These findings suggested that imprinting effects may be more important than that previously expected.

Reproductive traits

Except for LSW, adding the maternal imprinting effects to the model did not reduce the AIC values. The LSW displayed the most significant parent-of-origin effect originating from the maternal gene expression, explaining up to 7% of the overall phenotypic variance. Holl et al. (2004) demonstrated that maternal imprinting effects can influence the reproductive traits. Consistent with our findings, Mokhtari et al. (2022a) observed that maternal imprinting had no significant impact on the reproductive traits in Kermani sheep. Furthermore, Amiri Roudbar et al. (2018) found that maternal imprinting had higher influence on growth traits in Lori-Bakhtiari sheep compared to reproductive traits. It is possible that the sample size and data structure prevented the detection of imprinting effects or there are a small number of imprinting genes with small effects on reproduction traits.

Conclusions

Including the maternal imprinting effects in the model significantly improved the general properties of the models for WB and LSW in Murciano-Granadina goats. This is valuable for accurately estimating the genetic parameters related to economically important traits in this breed. Additionally, we found that some of the estimated additive genetic variance among animals can be attributed to imprinted effects, previously overlooked in assessing the economically relevant traits in goats. The findings emphasize the influence of the maternal imprinting on some growth and reproductive traits, and the necessity for breeding programs that consider these effects in selection decisions.

Conflict of interest

There is no conflict of interest.

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