

# Multiple-trait and structural equation modelling approaches to infer genetic relationships between tail length and weight traits in Merinoland sheep

Jennifer Oberpenning<sup>1</sup> | Mehdi Bohlouli<sup>1</sup> | Petra Engel<sup>1</sup> | Hannah Hümmelchen<sup>2</sup> | Henrik Wagner<sup>2</sup> | Axel Wehrend<sup>2</sup> | Sven König<sup>1</sup> 

<sup>1</sup>Institute of Animal Breeding and Genetics, Justus-Liebig-University Gießen, Gießen, Germany

<sup>2</sup>Clinic for Obstetrics, Gynaecology and Andrology of Large and Small Animals, University of Giessen, Giessen, Germany

## Correspondence

Sven König, Institute of Animal Breeding and Genetics, Justus-Liebig-University Gießen, Ludwigstraße 21b, 35390 Gießen, Germany.  
Email: [sven.koenig@agrar.uni-giessen.de](mailto:sven.koenig@agrar.uni-giessen.de)

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## Abstract

Tail docking is routinely conducted in long-tailed sheep breeds to prevent fly-strike infections, but it is not in agreement with legal guidelines and animal welfare issues. Selection on short tails is a sustainable alternative in this regard, but side effects on other breeding goal traits are unclear. In consequence, the present study aimed to estimate genetic parameters for tail length (TL) at birth, birth weight (BW), weaning weight (WW) and postweaning weight (PWW) at the slaughtering date considering single-trait (STM), multiple-trait (MTM) and structural equation models (SEM) with different random effects, and accordingly, different covariance structures. The SEM considered time-lagged recursive relationships among response variables in three different pathways. The first path pertained to the effect of TL on WW and of WW on PWW. The second path reflected the effect of BW on WW and of WW on PWW. The third path was the recursive effect of TL on PWW. The phenotypic data consisted of 2803 records for TL, 13,042 records for BW, 1556 records for WW and 3986 records for PWW from Merinoland lambs. Lambs were born in the period from 1995 to 2021 and kept at the university Gießen research station, Germany, with their naturally long tails. Genetic statistical model evaluation based on Bayesian and Akaike's information criteria suggested models simultaneously considering direct genetic, maternal genetic and maternal permanent environmental effects and respective covariances. For statistical models including the same random effects and covariance structures, SEM were superior over MTM. The direct heritability for TL from the best-fitting STM was  $0.60 \pm 0.08$ , indicating the potential for genetic reduction of tail length within a few generations. For growth traits, the direct heritabilities ranged from  $0.16 \pm 0.03$  for BW to  $0.31 \pm 0.09$  for PWW. The maternal heritabilities were  $0.03 \pm 0.03$  for TL,  $0.12 \pm 0.02$  for BW,  $0.04 \pm 0.03$  for WW and  $0.07 \pm 0.03$  for PWW, reflecting small, but the non-significant influence of uterine characteristics on the tail development. The direct genetic correlations between TL and

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all weight traits were positive and very similar to MTM and SEM but reflected antagonistic genetic relationships from a breeding perspective. Oppositely, the structural equation coefficients reflecting trait associations phenotypically were negative (favourable) for the time-lagged effects of TL on WW and on PWW. As an explanation, lambs with long and woolly tails have an increased risk for contamination with dirt and dust causing infections, which in turn impairs the body weight development. In conclusion, breeding on short tails should consider trait-associated environmental risk factors, for example, disease susceptibility, which can be mimicked via SEM approaches.

#### KEYWORDS

genetic parameters, sheep, structural equation models, tail length, weight traits

## 1 | INTRODUCTION

Merinoland sheep is the most commonly utilized 18th-century breed in Germany, which was generated by crossing Merino from Spain with local German breeds during the 18th century (Samraus, 2011). The aim of crossing was to improve female fertility and wool quality traits (Schiller et al., 2015). However, to fulfil local market demands, meat production gained increasing importance in breeding goals by neglecting wool quantity and quality (Strittmatter, 2005). Morphologically, Merinoland sheep are characterized by large body trait measurements and long tails. However, the long and woolly tail increases the risk of faecal contamination and induces susceptibility to flystrike (French et al., 1994; Lagler et al., 2022; Sutherland & Tucker, 2011). The official German statutes for animal protection (TierSchG, 2006) allow tail docking after birth only in specific cases, but it is a widespread management practice to minimize tail infections. Nevertheless, tail docking induces animal pain, and in consequence, it is not in line with farm animal welfare policies as defined in the EU Directive 2008/120/EG (European Union, 2008).

As an alternative to tail docking, breeding on short tails may be the most sustainable solution (Aikins-Wilson et al., 2021; Scobie & O'Connell, 2002). The observed quite a large amount of within-breed genetic variation for tail length offers the potential for successful purebred breeding strategies (Aikins-Wilson et al., 2021; Gizaw et al., 2008; Greeff et al., 2015). Accordingly, moderate to large heritabilities for tail length were estimated with 0.48 in Menz sheep (Gizaw et al., 2008), with 0.58 in Merino (Greeff et al., 2015) and with 0.82 in Finnish Landrace breeds (Scobie & O'Connell, 2002).

The complex breeding goal definition in Merinoland sheep requires genetic correlation estimates among all index and breeding goal traits, which are estimated via multiple-trait model (MTM) applications. However, genetic covariances might be biased in the case of

feedback and recursiveness among response variables. Consequently, Gianola and Sorensen (2004) suggested structural equation models (SEM) to infer genetic parameters for animal breeding objectives in the context of physiological relationships and biological systems. In the case of recursive relationships, trait A affects trait B by ignoring the reciprocal effect of trait B on trait A. The SEM framework mostly have been applied to infer genetic and phenotypic relationships among health, female fertility and productivity. For example, in dairy cows, König et al. (2008) modelled a recursive system including a two-way causal path. One path reflected the unfavourable effect of increasing test-day milk yield after calving on claw health, and the second path was the time-lagged and recursive effect of a claw disorder on milk yield decline in the ongoing lactation. In sheep, Jafaroghli et al. (2010) and Posht-e Masari et al. (2019) studied growth traits by modelling mutual relationships among response variables. In their studies, direct genetic correlations between weights from different periods and daily gain ranged from 0.37 to 0.85, and the structural equation coefficients reflecting trait associations phenotypically, were positive. With regard to tail length and weights of sheep, the biological justification of SEM modelling approaches based on (i) the relationships between tail length at birth and body size characteristics due to the variations in the number of the vertebra (Haverkamp et al., 2015), (ii) the associations between tail length and risks for infections with ongoing detrimental impact on feeding behaviour (Hümmelchen et al., 2022) and (iii) the effect of a changing nutritional supply from milk expressed via weaning weight on own roughage intake expressed via post weaning weight (Gernand et al., 2008).

Consequently, the aim of the present study was to apply different statistical modelling approaches for the estimation of direct and maternal-genetic effects on tail length and on weight traits recorded at birth, at the weaning date and at the slaughtering date. In ongoing multi-trait

analyses, we evaluated different MTM and focused on the estimation of genetic covariance components and genetic correlations for all trait combinations. Corresponding SEM including the three pathways as described above aimed at inferring genetic (co)variance components and structural equation coefficients for mutual direct and time-lagged trait associations.

## 2 | MATERIALS AND METHODS

The committee of animal care and protection as established by University of Giessen officially approved this study. The official number for this study is V 54–19c 20 15 h 01 GI 18/14 Nr. G 44/2021.

### 2.1 | Animals and traits

The present study considered the experimental purebred Merinoland sheep population from the University Gießen research station “Oberer Hardthof,” Germany, with their natural and undocked tails. The flock was kept in grazing (spring to fall) and high-input (fall to spring) production systems. The phenotypic records were collected over a period of 27 years (1995–2021) and included tail length at birth (TL) measured in cm, birth weight (BW) in kg, weaning weight (WW) in kg (average age of 62 days) and postweaning weight (PWW) in kg recorded at the slaughtering date (average age of 118 days). Year-month combinations with a small number of records (less than 10 lambs with records for TL, BW, WW or PWW) were discarded, implying the exclusion of records from 11-year-month combinations for the ongoing genetic analyses. In addition, all traits were checked for outliers by excluding records with values lower or higher than the mean  $\pm 3$  SD. After editing and discarding 11% of all initial records, the data consisted of 2803 records for TL, 13,042 records for BW, 1556 records for WW and 3986 records for PWW. All lambs with records for TL had records for the weight traits BW and PWW, and all lambs with records for WW had a TL measurement. The descriptive statistics for the traits are given in Table 1.

The pedigree of the lambs with trait records was traced back as many generations as possible and comprised 30,708 animals. In genetic analyses, all lambs with records could be traced back for at least three generations, but most of the lambs even had deeper pedigrees. Lourenco et al. (2014) evaluated the effects of pedigree depth on the accuracy of genetic evaluations, which depended on the data structure and the trait, but for genotyped animals,

TABLE 1 Descriptive statistics of tail length at birth, birth weight, weaning weight and postweaning weight

Trait	No. of records	Mean	SD	Min	Max
Tail length (TL, in cm)	2803	23.42	2.36	16.2	30.4
Birth weight (BW, in kg)	13,042	5.50	1.04	2.4	8.6
Weaning weight (WW, in kg)	1556	29.20	5.58	14.0	53.0
Postweaning weight (PWW, in kg)	3986	43.69	6.56	22.0	73.0

two or three generations of phenotypic records plus two additional pedigree generations were mostly sufficient in terms of accuracies. The pedigree completeness index was calculated according to MacCluer et al. (1983) and was 96.4%.

The lambs with phenotypic records were offspring from 169 different rams and different 4689 ewes. The average pedigree-based inbreeding coefficient of the lambs calculated with the CFC software package (Sargolzaei et al., 2006) was 6.5%, and increased from 2.8% in 1995 to 8.3% in 2021.

### 2.2 | Genetic-statistical analyses

Genetic parameters for all traits were estimated using the software package WOMBAT (Meyer, 2007) and applying restricted maximum likelihood. First, 6 different single-trait models (STM) were fitted including different random effects and considering different covariance structures for random effects. The single-trait models 1–6 (i.e., STM-1–STM-6) were defined as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (\text{STM-1})$$

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_c\mathbf{c} + \mathbf{e} \quad (\text{STM-2})$$

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{e} \text{ with } \text{Cov}(a, m) = 0 \quad (\text{STM-3})$$

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{e} \text{ with } \text{Cov}(a, m) = \mathbf{A}\sigma_{am} \quad (\text{STM-4})$$

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_c\mathbf{c} + \mathbf{e} \text{ with } \text{Cov}(a, m) = 0 \quad (\text{STM-5})$$

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_c\mathbf{c} + \mathbf{e} \text{ with } \text{Cov}(a, m) = \mathbf{A}\sigma_{am} \quad (\text{STM-6})$$

where  $\mathbf{y}$  was the observation vector for the lamb trait (TL, BW, WW or PWW);  $\mathbf{b}$  was the vector of fixed effects including year-month at recording, litter size, litter number and sex;  $\mathbf{a}$  was the vector of random direct genetic effects;  $\mathbf{c}$  was the vector of random maternal permanent environmental effects;  $\mathbf{m}$  was the vector of random maternal genetic effects and  $\mathbf{e}$  was the vector of random residual effects.  $\mathbf{X}$ ,  $\mathbf{Z}_a$ ,  $\mathbf{Z}_m$  and  $\mathbf{Z}_c$  were incidence matrices relating the records to fixed, additive direct genetic, maternal genetic and maternal permanent environmental effects, respectively.  $\mathbf{A}$  was the numerator relationship matrix and  $\sigma_{am}$  was the genetic covariance between direct and maternal genetic effects. It was assumed that the random effects are independent and normally disturbed. The (co)variance structure for random effects in model 6 (and correspondingly reduced in the remaining models with a smaller number of (co)variance components) was

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & 0 & 0 \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_c^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where  $\sigma_a^2$  and  $\sigma_m^2$  were the direct and maternal genetic variances, respectively;  $\sigma_{am}$  was the covariance between direct and maternal genetic effects;  $\sigma_c^2$  was the maternal permanent environmental variance;  $\sigma_e^2$  was the residual variance and  $\mathbf{I}$  was an identity matrix.

The phenotypic variance ( $\sigma_p^2$ ) was computed as the sum of the (co)variance components with  $\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_e^2$ . The direct heritability ( $h_d^2$ ), the maternal heritability ( $h_m^2$ ), the maternal permanent environmental variance as a proportion of the phenotypic variance ( $c^2$ ) and the direct-maternal genetic correlation ( $r_{gam}$ )

were calculated as  $h_d^2 = \sigma_a^2 / \sigma_p^2$ ,  $h_m^2 = \sigma_m^2 / \sigma_p^2$ ,  $c^2 = \sigma_c^2 / \sigma_p^2$

and  $r_{gam} = \sigma_{am} / \sqrt{\sigma_a^2 \times \sigma_m^2}$ , respectively. The effects from

STM-1 to STM-6 were considered in respective MTM by simultaneously including TL, BW, WW and PWW. For the most sophisticated model with all random effects, that is MTM-6, the matrix notation was as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \vdots \\ \mathbf{y}_4 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{X}_4 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \vdots \\ \mathbf{b}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{Z}_{a4} \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \vdots \\ \mathbf{a}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{m1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{Z}_{m4} \end{bmatrix} \begin{bmatrix} \mathbf{m}_1 \\ \vdots \\ \mathbf{m}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{c1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{Z}_{c4} \end{bmatrix} \begin{bmatrix} \mathbf{c}_1 \\ \vdots \\ \mathbf{c}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \vdots \\ \mathbf{e}_4 \end{bmatrix} \text{ with } \text{Cov}(a, m) = \mathbf{A}\sigma_{am}$$

(MTM-6)

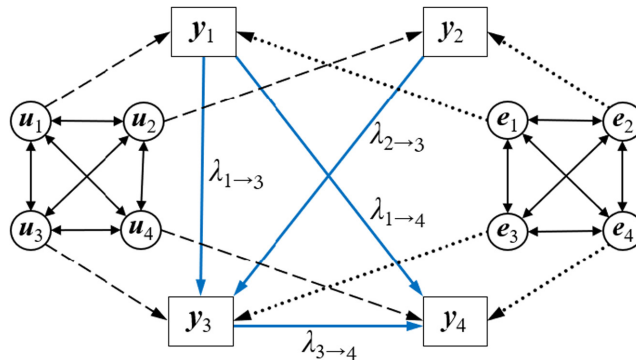


FIGURE 1 Recursive causal structure involving tail length at birth ( $y_1$ ), birth weight ( $y_2$ ), weaning weight ( $y_3$ ) and postweaning weight ( $y_4$ ) traits influenced by direct genetic effects ( $u_i$ ) and by residual ( $e_i$ ) effects. Bidirectional arrows indicate genetic or residual correlations between pairs of traits. Blue arrows represent the direct recursive effect of trait  $i$  on trait  $j$  ( $\lambda_{i \rightarrow j}$ ) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

where  $\mathbf{y}_1$  to  $\mathbf{y}_4$  were the observations for BW, TL, WW and PWW, respectively. For the remaining multiple-trait models MTM-1 to MTM-5 with a smaller number of effects and partly ignored covariance structures (see the STM definitions above), effects as defined in MTM-6 were excluded accordingly.

With regard to SEM, we hypothesized three pathways. The first path described the recursive and time-lagged effects of TL (trait 1) on WW (trait 3), and in the same path of WW (trait 3) on PWW (trait 4). A second pathway included the three weight traits simultaneously, that is, a recursive effect of BW (trait 2) on WW (trait 3), and in the ongoing process of ageing the causal recursive effect of WW (trait 3) on PWW (trait 4). The third pathway reflected the effect of TL (trait 1) on PWW (trait 4). From a biological and physiological perspective, such research objectives require a sheep population with undocked tails as kept on the research station of Oberer Hardthof, University of Giessen, Germany. The different recursive pathways are outlined in Figure 1.

Consequently, a matrix of structural equation coefficients ( $\Lambda$ ) was premultiplied with the observation vector. In analogy to the six STM and MTM, SEM-1 to SEM-6 were defined with the corresponding effects. Thus, SEM-6 was constructed as follows (and correspondingly reduced in the remaining five models with a smaller number of random effects):

$$\begin{bmatrix} \mathbf{y}_1 \\ \vdots \\ \mathbf{y}_4 \end{bmatrix} = \Lambda \begin{bmatrix} \mathbf{y}_1 \\ \vdots \\ \mathbf{y}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{X}_1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{X}_4 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \vdots \\ \mathbf{b}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{Z}_{a4} \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \vdots \\ \mathbf{a}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{m1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{Z}_{m4} \end{bmatrix} \begin{bmatrix} \mathbf{m}_1 \\ \vdots \\ \mathbf{m}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{e1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \mathbf{Z}_{e4} \end{bmatrix} \begin{bmatrix} \mathbf{c}_1 \\ \vdots \\ \mathbf{c}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \vdots \\ \mathbf{e}_4 \end{bmatrix} \quad \text{with Cov}(a, m) = \mathbf{A}\sigma_{am} \quad (\text{SEM-6})$$

and

$$\Lambda = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \mathbf{I}\lambda_{1 \rightarrow 3} & \mathbf{I}\lambda_{2 \rightarrow 3} & 0 & 0 \\ 0 & \mathbf{I}\lambda_{2 \rightarrow 4} & \mathbf{I}\lambda_{3 \rightarrow 4} & 0 \end{bmatrix}$$

where  $\mathbf{I}$  was the identity matrix and  $\lambda_{i \rightarrow j}$  represented direct effects of trait  $i$  on trait  $j$ . If all elements of the  $\Lambda$  matrix are equal to 0, then the SEM model is equal to an MTM model. Despite the difference in interpretations of MTM and SEM, the distribution of random effects was assumed to be the same for both models. Thus, the (co)variance structures for random effects using the model with all random effects (model 6) were

$$\text{var} \begin{bmatrix} \mathbf{a}_1 \\ \vdots \\ \mathbf{a}_4 \\ \mathbf{m}_1 \\ \vdots \\ \mathbf{m}_4 \end{bmatrix} = \mathbf{A} \otimes \begin{bmatrix} \sigma_{a_1}^2 & \dots & \sigma_{a_1, m_4} \\ \vdots & \ddots & \vdots \\ \sigma_{m_4, a_1} & \dots & \sigma_{m_4}^2 \end{bmatrix},$$

$$\text{var} \begin{bmatrix} \mathbf{c}_1 \\ \vdots \\ \mathbf{c}_4 \end{bmatrix} = \mathbf{I} \otimes \begin{bmatrix} \sigma_{c_1}^2 & \dots & \sigma_{c_1, c_4} \\ \vdots & \ddots & \vdots \\ \sigma_{c_4, c_1} & \dots & \sigma_{c_4}^2 \end{bmatrix},$$

$$\text{var} \begin{bmatrix} \mathbf{e}_1 \\ \vdots \\ \mathbf{e}_4 \end{bmatrix} = \mathbf{I} \otimes \begin{bmatrix} \sigma_{e_1}^2 & \dots & \sigma_{e_1, e_4} \\ \vdots & \ddots & \vdots \\ \sigma_{e_4, e_1} & \dots & \sigma_{e_4}^2 \end{bmatrix}$$

where  $\sigma_{a_i}^2$  and  $\sigma_{m_i}^2$  were direct and maternal genetic variances, respectively, for trait  $i$  ( $i = 1$  to 4);  $\sigma_{a_i, m_j}$  was the covariance between the direct genetic effect for trait  $i$  and the maternal genetic effect for trait  $j$  ( $j = 1$  and 4);  $\sigma_{c_i}^2$  was the maternal permanent environmental variance for trait  $i$ ;  $\sigma_{c_{ij}}$  was the maternal permanent covariance between traits  $i$  and  $j$ ;  $\sigma_{e_i}^2$  and  $\sigma_{e_{ij}}$  were residual variances and covariances, respectively and  $\mathbf{A}$  and  $\mathbf{I}$  were the numerator relationship and identity matrices, respectively.

In both MTM and SEM analyses, direct or maternal genetic correlations between traits  $i$  and  $j$  ( $r_{g_{ij}}$ ) were

$$r_{g_{ij}} = \sigma_{g_{ij}} / \sqrt{\sigma_{g_i}^2 \times \sigma_{g_j}^2}, \quad \text{where } \sigma_{g_{ij}} \text{ was the direct or mater-}$$

nal genetic covariance between traits  $i$  and  $j$ , and  $\sigma_{g_i}^2$  and  $\sigma_{g_j}^2$  were the direct or maternal genetic variances for trait  $i$  and trait  $j$ , respectively. Phenotypic correlations were calculated based on the estimated (co)variance components from the WOMBAT software package (Meyer, 2007). In

this regard, the phenotypic correlation is equal to the sum of the additive genetic, maternal genetic, permanent environmental and residual covariances between traits one and two, divided by the product of the square roots of the phenotypic variances for both traits.

The goodness of fit for the 6 models combined with the 3 approaches (i.e., STM, MTM and SEM) was determined based on Akaike's information criterion (AIC) and the Bayesian information criterion (BIC). The AIC was calculated as  $AIC = -2\log L + 2p$ , and  $BIC = -2\log L + p\log(N - r(x))$ , where  $\log L$  was the natural logarithm of the likelihood function value,  $p$  was the

**TABLE 2** Model evaluation of the six single-trait animal models (as described in the materials and methods) for tail length (TL), birth weight (BW), weaning weight (WW) and postweaning weight (PWW) according to the AIC and BIC evaluation criteria

Trait	Model	$p^a$	AIC	BIC
TL	STM-1	2	6817.2	6829.0
	STM-2	3	6813.4	6831.2
	STM-3	3	<b>6813.0</b>	<b>6830.7</b>
	STM-4	4	6815.4	6839.1
	STM-5	4	6813.0	6836.7
	STM-6	5	6814.7	6844.3
BW	STM-1	2	7850.5	7865.4
	STM-2	3	7634.0	7656.4
	STM-3	3	7620.7	7643.1
	STM-4	4	7617.8	7647.6
	STM-5	4	<b>7600.7</b>	<b>7632.6</b>
	STM-6	5	7601.4	7638.7
WW	STM-1	2	5937.1	5947.8
	STM-2	3	5937.9	5953.8
	STM-3	3	<b>5928.7</b>	<b>5944.6</b>
	STM-4	4	5938.6	5959.8
	STM-5	4	5930.7	5951.9
	STM-6	5	5929.1	5955.7
PWW	STM-1	2	16,666.0	16,678.6
	STM-2	3	16,659.4	16,678.2
	STM-3	3	16,658.4	16,677.2
	STM-4	4	<b>16,654.0</b>	<b>16,680.0</b>
	STM-5	4	16,657.4	16,682.5
	STM-6	5	16,654.0	16,685.3

Note: Values for model evaluation criteria (AIC and BIC) from the best model are highlighted in bold.

<sup>a</sup>Number of parameters.

**TABLE 3** Model evaluation of multiple-trait (MTM) and structural equation models (SEM) (as described in the materials and methods) considering AIC and BIC

Model	$p^a$	MTM		SEM		Diff <sup>b</sup>
		AIC	BIC	AIC	BIC	
1	20	35,691.5	35,850.5	35,678.2	35,837.3	13.2
2	30	35,467.5	35,706.0	35,452.3	35,690.9	15.1
3	30	35,455.7	35,602.3	35,438.2	35,679.8	17.5
4	46	35,448.7	35,814.5	35,431.0	35,796.8	17.8
5	40	35,444.4	35,762.5	35,427.1	35,745.1	17.4
6	56	35,441.3	35,786.6	35,427.3	35,682.6	14.0
Best <sup>c</sup>	33	35,439.2	35,694.6	35,422.3	35,674.7	16.9

<sup>a</sup>Number of parameters.

<sup>b</sup>AIC value from the MTM minus AIC from the respective SEM.

<sup>c</sup>The best MTM and SEM models were constructed using the most appropriate single-trait models (i.e., STM-3 for TL, STM-5 for BW, STM-3 for WW and STM-4 for PWW).

number of parameters in the model,  $N$  was the number of observations and  $r(x)$  was the rank of the fixed effect incidence matrix. The model with the lowest AIC and BIC values was considered the most appropriate model.

### 3 | RESULTS

#### 3.1 | Model comparison

AIC and BIC values for STM-1 to STM-6 from the genetic analyses of all four traits are given in Table 2. For TL, the largest AIC value was obtained for STM-1, and no significant differences were identified among models STM-2 to STM-6. For the growth traits, models with maternal genetic effects indicated lower AIC and BIC values compared to STM-1 and STM-2. For BW, the best fitting model was STM-5, considering direct genetic, maternal genetic and permanent environmental effects. Model STM-3 was favourable for WW, and STM-4 for PWW. The same favourable STM were selected based on AIC and on BIC.

Table 3 shows the AIC and BIC values for the different MTM and SEM. In the last row for the “best model,” we considered the effects and covariance structure for each trait from the respective superior STM for each trait, that is, STM-3 for TL, STM-5 for BW, STM-3 for WW and STM-4 for PWW. Regarding model comparisons with a focus on the same traits and same effects, SEM displayed lower AIC and BIC values compared to MTM, and thus, SEM improved the goodness of fit. Due to the small differences in AIC and BIC values from the full models 6 compared to the “best” MTM or STM, we chose the results from STM-6, MTM-6 and SEM-6 for the ongoing interpretations and discussions in this manuscript. Such an approach allows the deepest insights into all possible covariances for all random effects and trait combinations.

#### 3.2 | (Co)variance components and heritabilities

The STM-6 generates all possible estimates for variance and covariance components of all random effects and displays almost the same AIC and BIC values for all traits compared to the best-fitting model (see Table 3). Genetic parameter estimates for all traits from the full single-trait model (STM-6) are given in Table 4. Additive genetic variances were  $3.15 \pm 0.87$  for TL,  $0.11 \pm 0.02$  for BW,  $5.48 \pm 2.21$  for BW and  $8.43 \pm 2.68$  for PWW. A quite large direct heritability of  $0.60 \pm 0.08$  was estimated for TL. For body weight traits, direct heritabilities ranged from  $0.16 \pm 0.03$  for BW to  $0.31 \pm 0.09$  for PWW. In comparison to the models STM-3 and STM-5, consideration of the direct-maternal genetic covariances in single-trait models (STM-4 and STM-6) was associated with an increase of maternal heritabilities for the studied traits of 20%–50%. Using STM-6, maternal heritability estimates were  $0.03 \pm 0.03$  for TL,  $0.12 \pm 0.02$  for BW,  $0.04 \pm 0.03$  for WW and  $0.07 \pm 0.03$  for PWW. The maternal permanent environmental variance as the proportion of the phenotypic variance ( $c^2$ ) ranged from  $0.04 \pm 0.02$  for TL to  $0.13 \pm 0.04$  for WW. For TL, a negative correlation of  $-0.26 \pm 0.20$  was estimated between direct and maternal genetic effects. The antagonistic direct-maternal correlations were stronger for the weight traits, that is,  $-0.33 \pm 0.15$  for BW,  $-0.65 \pm 0.23$  for WW and  $-0.74 \pm 0.13$  for PWW.

#### 3.3 | Phenotypic and genetic correlations between tail length and body weight traits

Estimates of phenotypic and genetic correlations between the traits from the models MTM-6 and SEM-6 are shown in Table 5. Using MTM-6, the smallest phenotypic correlation was estimated between TL and PWW ( $0.16 \pm 0.03$ ),

**TABLE 4** Genetic parameters ( $\sigma_p^2$  = phenotypic variance;  $\sigma_a^2$  = additive genetic variance;  $\sigma_m^2$  = maternal genetic variance;  $\sigma_e^2$  = residual variance;  $\sigma_{am}^2$  = covariance between direct and maternal genetic effects;  $\sigma_c^2$  = maternal permanent environmental variance;  $\sigma_e^2$  = direct heritability;  $h_d^2$  = direct heritability;  $h_m^2$  = maternal heritability;  $r_{g,am}$  = correlation between direct and maternal genetic effects and  $c^2$  = maternal permanent environmental variance as a proportion of the phenotypic variance) from the full single-trait animal model (STM-6) for tail length at birth (TL), birth weight (BW), weaning weight (WW) and postweaning weight (PWW)

Genetic parameters										
Trait	$\sigma_p^2$	$\sigma_a^2$	$\sigma_m^2$	$\sigma_{am}^2$	$\sigma_c^2$	$\sigma_e^2$	$h_d^2$	$h_m^2$	$r_{g,am}$	$c^2$
TL	5.24 (0.25)	3.15 (0.87)	0.16 (0.14)	-0.19 (0.10)	0.19 (0.10)	1.92 (0.45)	0.60 (0.08)	0.03 (0.03)	-0.26 (0.11)	0.04 (0.02)
BW	0.70 (0.01)	0.11 (0.02)	0.08 (0.01)	-0.03 (0.02)	0.05 (0.01)	0.49 (0.02)	0.16 (0.03)	0.12 (0.02)	-0.33 (0.15)	0.07 (0.01)
WW	18.32 (0.99)	5.48 (2.21)	0.72 (0.44)	-1.28 (0.58)	2.47 (0.77)	11.64 (1.78)	0.30 (0.11)	0.04 (0.03)	-0.65 (0.23)	0.13 (0.04)
PWW	27.03 (0.83)	8.43 (2.68)	2.02 (1.23)	-3.07 (1.04)	0.97 (0.56)	18.68 (1.53)	0.31 (0.09)	0.07 (0.03)	-0.74 (0.13)	0.04 (0.02)

Note: Corresponding standard errors of estimates as generated by the WOMBAT software package (Meyer, 2007) are given in brackets.

**TABLE 5** Phenotypic, direct genetic and maternal genetic covariances (above the diagonal) and respective correlations (below the diagonal) between traits from the full multiple-trait (MTM-6) and full structural equation model (SEM-6)

Model	Trait	Phenotypic				Direct genetic				Maternal genetic			
		TL	BW	WW	PWW	TL	BW	WW	PWW	TL	BW	WW	PWW
MTM	TL												
	BW	0.41 (0.02)				0.33 (0.14)				0.70 (0.16)			
	WW	0.20 (0.04)	0.42 (0.02)			0.23 (0.12)	0.67 (0.18)			0.25 (0.15)	0.72 (0.13)		
SEM	PWW	0.16 (0.03)	0.31 (0.02)	0.78 (0.01)		0.38 (0.22)	0.43 (0.10)	0.66 (0.19)		0.10 (0.04)	0.58 (0.11)	0.98 (0.07)	
	TL				4.24 (0.40)				1.89 (0.68)				0.12 (0.03)
	BW	0.43 (0.02)			1.51 (0.08)	0.34 (0.15)			0.28 (0.12)	0.67 (0.15)			0.18 (0.07)
SEM	WW	0.15 (0.04)	0.17 (0.03)		16.84 (0.61)	0.23 (0.13)	0.50 (0.24)		1.67 (0.94)	0.14 (0.15)	0.55 (0.19)		1.95 (0.46)
	PWW	0.34 (0.03)	0.35 (0.02)	0.78 (0.01)		0.62 (0.18)	0.48 (0.07)	0.66 (0.19)		0.25 (0.19)	0.62 (0.11)	0.99 (0.10)	

Note: Corresponding standard errors of estimates as generated by the WOMBAT software package (Meyer, 2007) are given in brackets.

**TABLE 6** Structural coefficients  $\lambda$  estimated with different structural equation models (SEM-1 to SEM-6)

Path <sup>a</sup>	Model <sup>b</sup>						Best <sup>c</sup>
	SEM-1	SEM-2	SEM-3	SEM-4	SEM-5	SEM-6	
$\lambda_{1 \rightarrow 3}$	-0.07	-0.08	-0.12	-0.11	-0.12	-0.08	-0.13
$\lambda_{1 \rightarrow 4}$	-0.39	-0.41	-0.49	-0.49	-0.47	-0.24	-0.47
$\lambda_{2 \rightarrow 3}$	1.21	1.25	0.98	0.66	1.51	1.37	1.49
$\lambda_{3 \rightarrow 4}$	-0.18	-0.19	-0.19	-0.18	-0.19	-0.14	-0.19

<sup>a</sup> $\lambda_{i \rightarrow j}$  represents the change in trait  $j$  per 1-unit increase of trait  $i$ . Traits are TL (trait 1), BW (trait 2), WW (trait 3) and PWW (trait 4).

<sup>b</sup>Effects of the different models are specified in the materials and methods.

<sup>c</sup>The best SEM was constructed using the effects from the most appropriate single-trait models (i.e., STM-3 for TL, STM-5 for BW, STM-3 for WW and STM-4 for PWW).

and the largest phenotypic correlation was between WW and PWW ( $0.78 \pm 0.01$ ). Similarly, phenotypic correlations among all traits were positive when fitting SEM-6. Direct genetic correlations from MTM-6 ranged from  $0.23 \pm 0.12$  between TL and WW to  $0.67 \pm 0.19$  between BW and WW. With regard to SEM-6, the direct genetic correlations ranged from  $0.23 \pm 0.13$  between TL and WW to  $0.66 \pm 0.19$  between WW and PWW. Maternal genetic correlations were strong and positive among body weight traits with the largest estimates of  $0.98 \pm 0.07$  and  $0.99 \pm 0.10$  between WW and PWW from MTM-6 and from SEM-6, respectively. Strong positive maternal genetic correlations ( $0.70 \pm 0.16$  from MTM-6 and  $0.67 \pm 0.15$  from SEM-6) were estimated between TL and BW, but the correlations were smaller between TL and the weight traits WW and PWW recorded at later ages.

### 3.4 | Structural equation coefficients

Estimated structural coefficients for the effects of TL on WW ( $\lambda_{1 \rightarrow 3}$ ) and on PWW ( $\lambda_{1 \rightarrow 4}$ ) were negative (Table 6). The negative effect of TL on weight traits increased with ageing. In SEM-6, for instance, structural coefficients of  $-0.08$  ( $\lambda_{1 \rightarrow 3}$ ) and of  $-0.24$  ( $\lambda_{1 \rightarrow 4}$ ) indicate that 1 cm increase in TL was associated with a decline of 0.08 kg for WW and 0.24 kg for PWW. With regard to the different SEM, positive structural coefficients were estimated for the effect of BW on WW in the range from 0.66 to 1.49. In contrast, structural coefficients for the effect of WW on PWW ( $\lambda_{3 \rightarrow 4}$ ) were negative in the range from  $-0.14$  to  $-0.19$ .

## 4 | DISCUSSION

### 4.1 | Genetic parameters and heritabilities for tail length and body weight traits

The quite large direct heritability (0.60) for TL reflects estimates as previously reported for different sheep breeds

(e.g., Gizaw et al., 2008; Greeff et al., 2015). Especially the direct heritability of 0.58 for TL in another Merino population (Greeff et al., 2015) is very similar to the estimate of 0.60 from the present study. An even larger heritability of 0.82 was reported for crosses of short-tailed Finnish Landrace and long-tailed Cheviot sheep (Scobie & O'Connell, 2002). In the context of this study, Scobie and O'Connell (2002) addressed the favourable allele frequencies of major genes for TL in this specific population. A crossing focus only on TL might be associated with indirect losses in genetic gain for other breeding goal traits, which have been improved in purebred Merino sheep based on additive-genetic effects during the past decades. Nevertheless, the large heritability for TL in our study indicates the possibility to generate a short-tailed sheep population within a few generations also for intra-breed selection strategies. In a recent study conducted in Merino sheep, Lagler et al. (2022) proved a strong quantitative-genetic background for TL, because a large number of genome-wide markers explained a large proportion of TL variation. Nevertheless, in ongoing gene annotations, Lagler et al. (2022) identified *HOXB13* on chromosome 11 as a potential candidate gene and suggested gene-assisted selection on shorter tails. From a physiological perspective, Fowden et al. (2006) addressed the effects of uterus characteristics of the dam on morphological traits in offspring, possibly explaining the maternal heritability for TL of 0.03. However, the maternal heritability for TL was quite small in the range of the respective standard error, and non-significantly different from zero.

The direct heritability for BW of 0.16 in the present study for Merino is very similar compared to estimates reported for Baluchi sheep (Abbasi et al., 2012), Chinese Merino (Di et al., 2011), Dorper (Kariuki et al., 2010) and the Horro sheep breed (Gowane et al., 2015). In various sheep breeds, the direct heritability for weight traits tended to increase with ageing and ranged from 0.09 to 0.39 for WW and from 0.14 to 0.55 for PWW (Di et al., 2011; Gowane et al., 2015; Jafaroghli et al., 2010), confirming the results from the present study. Especially from the most complex model STM-6, the maternal heritabilities

for body weight traits were in agreement with estimates reported by several authors (e.g., Abbasi et al., 2012; Di et al., 2011). Even larger maternal heritabilities were estimated by El Fadili et al. (2000) for BW (0.59) in Moroccan Timahdit breeds and by Areb et al. (2021) for BW (0.34) and WW (0.20) in Bonga sheep. In agreement with our findings, several studies (e.g., Areb et al., 2021; El Fadili et al., 2000) estimated negative direct-maternal genetic covariances for body weight traits. The negative covariances implied increased maternal heritabilities as outlined by Areb et al. (2021), in comparison to maternal heritabilities from models ignoring a direct-maternal covariance structure. From a statistical modelling perspective, Solanes et al. (2004) assumed biased genetic evaluations when ignoring maternal genetic effects and maternal-direct genetic covariances. The antagonism between direct and maternal genetic effects for TL and body weight traits might be due to natural selection for an intermediate optimum (Tosh & Kemp, 1994). From an evolutionary point of view, the genetic background of the physiological and uterine capacities of ewes may prevent oversized body proportions of lambs.

The estimate of  $c^2$  for BW (0.07 from both STM-5 and STM-6) was in accordance with ratios for permanent environmental variances in studies by Abbasi et al. (2012) in Baluchi sheep (0.08), by Areb et al. (2021) in Bonga sheep (0.15), by Gowane et al. (2015) in Malpura sheep (0.09) and by Mandal et al. (2015) in Muzaffarnagari sheep (0.09). For the weight traits WW and PWW recorded later in life, the inclusion of the maternal permanent environmental effect in STM-5 and STM-6 did not improve the goodness of fit when compared to AIC and BIC for STM-3 and STM-4. The significant effect of the maternal permanent environment on BW is mainly due to the uterine capacity and nutritional quality, especially during late gestation. The permanent maternal environmental variance consistently decreased with lamb ageing, especially when altering the feeding behaviour from milk to roughage (Mandal et al., 2012; Zishiri et al., 2013).

## 4.2 | Genetic correlations between tail length and body weight traits

Direct genetic and maternal genetic correlations between TL and body weight traits from both modelling approaches MTM and SEM were positive, genetically indicating that heavier lambs have longer tails. However, the direct genetic correlations between TL and weight traits were only low to moderate. Thus, selection on shorter tails will not significantly impair body weight development, especially with regard to only small detrimental effects on WW. Genetic correlations among body weight traits decreased

with increasing age distances, which is in agreement with estimates in other sheep breeds (Abbasi et al., 2012; Areb et al., 2021; Mohammadi et al., 2015). The positive genetic correlations among the weight traits are evidence for common genetic and physiological mechanisms. Hence, selection for increased WW implies associated calving difficulties due to the positive correlation with BW. Weaning weight can be used as an indicator trait for PWW, especially in the context of the quite large maternal genetic correlations (i.e., 0.98 and 0.99 from MTM-6 and SEM-6, respectively).

## 4.3 | Structural equation coefficients

We found negative recursive relationships from TL on WW, and from TL on PWW ( $\lambda_{1 \rightarrow 3}$  and  $\lambda_{1 \rightarrow 4}$ , respectively). Lambs with longer tails are more susceptible to breech and tail strikes, which in turn can impair their body weight development. The long and woolly tails imply an increased risk for contamination with dirt and dust, and in causality, causing infections with fly larvae, the so-called myiasis (Pijpers et al., 2006). Physiologically, the contamination caused by excrement residues provides space for the accumulation of fly larvae in the host's skin and subcutaneous membrane. The fly larvae grow inside the host while feeding on its tissue, causing considerable tissue destruction and potential losses of appetite and associated weight losses (Wall, 2012). The different signs in structural equation coefficients and genetic correlations for the same trait combinations impressively demonstrate the advantage of SEM to infer phenotypic trait causalities from genetic mechanisms. The positive genetic correlations between TL and body weight traits indicate that lambs with longer tails may carry the favourable genes for body weight development and would be heavier later in life when ignoring negative recursive relationships at the phenotypic level. Such recursive effects might be induced by additional external risk factors such as tail infections hampering animal performance.

Interestingly, the pure phenotypic correlations between TL and body weight traits were positive, indicating biased estimates when ignoring recursive relationships and feedback mechanisms among traits as outlined by König et al. (2008) in the case of claw health and milk yield. Thus, the magnitude and sign of selection response in trait A by indirect selection on trait B strongly depend on the level of recursiveness and genetic covariances between both traits. In agreement with our results, Razmkabir et al. (2020) and Jafaroghli et al. (2021) reported positive structural equation coefficients of 1.24 and 1.19 for the recursive effect of BW on WW in Markhoz goats and in Moghani sheep, respectively. In the present study, both the recursive relationship and the genetic covariance between BW and WW were

positive, indicating correlated genetic gain in WW for an early selection strategy on BW. In contrast to our results for the recursive effect of WW on PWW, positive structural equation coefficients of 0.79 were reported by Razmkabir et al. (2020) and of 0.67 by Jafaroghli et al. (2021). A negative recursive effect of WW on PWW indicates that heavy lambs until weaning (due to the favourable milk supply of their mother) may face difficulties when switching the feeding strategy to own roughage intake, especially for sheep kept in harsh grazing systems (Gernand et al., 2008). Vice versa, lambs with low WW may respond with compensatory growth after weaning (Homem et al., 2007), implying a stronger growth rate increase after weaning compared to heavy lambs with high WW. Furthermore, Valente et al. (2013) pointed out that environmental conditions may determine the sign and magnitude of recursive relationships among phenotypes. In merino sheep, for instance, Dakhlan et al. (2018) and Kelman et al. (2022) reported stronger compensatory growth after weaning for multiple-born lambs compared to single-born lambs, especially in the case of nutritional restrictions.

In contrast to MTM, a great advantage of SEM is the ability to discriminate genetic correlations and recursive relationships among traits (e.g., König et al., 2008; Rosa et al., 2011). From a practical breeding perspective, genetic correlations classically determine the success of breeding goal definitions and genetic gain in single traits. However, it should be kept in mind that recursive relationships between traits of interest can affect selection response. For instance, the sign and magnitude of the response to selection for WW depend on two pathways of relationships: one representing an antagonistic path (i.e., a negative recursive relationship and positive genetic covariance between TL and WW), and another pathway including positive recursive and genetic relationships between BW and WW. As mentioned above, a large heritability for TL and small direct and maternal correlations between TL and WW indicate successful genetic selection on short tails without unfavourable effects on WW. Furthermore, the negative recursive effect of TL on WW indicates short tails in the context of improved body weight development. Especially in the ongoing postweaning period, long-tailed lambs have a greater risk to suffer due to the unfavourable side effects of long tails including breech, tail strikes and infections. Thus, ignoring recursive effects can hamper selection efficiency in a long-term perspective.

## 5 | CONCLUSION

Different modelling approaches favoured models considering both direct-genetic and maternal-genetic effects plus respective covariance components for the genetic

evaluation of TL and body weight traits in Merinoland sheep. The direct heritability for TL from the best-fitting STM was  $0.60 \pm 0.08$ , indicating the potential for genetic reduction of tail length within a few generations. For TL, also a small maternal heritability of  $0.03 \pm 0.03$  was estimated, maybe due to intrauterine effects determining the embryonic development. As expected, the maternal heritabilities for body weight traits decreased with ageing. The direct genetic correlations between TL and body weight traits from MTM were positive, indicating unfavourable relationships from a breeding perspective. Genetic correlations between the same traits were very similar when applying SEM. Nevertheless, the structural equation coefficients reflecting trait associations phenotypically were negative (favourable) for the time-lagged effects of TL on WW and on PWW. As an explanation, lambs with long and woolly tails have an increased risk for tail contaminations with dirt and dust causing infections, which in turn impairs the body weight development. The mutual relationships depicted via structural equation coefficients differed in sign and magnitude from the pure phenotypic and genetic correlations. Hence, optimized breeding strategies imply consideration of environmental risk factors, that is, alterations in disease susceptibility when breeding short-tailed Merinoland sheep.

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## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

## ORCID

Sven König  <https://orcid.org/0000-0002-1716-2511>

## REFERENCES

- Abbasi, M. A., Abdollahi-Arpanahi, R., Maghsoudi, A., Torshizi, R. V., & Nejati-Javaremi, A. (2012). Evaluation of models for estimation of genetic parameters and maternal effects for early growth traits of Iranian Baluchi sheep. *Small Ruminant Research*, 104(1–3), 62–69.
- Aikins-Wilson, S., Bohlouli, M., & König, S. (2021). Maternal and direct genetic parameters for tail length, tail lesions, and growth traits in pigs. *Journal of Animal Science*, 99(1), skaa398. <https://doi.org/10.1093/jas/skaa398>
- Areb, E., Getachew, T., Kirmani, M. A., Abate, Z., & Haile, A. (2021). Estimation of (co)variance components, genetic parameters,

- and genetic trends of growth traits in community-based breeding programs of Bonga sheep. *Animal*, 15(5), 100202.
- Dakhlan, A., Moghaddar, N., & van der Werf, J. H. J. (2018). Genotype  $\times$  birth type or rearing-type interactions for growth and ultrasound scanning traits in merino sheep. *Animal Production Science*, 59(6), 1016.
- Di, J., Zhang, Y., Tian, K. C., Lazate, J. F., Liu, X. M., Xu, Y. J. Z., & Zhang, T. H. (2011). Estimation of (co)variance components and genetic parameters for growth and wool traits of Chinese superfine merino sheep with the use of a multi-trait animal model. *Livestock Science*, 138(1–3), 278–288.
- El Fadili, M., Michaux, C., Detilleux, J., & Leroy, P. L. (2000). Genetic parameters for growth traits of the Moroccan Timahdit breed of sheep. *Small Ruminant Research*, 37(3), 203–208.
- European Union. (2008). Richtlinie 2008/120/EG des Rates vom 18. Dezember 2008 über Mindestanforderungen für den Schutz von Schweinen. <https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A32008L0120> Accessed July 14, 2020.
- Fowden, A. L., Ward, J. W., Wooding, F. P. B., Fordhead, A. J., & Christensen, O. F. (2006). Programming placental nutrient transport capacity. *The Journal of Physiology*, 572(1), 5–15.
- French, N. P., Wall, R., & Morgan, K. L. (1994). Lamb tail docking: A controlled field study of the effects of tail amputation on health and productivity. *The Veterinary Record*, 134(18), 463–467.
- Gernand, E., Wassmuth, R., Lenz, H., von Borstel, U. U., Gauly, M., & König, S. (2008). Impact of energy supply of ewes on genetic parameters for fertility and carcass traits in merino long wool sheep. *Small Ruminant Research*, 75, 80–89.
- Gianola, D., & Sorensen, D. (2004). Quantitative genetic models for describing simultaneous and recursive relationships between phenotypes. *Genetics*, 167(3), 1407–1424.
- Gizaw, S., Komen, H., & van Arendonk, J. A. M. (2008). Selection on linear size traits to improve live weight in Menz sheep under nucleus and village breeding programs. *Livestock Science*, 118(1–2), 92–98.
- Gowane, G. R., Prince, L. L. L., Lopes, F. B., Paswan, C., & Sharma, R. C. (2015). Genetic and phenotypic parameter estimates of live weight and daily gain traits in Malpura sheep using Bayesian approach. *Small Ruminant Research*, 128, 10–18.
- Greeff, J. C., Karlsson, L. J. E., & Schlink, A. C. (2015). *Inheritance of tail length in merino sheep* (pp. 237–240). Association for the Advancement of Animal Breeding and Genetics, University of New England.
- Haverkamp, H., Brandt, H., & Erhardt, G. (2015). *Variation in der Schwanzlänge beim Merinolandschaf als Basis für züchterische Aktivitäten*. Vortragstagung der DGfZ/GfT September 16–17.
- Homem, A. R., da Silva Sobrinho, A. G., Yamamoto, S. M., Pinheiro, R. S. B., Buzzulini, C., & Alves de Lima, C. S. (2007). Compensatory body weight gain in growing lambs: Performance and biometrical measurements. *Revista Brasileira de Zootecnia*, 36(1), 111–119.
- Hümmelchen, H., Wagner, H., König, S., & Wehrend, A. (2022). Importance of tail length in sheep and the breeding for short tails. *Tierarztl Prax Grosstiere*, 50(3), 187–194. <https://doi.org/10.1055/a-1851-9402>
- Jafaroghli, M., Rashidi, A., Mokhtari, M. S., & Shadparvar, A. A. (2010). (Co)variance components and genetic parameter estimates for growth traits in Moghani sheep. *Small Ruminant Research*, 91(2–3), 170–177.
- Jafaroghli, M., Soflaee Sharbabak, M., Ghafouri Kesbi, F., & Mokhtari, M. (2021). Estimation of the autosomal and sex-linked genetic parameters for growth rate and efficiency related traits in Moghani sheep. *Journal of Livestock Science and Technologies*, 9(1), 69–75.
- Kariuki, C. M., Ilatsia, E. D., Kosgey, I. S., & Kahi, A. K. (2010). Direct and maternal (co)variance components, genetic parameters and annual trends for growth traits of dorper sheep in semi-arid Kenya. *Tropical Animal Health and Production*, 42(3), 473–481.
- Kelman, K. R., Alston-Knox, C., Pethick, D. W., & Gardner, G. E. (2022). Sire breed, litter size, and environment influence genetic potential for lamb growth when using sire breeding values. *Animals an open access journal from MDPI*, 12(4), 501.
- König, S., Wu, X. L., Gianola, D., Heringstad, B., & Simianer, H. (2008). Exploration of relationships between claw disorders and milk yield in Holstein cows via recursive linear and threshold models. *Journal of Dairy Science*, 91(1), 395–406.
- Lagler, D. K., Hannemann, E., Eck, K., Klawatsch, J., Seichter, D., Russ, I., Mendel, C., Lühken, G., Krebs, S., Blum, H., Upadhyay, M., & Medugorac, I. (2022). Fine-mapping and identification of candidate causal genes for tail length in the Merinolandschaf breed. *bioRxiv Preprint*. <https://doi.org/10.1101/2022.02.27.481613>
- Lourenco, D. A., Misztal, I., Tsuruta, S., Aguilar, I., Lawlor, T. J., Forni, S., & Weller, J. I. (2014). Are evaluations on young genotyped animals benefiting from the past generations? *Journal of Dairy Science*, 97(6), 3930–3942. <https://doi.org/10.3168/jds.2013-7769>
- MacCluer, J. W., Boyce, A. J., Dyke, B., Weitkamp, L. R., Pfennig, D. W., & Parson, C. J. (1983). Inbreeding and pedigree structure in standardbred horses. *Journal of Heredity*, 74, 394–399.
- Mandal, A., Dass, G., & Rout, P. K. (2012). Model comparisons for estimation of genetic parameters of pre-weaning daily weight gains in Muzaffarnagari sheep. *Small Ruminant Research*, 106(2–3), 118–124.
- Mandal, A., Karunakaran, M., Sharma, D. K., Baneh, H., & Rout, P. K. (2015). Variance components and genetic parameters of growth traits and Kleiber ratio in Muzaffarnagari sheep. *Small Ruminant Research*, 132, 79–85.
- Meyer, K. (2007). WOMBAT—A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *Journal of Zhejiang University Science*, 8, 815–821.
- Mohammadi, K., Abdollahi-Arpanahi, R., Amraei, F., Mohamadi, E. M., & Rashidi, A. (2015). Genetic parameter estimates for growth and reproductive traits in Lori sheep. *Small Ruminant Research*, 131, 35–42.
- Pijpers, A., A. Stegemann, H. Hopster. 2006. Het is in de Nederlandse situatie mogelijk om met goed management verantwoord schapen te houden zonder het couperen van staarten. [library.wur.nl/ebooks/minlnv/rapporten/1883153.pdf](http://library.wur.nl/ebooks/minlnv/rapporten/1883153.pdf). Accessed October 12, 2021.
- Posht-e Masari, H. A., Hafezian, S. H., Abdollahi-Arpanahi, R., Mokhtari, M. S., Mianji, G. R., & Yeganeh, A. T. (2019). The comparison of alternative models for genetic evaluation of growth traits in Lori-Bakhtiari sheep: Implications on predictive ability and ranking of animals. *Small Ruminant Research*, 173, 59–64.
- Razmkabir, M., Mokhtari, M., Mahmoudi, P., & Rashidi, A. (2020). The comparison of standard and fully recursive multivariate models for genetic evaluation of growth traits in Markhoz goat: Predictive ability of models and ranking of animals. *The Journal of Agricultural Science*, 158(6), 511–517.

- Rosa, G. J. M., Valente, B. D., de los Campos, G., Wu, X. L., Gianola, D., & Silva, M. A. (2011). Inferring causal phenotype networks using structural equation models. *Genetics Selection Evolution GSE*, 43, 6.
- Samraus, H. H. (2011). Sheep. In *Color atlas of livestock breeds* (7th ed., pp. 160–181). Eugen Ulmer KG.
- Sargolzaei, M., Iwaisaki, H., & Colleau, J. J. (2006). CFC: A tool for monitoring genetic diversity. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Brazil, CD-Rom comm. No. 27-28.
- Schiller, K. F., Grams, V., & Bennewitz, J. (2015). Analysis of growth and feed conversion in purebred and crossbred German Merinolandschaf lambs. *Acronym Animal Breed*, 58(1), 177–183.
- Scobie, D., & O'Connell, D. (2002). Genetic reduction of tail length in New Zealand sheep. *Proceedings of the New Zealand Society of Animal Production*, 62, 195–198.
- Solanes, F. X., Grandinson, K., Rydhmer, L., Stern, S., Andersson, K., & Lundeheim, N. (2004). Direct and maternal influences on the early growth, fattening performance, and carcass traits of pigs. *Livestock Production Science*, 88(3), 199–212. <https://doi.org/10.1016/j.livprodsci.2003.12.002>
- Strittmatter, K. (2005). Development, situation and perspectives of the sheep production in Germany. *Züchtungskunde*, 77, 496–501.
- Sutherland, M. A., & Tucker, C. B. (2011). The long and short of it: A review of tail docking in farm animals. *Applied Animal Behaviour Science*, 135(3), 179–191.
- TierSchG. 2006. §5 Absatz 3 Satz 4, §6: Tierschutzgesetz in der Fassung der Bekanntmachung vom 18. Mai 2006 (BGBl. I S. 1206, 1313), das zuletzt durch Artikel 105 des Gesetzes vom 10. August 2021 (BGBl. I S. 3436) geändert worden ist. Im Internet: <https://www.gesetze-im-internet.de/tierschg/BJNR012770972.html>. Accessed: 02.12.2021
- Tosh, J. J., & Kemp, R. A. (1994). Estimation of variance components for lamb weights in three sheep populations. *Journal of Animal Science*, 72(5), 1184–1190.
- Valente, B. D., Rosa, G. J. M., Gianola, D., Wu, X. L., & Weigel, K. (2013). Is structural equation modeling advantageous for the genetic improvement of multiple traits? *Genetics*, 194(3), 561–572.
- Wall, R. (2012). Ovine cutaneous myiasis: Effects on production and control. *Veterinary Parasitology*, 189(1), 44–51.
- Zishiri, O. T., Cloete, S. W. P., Olivier, J. J., & Dzama, K. (2013). Genetic parameters for growth, reproduction and fitness traits in the south African dorper sheep breed. *Small Ruminant Research*, 112(1–3), 39–48.

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