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The influence of parental imprinting on some economic traits in Markhoz goats

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Abstract Parental effects refer to the phenomenon whereby gene expression is influenced by the parent of origin, a process known as genomic imprinting. These effects may significantly affect phenotypic traits and shape the genetic architecture of individuals, making them an important factor in animal breeding and genetic evaluation programs. This study aimed to examine the impact of parental imprinting effects on genetic variation in a Markhoz goat population, with emphasis on body weight traits at birth (BW), weaning (WW), six months (6MW), nine months (9MW), yearling (YW), and yearling fleece weight (YFW). The analysis was conducted in two phases. Initially, each trait was modeled using 12 univariate animal models incorporating various combinations of direct and maternal genetic effects. The best-fitting model for each trait was selected using the Akaike Information Criterion (AIC). In the second phase, three additional models were constructed by integrating maternal imprinting, paternal imprinting, or both into the selected model, and the resulting changes in AIC values were evaluated. The results revealed that including the paternal imprinting effects substantially improved model fit for BW and 9MW, as these models showed the lowest AIC values. Conversely, for WW, 6MW, YW, and YFW, imprinting variances were negligible, suggesting limited influence of parental origin and supporting the exclusion of these effects from genetic evaluation models for these traits. Across all traits analyzed, paternal imprinting effects accounted for 0.7% to 11% of the phenotypic variance, while maternal imprinting effects contributed between 1.5% and 9%. Furthermore, incorporating the parental imprinting effects into the analysis led to reductions in both the direct and maternal heritability estimates. These findings highlighted the necessity of accounting for parental imprinting, particularly paternal effects, in genetic evaluation of body weight traits in Markhoz goats.

Keywords: epigenetics, genomic imprinting, parent-of-origin effects, variance components

Introduction

Integrating goat farming with sheep and cattle on underperforming pastureland is an effective strategy for optimizing livestock productivity (Mohammadabadi and Tohidinejad, 2017). Among native breeds, Markhoz goats play a vital role in Kurdistan, western Iran, contributing significantly to mohair and meat production. Given that sheep and goats account for over 57% of Iran's livestock units, understanding the factors influencing their genetic and phenotypic traits is essential for sustainable breeding programs and highlights the need for more precise genetic evaluation methods (Valizadeh, 2010). The Markhoz and Raeini breeds, in particular, are valued for their production of high-quality mohair and Kashmir fibers (Mueller et al., 2015).

Epigenetics plays a pivotal role in animal genetics,

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referring to heritable changes in gene function that do not involve alterations in the DNA sequence itself (Herman and Sultan, 2011). These modifications can influence gene expression and lead to significant phenotypic variation without altering the genetic code. One critical dimension of epigenetic regulation is the parent-of-origin effect, whereby gene expression is influenced by whether the gene is inherited maternally or paternally. This phenomenon, known as genomic imprinting, results in differential activation or silencing of specific alleles depending on the parental source, and has been shown to significantly impact livestock traits such as growth, reproduction, and health (Barlow and Bartolomei, 2014).

Parental effects go beyond simple genetic inheritance, encompassing influences of the parental phenotype and environment, such as nutrition, physiological status, and epigenetic markers that shape the development and productivity of offspring (Schaeffer et al., 1989). These effects can manifest throughout various life stages, leading to shifts in gene expression patterns that affect growth trajectories, body composition, and metabolic functions. For example, maternal overnutrition during critical periods like pre-conception and gestation has been linked to increased visceral fat deposition and altered feeding behavior in offspring, with sex-specific outcomes driven by differential DNA methylation patterns (Zhang et al., 2011; Feil and Fraga, 2012). Importantly, the dynamic interaction between environmental inputs and epigenetic mechanisms highlights the complexity of trait heritability in livestock. Such insights are particularly relevant in the context of sheep and goat breeding, where animals constitute a substantial portion of Iran's livestock industry. Integrating knowledge of epigenetic regulation, including imprinting and parental effects, into genetic evaluation frameworks can improve the precision of selection strategies and promote sustainable breeding practices. This comprehensive understanding underscores the importance of considering both genetic and non-genetic factors when predicting animal performance and designing programs aimed at long-term productivity enhancement.

A variety of models have been proposed to analyze parent-of-origin effects in animal genetics. Early models primarily assessed imprinting from one parent (Schaeffer et al., 1989; de Vries et al., 1994), whereas more recent studies account for both parental influences (Neugebauer et al., 2010a, 2010b; Meyer and Tier, 2012; Tier and Meyer, 2012). The animal model that incorporates the gametic effects enables the estimation of gene expression variability from both parents, offering a robust framework for analyzing genetic inheritance patterns. Meyer and Tier (2012) identified key parameters for imprinting analysis, though practical limitations restrict differentiation of multiple gene groups, necessitating simplifications in imprinting assumptions. Genomic imprinting has emerged as a pivotal consideration in animal breeding programs, as its exclusion may introduce significant biases into the estimation of genetic parameters (Meyer and Tier, 2012; Tier and Meyer, 2012). Empirical evidence has demonstrated the pronounced role of imprinted parental alleles in shaping complex traits in both sheep (Amiri Roudbar et al., 2017, 2018; Ghafouri-Kesbi et al., 2022a, 2022b) and goats (Ehsaninia and Ghafouri-Kesbi, 2024). Collectively, these studies underscore those genetic models neglecting imprinting effects may lead to inflated estimates of direct heritability, thereby compromising the accuracy of predicted selection responses.

This study evaluates the contribution of parental imprinting to phenotypic and genetic variation in growth-related traits, including body weight from birth to one year and yearling greasy fleece weight (YFW), in Markhoz goats. Despite YFW’s economic relevance, its relationship to imprinting has not been previously explored in this breed. By applying a gametic relationship model, maternal and paternal genetic influences are disentangled from overall phenotypic variance, addressing a notable gap in livestock genetic evaluation frameworks, where imprinting effects are often overlooked. The findings aim to advance our understanding of epigenetic inheritance and support the development of more accurate selection strategies for key traits in small ruminants.

Materials and methods

As the analyses were conducted using previously acquired field data under standard farm management practices, this study was exempt from Animal Care and Use Committee approval.

Data

This study collected extensive pedigree and performance data from 1992 to 2018 at the Markhoz Goat Breeding Station in Kurdistan, Iran. Newborn kids were ear-tagged and weighed at birth, with detailed records of pedigree, gender, birth year, and birth type. For the first 15 days, kids nursed exclusively from their mothers, then transitioned to partial weaning, suckling twice a day for one hour each session, and fed high-quality alfalfa. At three months, they were weaned and allowed to graze. Body weight was recorded every three months until they reached one year of age. Mating occurred from October to November, with births from February to March. Does were introduced to males at around 18 months, with each male mating with 10 to 15 females for two to three seasons (Rashidi et al., 2008). The pedigree dataset included 5232 individuals, comprising 242 sires and 1499 dams. A total of 4886 individuals had known parentage, providing a comprehensive genealogical record. After pruning, the number of animals was reduced to 5175, including 2898 inbred individuals. The dataset also contained 1684 individuals with progeny and 3491 without progeny. Among them, 345 were classified as founder animals, while 4887 were non-founders. Table 1 presents summary statistics, including the number of observations, minimum/maximum values, mean, and standard deviation. This study examines body weight traits at various stages of development: birth (BW), weaning (WW), six months (6MW), nine months (9MW), and yearling (YW). It also evaluates yearling greasy fleece weight (YFW).

Table 1. Statistical descriptions of the examined characteristics in Markhoz goats

Traits[1]	# of records	Minimum (kg)	Maximum (kg)	Mean (kg)	SD (kg)
BW	4887	1.10	4.50	2.50	0.47
WW	4077	3.80	28.50	15.27	4.40
6MW	3764	6.00	31.00	17.69	4.38
9MW	3337	7.00	39.00	21.05	5.10
YW	2899	8.00	48.00	25.36	6.83
YFW	2578	0.10	0.99	0.40	0.16

[1] BW: Birth weight, WW: Weaning weight, 6MW: Six-month weight, 9MW: Nine-month weight, YW: Yearling weight, YFW: Yearling greasy fleece weight

Statistical analysis

All genetic analyses in this study aimed to estimate variance components and genetic parameters associated with parental imprinting effects, as well as to determine their statistical significance. The analyses were conducted in two phases. Before the first phase, the GLM method in SAS software (version 9.1, 2004) was applied to identify significant fixed effects. These included sex (male and female), dam age at kidding (2-7 years), birth type (single, twin, or triplet), and birth year (1992–2018). All fixed factors were statistically significant ($P< 0.01$) for each trait, necessitating their inclusion in subsequent models. Additionally, kids' age in days at weighing was incorporated as a linear covariate for all traits except BW.

In the first phase, twelve animal models were employed to examine their characteristics and identify the most suitable model for imprinting analysis. Conventional univariate models, which did not account for parental effects, were used to determine the optimal model for each trait. Models were fitted as follows:

Model 1: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{e}$
Model 2: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_c c} + \mathbf{e}$
Model 3: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{e}, \quad \sigma_{\mathrm{am}} = 0$
Model 4: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{e}, \quad \sigma_{\mathrm{am}} \neq 0$
Model 5: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{e}, \quad \sigma_{\mathrm{am}} = 0$
Model 6: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{e}, \quad \sigma_{\mathrm{am}} \neq 0$
Model 7: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_l l} + \mathbf{e}$
Model 8: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_c c} + \mathbf{Z_l l} + \mathbf{e}$
Model 9: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_l l} + \mathbf{e}, \quad \sigma_{\mathrm{am}} = 0$
Model 10: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_l l} + \mathbf{e}, \quad \sigma_{\mathrm{am}} \neq 0$
Model 11: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{Z_l l} + \mathbf{e}, \quad \sigma_{\mathrm{am}} = 0$
Model 12: $\mathbf{y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{Z_l l} + \mathbf{e}, \quad \sigma_{\mathrm{am}} \neq 0$

In the aforementioned models, **y** represents the observations, and **b** represents the fixed effects of birth year, birth type, dam age, and sex. The vectors **a**, **m**, **c**, **l**, and **e** denote additive genetic, maternal genetic, permanent environmental maternal, common environmental maternal and residual effects, respectively. In addition, **X**, $\mathbf{Z_a}$, $\mathbf{Z_m}$, $\mathbf{Z_c}$, $\mathbf{Z_l}$ and σ_{am} are the incidence matrices for the fixed effects, additive genetic, maternal genetic, permanent environmental maternal, common environmental maternal and direct-maternal genetic covariance, respectively.

In the second phase, the optimal model (Model S1) from the preceding analysis was utilized to investigate parental imprinting effects, incorporating and assessing both paternal and maternal imprinting effects. Three models were used to estimate variance components for parental effects, precisely quantifying their contribution to total trait variation. These models were incorporated into the analysis outlined below.

Model MI: $\mathbf{y} = S1 + \mathbf{Z_{mi} mi} + \mathbf{e}$
Model PI: $\mathbf{y} = S1 + \mathbf{Z_{pi} pi} + \mathbf{e}$
Model MPI: $\mathbf{y} = S1 + \mathbf{Z_{mi} mi} + \mathbf{Z_{pi} pi} + \mathbf{e}$

In these models, S1 represents fixed and random effects from the initial analysis stage. Design matrices $\mathbf{Z_{mi}}$ and $\mathbf{Z_{pi}}$ link observations to dam and sire imprinting effects. Vectors **mi** and **pi** indicate maternally and paternally imprinted effects, respectively. These vectors are assumed to follow a certain distribution, $\mathbf{m}_i \sim \mathrm{N}(0.\ G\sigma_{mi}^2)$ and, $\mathbf{p}_i \sim \mathrm{N}(0.\ G\sigma_{pi}^2)$, which can be described as having a mean of zero and a covariance structure determined by the gametic relationship matrix (GRM) of Smith and Allaire (1985) introduced the GRM to estimate the probability of genes being identical by descent in inbred populations. The GRM shows expected genetic material shared among individuals due to common ancestry. Diagonal elements represent self-relatedness (always one), while off-diagonal elements show the probabilities of genes being identical by descent. All gametic models used the inversion of the gametic relationship matrix to derive the covariance matrix (Tier and Meyer, 2012), considering both maternal and paternal gamete contributions to animal models. Model MI and Model PI were structurally similar to Model S1, but accounted separately for maternal and paternal imprinting effects, respectively. Model MPI incorporated both effects simultaneously.

The AI-REML algorithm in the Wombat program (Meyer 2007), was used to estimate (co)variance components and genetic parameters for each characteristic. The Akaike Information Criterion (AIC) was used to determine the best model among twelve models (Akaike, 1974). AIC is calculated as AIC=-2logL+2p, where logL is the maximized likelihood function and p is the number of model parameters. The model with the lowest AIC is considered the best.

Results

Comparison of models without parental imprinting effects

The effects of sex, birth year, birth type, and dam age significantly affected all traits (P<0.01). In the first phase, twelve animal models were tested for six traits, excluding parental imprinting (Table 2). AIC-based model comparisons indicated that Models 12, 5, and 8 were optimal for BW, WW, and 6MW, respectively. Model 5 incorporated additive genetic, maternal genetic, and permanent maternal environmental effects, under the assumption of zero direct–maternal genetic covariance. Model 8 included additive genetic, permanent maternal environmental, and common maternal environmental effects. Model 12 represented a comprehensive model, encompassing additive genetic, maternal genetic, permanent maternal environmental, and common maternal environmental effects, with direct–maternal genetic covariance assumed to be non-zero. Model 7 was identified as the best-fitting model for 9MW, YW, and YFW, incorporating additive genetic and common maternal environmental effects. These selected models formed the basis for estimating genetic parameters and served as reference models for subsequent analyses (Model S1).

Table 2. AIC-based comparison of 12 animal models in Markhoz goats with best model highlighted

	Model											
Trait[1]	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
BW	-4280.57	-4361.26	-4339.53	-4347.46	-4362.03	-4370.02	-4609.56	-4630.49	-4626.59	-4630.40	-4630.80	**-4634.68**
WW	13946.37	13927.60	13927.22	13929.00	**13925.87**	13927.65	13944.27	13929.25	13928.49	13930.20	13927.59	13929.33
6MW	12997.16	12985.00	12987.36	12989.29	12985.60	12987.50	12984.73	**12978.95**	12979.67	12981.67	12979.73	12981.72
9MW	12200.99	12201.34	12202.23	12203.63	12203.33	12204.66	**12198.01**	12199.60	12199.82	12201.36	12201.59	12203.07
YW	11847.95	11847.98	11849.87	11851.72	11849.98	11851.95	**11847.70**	11848.73	11849.70	11851.59	11850.73	11852.72
YFW	27822.62	27824.29	27824.22	27826.20	27826.16	27828.13	**27822.31**	27824.31	27824.16	27826.13	27826.16	27828.13

[1] BW: Birth weight, WW: Weaning weight, 6MW: Six-month weight, 9MW: Nine-month weight, YW: Yearling weight, YFW: Yearling greasy fleece weight

Comparison of models with parental imprinting

The second phase results show significant variation in growth traits linked to parental effects (Table 3). Paternal imprinting effects explained between 0.7% and 11% of the observed phenotypic variance across the evaluated traits, whereas maternal imprinting effects contributed a range of 1.5% to 9%. Incorporating paternal imprinting enhanced the model fit for both BW and 9MW, as evidenced by a reduction in their respective AIC values. Furthermore, paternal imprinting had the most significant impact on BW, contributing to 11% of the phenotypic variation. The direct heritability experienced a decrease from 0.21 to 0.03 following the inclusion of paternal imprinting effects into the model for BW, indicating that a substantial portion of the previously estimated additive genetic variance may have been confounded with imprinting. After BW, the highest paternally imprinted genetic effect was associated with the 9MW trait, accounting for 6% of the phenotypic variation. However, incorporating paternal imprinting lowered the AIC for 9MW and decreased direct heritability from 0.28 to 0.24. Conversely, disregarding parental effects led to better performance in modeling WW, 6MW, YW, and YFW traits.

Maternal imprinting did not enhance model adequacy for any traits, as indicated by AIC values. Although its variance component was greater than that of paternal imprinting, most notably accounting for 9% of phenotypic variability in WW, this did not translate into an improved model fit. BW showed the next highest maternal imprinting effect, contributing 6%. Incorporating maternal imprinting into the model reduced the proportion of phenotypic variance attributed to maternal genetic effects for BW, decreasing from 7% as estimated in the base model derived from the first stage of analyses to 5%, and for WW, from 4% to 0%. Both imprinting effects did not affect the variance of permanent and common environmental effects.

However, for all other traits, paternal imprinting had a greater impact. Table 3 reveals that yearling greasy fleece weight (YFW) is scarcely influenced by parental imprinting. Maternal imprinting accounts for 0.78% and 1.40% of phenotypic variation in the MI and MPI models, respectively. Similarly, paternal imprinting contributes 1.35% and 1.79% in the PI and MPI models, respectively. The inclusion of parental imprinting effects in the models for all analyzed traits resulted in reduced estimates of both direct and maternal heritability, enabling more accurate partitioning of genetic and maternal variance components. This refinement improved the precision of variance estimations and led to streamlined component values.

Discussion

Direct heritability estimations for BW, WW, 6MW, 9MW, YW, and YFW from model S1 were 0.21, 0.13, 0.13, 0.28, 0.30, and 0.18, respectively, indicating generally moderate heritability across traits, with YW showing the highest potential for genetic improvement (Table 3). Rashidi et al. (2008) studied the Markhoz breed using five animal models, reporting direct heritability estimates for weight at various stages and yearling fleece weight of 0.19, 0.15, 0.19, 0.33, 0.41, and 0.16, respectively. Compared to the current study, the estimates for WW, 6MW, 9MW, and YW showed slight increases, whereas those for BW and YFW decreased. Although both studies relied on datasets from the same animal breeding station, these differences may primarily stem from structural elements within the data, particularly factors such as sample size, and pedigree depth (Su et al., 2018). Such components are known to influence the accuracy of additive genetic variance estimates in livestock, and their effects may outweigh those of environmental or genetic variation. In Table 3, maternal heritability (h_m^2) was estimated at 0.07 for birth weight and 0.04 for weaning weight. These values are relatively low, yet consistent with previous findings by Rashidi et al. (2008), who reported estimates of 0.06 and 0.02 for the same traits in the Markhoz breed. Such low maternal heritability values suggest that maternal genetic effects contribute modestly to phenotypic variation in early growth traits. Since this study focuses on parental imprinting effect, the variance components and genetic parameters of the best models from the initial stage of analysis were not examined further.

Table 3. Estimates of genetic parameters and variance components with parental imprinting in Markhoz goats: Best model components highlighted

			Components[2]									
Traits[1]	**Models**	**AIC**	σ_a^2	σ_m^2	σ_{mi}^2	σ_{pi}^2	pe^2	ce^2	h_a^2	h_m^2	h_{mi}^2	h_{pi}^2
BW	S1-12	-4634.68	0.03	0.01	-	-	0.06	0.46	0.21	0.07	-	-
	MI	-4633.33	0.03	0.01	0.01	-	0.06	0.46	0.21	0.05	0.06	-
	PI	**-4636.61**	**0.01**	**0.01**	**-**	**0.02**	0.06	0.46	**0.04**	**0.03**	**-**	**0.11**
	MPI	-4634.89	0.01	0.00	0.01	0.02	0.06	0.46	0.03	0.02	0.05	0.11
WW	**S1-5**	**13925.87**	**1.43**	**0.46**	**-**	**-**	0.04	**-**	**0.13**	**0.04**	**-**	**-**
	MI	13927.41	1.30	0.00	0.93	-	0.05	-	0.11	0.00	0.08	-
	PI	13928.29	1.33	0.48	-	0.09	0.04	-	0.12	0.04	-	0.01
	MPI	13929.02	1.05	0.00	1.05	0.20	0.04	-	0.09	0.00	0.09	0.02
6MW	**S1-8**	**12978.95**	**1.56**	-	-	-	0.05	0.10	0.13	-	-	-
	MI	13177.43	1.50	-	0.39	-	0.04	0.11	0.12	-	0.03	-
	PI	13176.84	1.35	-	-	0.39	0.05	0.11	0.11	-	-	0.03
	MPI	13177.39	0.94	-	0.63	0.55	0.04	0.10	0.08	-	0.05	0.05
9MW	S1-7	12198.01	4.13	-	-	-	-	0.08	0.28	-	-	-
	MI	12199.57	3.95	-	0.30	-	-	0.08	0.26	-	0.02	-
	PI	**12196.50**	**3.67**	**-**	**-**	**0.83**	**-**	0.08	**0.24**	**-**	**-**	**0.06**
	MPI	12197.97	3.31	-	0.41	0.90	-	0.07	0.22	-	0.03	0.06
YW	**S1-7**	**11847.698**	**6.99**	**-**	**-**	**-**	**-**	0.06	**0.30**	**-**	**-**	**-**
	MI	11849.562	6.75	-	0.34	-	-	0.06	0.29	-	0.02	-
	PI	11849.292	6.63	-	-	0.48	-	0.06	0.29	-	-	0.02
	MPI	11851.038	6.15	-	0.51	0.58	-	0.06	0.27	-	0.02	0.03
YFW	**S1-7**	**27822.308**	**3575.53**	**-**	**-**	**-**	**-**	0.07	**0.18**	**-**	**-**	**-**
	MI	27824.254	3469.24	-	152.86	-	-	0.07	0.18	-	0.01	-
	PI	27824.128	3413.18	-	-	265.67	-	0.07	0.17	-	-	0.01
	MPI	27825.99	3158.60	-	275.13	350.28	-	0.07	0.16	-	0.01	0.02

[1] For trait abbreviations see footnote of Table 1

[2] σ_a^2: Additive genetic variance, σ_m^2: Genetic maternal variance, σ_{mi}^2: Maternal imprinting variance, σ_{pi}^2: Paternal imprinting variance, pe^2: Ratio of maternal permanent environment effect, ce^2: Ratio of maternal common environment effect, h_a^2: Direct heritability, h_m^2: Maternal heritability, h_{mi}^2: Maternal imprinting heritability, h_{pi}^2: Paternal imprinting heritability, AIC: Akaike Information Criterion

The current research indicates that parental imprinting significantly influenced growth traits in Markhoz goats, with paternal imprinting having a greater impact than maternal imprinting. Incorporating paternal imprinting improved model fit for BW and 9MW, accounting for 11% and 6% of the phenotypic variation, respectively. In contrast, maternal imprinting showed higher variance components but did not enhance model adequacy. Paternally imprinted genes, expressed only when inherited from the father, may influence body weight traits. When inherited from the mother, these genes typically remain inactive, though they may be expressed in future generations depending on imprinting status. Additionally, paternal imprinting regulates certain genes in a manner distinct from additive genetic effects, which should be considered in breeding programs to improve selection accuracy and maximize genetic gain. The findings emphasize the importance of paternal imprinting in growth traits, suggesting that focusing on breeding values related to paternal imprinting when selecting sires could improve genetic response.

The findings of Amiri Roudbar et al. (2018) highlight that both maternal and paternal imprinting significantly affect growth traits in sheep. Maternal imprinting explained 10.5% to 23.3% of phenotypic variability, most notably in birth and weaning weights, and improved model fit by reducing the Bayesian Information Criterion (BIC) for all traits except 6-month weight and yearling weight. Its inclusion also lowered direct heritability estimates across traits. Paternal imprinting showed a notable impact on average daily gain from birth to weaning and contributed to a 44.5% reduction in additive genetic variance, underscoring its relevance in genetic modeling. Studies have also observed paternal imprinting effects across various traits and farm animals (Neugebauer et al., 2010a; Imumorin et al., 2011; Meyer and Tier, 2012; Tier and Meyer, 2012). Recent findings indicate that paternal imprinting affects goat growth traits by altering the expression of specific genes depending on their parental origin. Parental effects play a crucial role in shaping complex traits and significantly contribute to phenotypic variance, as demonstrated in studies on domesticated animals including pigs, cattle, sheep, and goats (Neugebauer et al., 2010a, 2010b; Imumorin et al., 2011; Meyer and Tier, 2012; Tier and Meyer, 2012; Hu et al., 2015; Amiri Roudbar et al., 2017, 2018; Ghafouri-

Kesbi et al., 2022a, 2022b; Ehsaninia and Ghafouri-Kesbi, 2024).

In the Iran-Black sheep study, maternal imprinting effects accounted for 12–23% of phenotypic variation, enhancing model accuracy for traits such as weaning and 6-month body weight (Amiri Roudbar et al., 2017). In contrast, our findings in Markhoz goats showed more modest maternal imprinting effects, explaining between 1.5% and 9% of the phenotypic variance across evaluated traits. In Lori-Bakhtiari sheep, models incorporating maternal imprinting showed enhanced variance estimation and improved BIC, except for the 6MW and YW traits. Maternal imprinting effects accounted for 10.5% of phenotypic variation in WW and up to 23.3% in BW. Including maternal imprinting in the models resulted in reduced direct heritability estimates: BW decreased by 21.3%, WW by 26.5%, 6MW by 13.8%, 9MW by 41%, and YW by 25.8% (Amiri Roudbar et al., 2018).

Ehsaninia and Ghafouri-Kesbi (2024) reported that among growth traits in Murciano-Granadina kids, maternal imprinting influenced only birth weight. Incorporating this effect into the optimal initial model reduced additive genetic variance by 6.29% and maternal genetic variance by 85.71%. In Baluchi sheep, significant maternal imprinting effects on birth weight were observed, explaining 12% of phenotypic variation (Ghafouri-Kesbi et al., 2022a). By contrast, such effects were absent in Makuie sheep (Ghafouri-Kesbi et al., 2022a). In Zandi sheep, both maternal and paternal imprinting contributed to variation in birth and weaning weights, with imprinting-inclusive models providing better data fit and accounting for approximately 8% of phenotypic variation (Ghafouri-Kesbi et al., 2022b).

In beef cattle, maternal imprinting affects birth and weaning weights (0-11%) and yearling and final weights (7-8%). Paternal imprinting impacts birth and weaning weights (5-7%) but has little effect on yearling and final weights (0-1%) (Meyer and Tier, 2012). Neugebauer et al. (2010b) reported that total imprinting effects accounted for 8–25% of the additive genetic variance in beef carcass traits. Karami et al. (2019) showed that parental effects significantly impact body weight in Iranian indigenous poultry, improving parameter estimation accuracy at 8 and 12 weeks. The study found paternal and maternal imprinting effects explained 4% and 5% of the variability in BW8 and BW12, respectively.

Variations in parental effects on body weight traits across breeds and species may stem from differences in genetic architecture, management practices, and data structure. For instance, studies in cattle (Neugebauer et al., 2010b), sheep (Ghafouri-Kesbi, 2022a; Amiri Roudbar et al., 2018), and goats (Ehsaninia and Ghafouri-Kesbi, 2024) have reported varying contributions of imprinting effects. These differences may reflect breed-specific genetic backgrounds, management systems, and trait recording strategies.

Parent-of-origin effects, such as genomic imprinting, can substantially influence economically important traits, including growth performance, reproductive efficiency, and carcass quality. These effects have been reported across multiple livestock species, with varying contributions depending on breed, trait type, and genetic architecture (e.g., Neugebauer et al., 2010b; Ghafouri-Kesbi, 2022a; Ehsaninia and Ghafouri-Kesbi, 2024). In the study of Markhoz goats, maternal imprinting had no detectable effect on body weight traits or fleece weight, whereas paternal imprinting significantly influenced birth weight and nine-month weight. This may reflect breed-specific genetic architecture or potential differences in epigenetic regulation pathways, with paternal alleles exerting a stronger imprinting effect in these particular traits. Other research indicates maternal imprinting has a stronger influence on body weight characteristics than paternal imprinting (Meyer and Tier, 2012; Amiri Roudbar et al., 2017, 2018). During embryonic development, maternal imprinting influences placental growth, while paternal imprinting drives embryonic tissue development, both of which can have lasting effects on postnatal growth traits and metabolic outcomes (Barlow and Bartolomei, 2014).

A confounding effect was observed between maternal genetic contributions and maternal imprinting influences on the weaning weight trait, complicating the distinction between variations driven by true imprinting and those resulting from maternal genetic factors. This was evidenced by the reduction of maternal genetic variance to zero in the weaning weight statistical model when maternal parent-of-origin effects were included, suggesting that neglecting maternal imprinting may lead to an overestimation of maternal genetics. Interestingly, the reduction in maternal genetic variance was less pronounced for the BW trait compared to WW, likely due to the stronger influence of maternal environmental factors and imprinting during the postnatal period, which more heavily affect WW than BW. We were unable to examine this issue in other growth traits due to our study being restricted to BW and WW traits, which are the only ones affected by maternal genetic variance.

Paternal imprinting reduced direct heritability estimates for BW, WW, 6MW, 9MW, YW, and YFW by 83.7%, 6.7%, 17.7%, 11.7%, 5.4%, and 4.7%, respectively. Maternal imprinting caused declines of 0.7%, 9.1%, 8.3%, 4.3%, 3.5%, and 3% in direct heritability for these traits. The reduction in direct heritability was more pronounced with paternal imprinting compared to maternal imprinting, aligning with previous research by Meyer and Tier (2012), Tier and Meyer (2012), and Amiri Roudbar et al. (2017, 2018). This suggests that certain imprinting effects may confound or reduce the accuracy of estimating direct additive genetic effects, particularly for traits that are strongly influenced by parental factors. Due to the dissimilar nature of imprinting and additive genetic heritabilities, including this variation in the analysis of growth traits could potentially benefit breeding programs. Thus, a portion of growth trait variation in goats may be due to the differential gene expression from both parental sources. The present study showed that parental imprinting has a lesser impact on yearling greasy fleece weight than on growth traits in Markhoz goats, possibly because fleece development is more influenced by postnatal environmental factors and polygenic inheritance than by parent-of-origin effects. Including parental imprinting effects from both parents did not alter estimates of maternal permanent and common environmental variances, aligning with findings by Meyer and Tier (2012), but contrasting with Amiri Roudbar et al. (2017), a difference that may stem from variations in data structure, breed-specific imprinting patterns, or model specifications used in the respective studies. Meyer and Tier found no impact on weight traits in beef, while Amiri Roudbar reported a decrease in maternal permanent variance with maternal imprinting effects included. Parental effects, like genomic imprinting, can result in transgenerational inheritance of epigenetic traits, leading to phenotypic changes over generations without affecting allele frequencies (Bonduriansky and Day, 2009). This aspect of epigenetics can be utilized in animal breeding by selecting for epigenetically controlled traits. Imprinted genes show distinct expression patterns in various tissues during development, influencing a range of traits. Studying epigenetic inheritance in livestock production is crucial, especially for understanding hybrid vigor, although conflicting findings, such as those reported by Groszmann et al. (2013), may arise due to differences in species-specific epigenetic mechanisms, environmental influences, or the complexity of gene expression regulation in hybrids. Research in this area could improve breeding methods and reduce disease prevalence, meeting production standards (Feeney et al., 2014).

Conclusions

This study highlights the importance of incorporating parental imprinting effects into genetic evaluation models for body weight traits in Markhoz goats. Imprinting effects accounted for 0.7% to 11% of phenotypic variance and reduced direct and maternal genetic variance estimates, underscoring their relevance in genetic assessments. These findings emphasize the role of epigenetics in enhancing breeding program efficiency and refining selection strategies. Future research into the molecular mechanisms of imprinting and its integration with conventional genetic evaluations may offer more precise tools for modeling complex traits and optimizing livestock performance.

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Conflict of interest

The author declares no conflicts of interest with any companies or organizations related to the content of this article.

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