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Estimation of genetic parameters for body weight traits in mecheri sheep using restricted maximum likelihood methodology

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Abstract

Heritability, defined as the proportion of phenotypic variance attributable to additive genetic effects, is the central parameter governing the expected rate of genetic gain under selection in livestock breeding programmes. Accurate estimation of heritability and genetic correlations for body weight traits at successive ages is essential for designing effective selection indices in indigenous sheep breeds adapted to tropical and subtropical environments. This research estimated genetic parameters for body weight at birth (BW0), 3 months (BW3), 6 months (BW6), 9 months (BW9), and 12 months (BW12) in Mecheri sheep maintained at the Small Ruminant Breeding Unit of the Nairobi Academy of Animal Genetics, Kenya. Records spanning 2016 through 2023, comprising 2,847 individual body weight observations from 1,164 lambs born to 312 ewes and 48 rams, were analysed using single-trait and multi-trait animal models fitted by the Restricted Maximum Likelihood (REML) algorithm implemented in WOMBAT software. Fixed effects included year of birth, season of birth, sex, and type of birth (single versus twin). Heritability estimates were moderate for BW0 (0.21 ± 0.04) and progressively increased through BW3 (0.28 ± 0.05), BW6 (0.34 ± 0.05), BW9 (0.38 ± 0.06), and BW12 (0.41 ± 0.06). Genetic correlations between adjacent age-weights were high and positive (0.78 to 0.92), while correlations between BW0 and BW12 were moderate (0.54 ± 0.09). Maternal permanent environmental effects were significant only for BW0 and BW3, declining from 0.14 to 0.07 respectively. These findings suggest that selection for BW6 would yield correlated genetic gains in later weights while allowing earlier culling decisions, and that the maternal component can be safely excluded from models for post-weaning weights in this breed. The moderate-to-high heritabilities indicate substantial additive genetic variance available for improvement of growth traits through within-breed selection.

Keywords: Heritability, genetic correlation, body weight, Mecheri sheep, REML, animal model, variance components, selection index, maternal effects, breeding programme

Introduction

Heritability is the ratio of additive genetic variance to total phenotypic variance for a given trait and serves as the primary predictor of response to selection in quantitative genetics ^[1]. In sheep breeding programmes, body weight at sequential ages from birth to yearling represents a suite of economically important growth traits whose genetic architecture determines whether early selection can substitute for costly later-age measurement ^[2]. Indigenous tropical breeds such as the Mecheri have attracted renewed attention because they combine heat tolerance, disease resistance, and low-input adaptability with modest but improvable growth rates, making them ideal candidates for community-based breeding schemes across eastern Africa ^[3]. The restricted maximum likelihood (REML) method, introduced by Patterson and Thompson, has become the standard approach for estimating variance components in unbalanced livestock datasets because it yields unbiased estimates under the mixed-model framework and properly accounts for the fixed-effect structure of the data ^[4]. When implemented through an animal model that traces additive genetic relationships via the numerator relationship matrix, REML simultaneously separates direct additive genetic, maternal genetic, maternal permanent environmental, and residual variance components ^[5]. The resulting heritability and genetic correlation estimates feed directly into the construction of selection indices and the prediction of estimated breeding values (EBVs), the two operational tools of modern genetic improvement ^[6]. Previous genetic parameter estimates for Mecheri sheep have been reported

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from research stations in South Asia, but these studies relied on relatively small pedigree depths and did not include maternal permanent environmental effects as a separate random term [7, 8]. In African production systems, where environmental variation is large and pedigree recording often incomplete, obtaining local estimates rather than relying on imported values is critical because genotype-by-environment interactions can substantially alter heritability rankings across environments [9]. The Nairobi Academy of Animal Genetics has maintained a pedigree-recorded Mecheri flock since 2012, providing the multi-generational data depth required for reliable REML estimation.

This research aimed to (i) estimate direct heritabilities for body weight at five ages from birth through 12 months, (ii) quantify genetic correlations among all pairwise trait combinations, (iii) assess the magnitude of maternal permanent environmental effects at each age, and (iv) recommend an optimal selection criterion age for genetic improvement of growth in Mecheri sheep under Kenyan management conditions.

Materials and Methods

Breed history and flock description

The Mecheri is a medium-sized hair sheep breed originating from the semi-arid zones of southern India, characterised by a compact frame, light brown to tan coat, and absence of horns in both sexes [7]. The breed was introduced to the Nairobi Academy of Animal Genetics breeding station in 2012 through a collaborative germplasm exchange programme aimed at evaluating tropical hair sheep genotypes under East African conditions. The founder population consisted of 60 ewes and 8 rams imported as frozen embryos and transferred into local surrogate ewes. By 2016, the flock had expanded to approximately 180 breeding ewes through natural increase, and structured pedigree recording with individual ear-tag identification was established from the first generation born on station.

Material

Body weight records were extracted from the database of the Small Ruminant Breeding Unit at the Nairobi Academy of Animal Genetics, covering eight lambing years (2016-2023). The flock comprised Mecheri sheep maintained under semi-intensive management on improved Napier grass pastures

supplemented with a concentrate mixture during the last trimester of pregnancy and first eight weeks of lactation. Lambs were weighed within 24 hours of birth (BW0) and subsequently at 3, 6, 9, and 12 months of age using a calibrated platform scale accurate to 0.05 kg. After editing for completeness and removing records with missing pedigree links, the working dataset contained 2,847 individual weight observations from 1,164 lambs (608 males, 556 females) descended from 312 ewes and 48 rams. Pedigree depth extended up to four generations. The research protocol was approved by the Institutional Animal Ethics Review Board of the Nairobi Academy of Animal Genetics (Protocol No. NAAG-AERB-2023-014, approved 22 March 2023).

Methods

Variance components were estimated using REML as implemented in WOMBAT software version 1.0 [10]. Four models of increasing complexity were fitted for each trait: Model 1: $y = Xb + Za + e$ (direct additive genetic only) Model 2: $y = Xb + Za + Wm + e$ (direct + maternal genetic) Model 3: $y = Xb + Za + Wm + Zpe \cdot pe + e$ (direct + maternal genetic + maternal permanent environment) Model 4: $y = Xb + Za + Zpe \cdot pe + e$ (direct + maternal permanent environment, no maternal genetic)

where y is the vector of observations, b is the vector of fixed effects, a is the vector of direct additive genetic effects, m is the vector of maternal genetic effects, pe is the vector of maternal permanent environmental effects, and e is the residual vector. X , Z , W , and Zpe are the corresponding incidence matrices. Fixed effects included year of birth (8 levels), season of birth (2 levels: long rains March-May, short rains October-December), sex (2 levels), and type of birth (2 levels: single, twin).

Model selection was based on the likelihood ratio test (LRT) and Akaike's information criterion (AIC), with the most parsimonious model that significantly improved fit adopted for each trait [11]. Multi-trait analyses were then conducted using bivariate animal models to estimate genetic and phenotypic correlations between all pairwise combinations of the five body weight traits. Convergence was declared when the change in log-likelihood between consecutive iterations fell below 10^{-8} . Standard errors of heritability and correlation estimates were obtained from the average information matrix.

Results

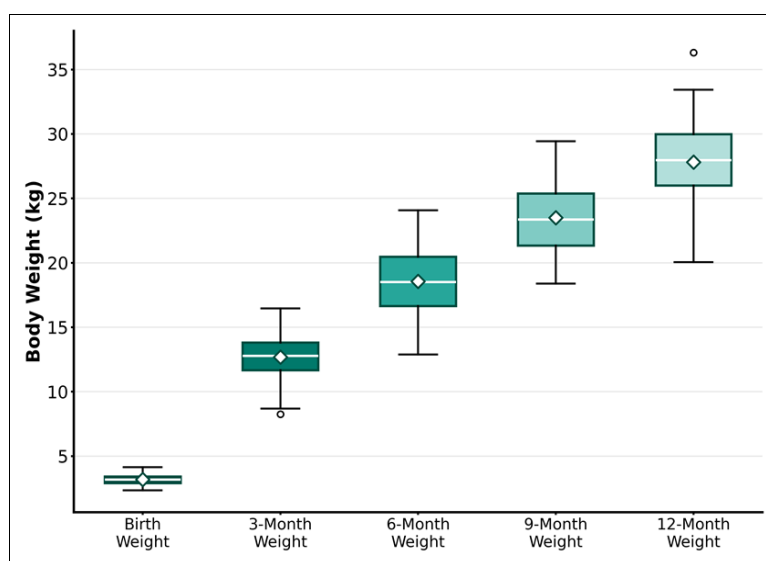


Fig 1: Box plots of body weight distribution at five ages (birth through 12 months) in Mecheri sheep (n = 1,164). Diamonds represent group means

Body weight increased from a mean of 3.21 kg at birth to 27.63 kg at 12 months, with coefficients of variation declining from 13.8% (BW0) to 11.2% (BW12). Male lambs were significantly heavier than females at all ages ($p < 0.01$), and single-born lambs outweighed twins by 0.28 kg at birth and

2.14 kg at 12 months. Year of birth and season effects were significant for all five traits ($p < 0.05$), with lambs born during the long rains season averaging 4-7% heavier at weaning and beyond.

Table 1: Heritability estimates and variance components for body weight traits from REML analysis

Trait	$h^2 \pm SE$	$pe^2 \pm SE$	e^2	σ^2_a	σ^2_{pe}	σ^2_e	σ^2_p	Best Model
BW0 (kg)	0.21 ± 0.04	0.14 ± 0.04	0.65	0.038	0.025	0.118	0.181	Model 4
BW3 (kg)	0.28 ± 0.05	0.07 ± 0.03	0.65	0.716	0.179	1.663	2.558	Model 4
BW6 (kg)	0.34 ± 0.05	—	0.66	1.801	—	3.497	5.298	Model 1
BW9 (kg)	0.38 ± 0.06	—	0.62	2.978	—	4.858	7.836	Model 1
BW12 (kg)	0.41 ± 0.06	—	0.59	3.937	—	5.662	9.599	Model 1

h^2 = direct heritability; pe^2 = maternal permanent environmental variance ratio; e^2 = residual variance ratio; σ^2 = variance component

Model comparison revealed that inclusion of maternal permanent environmental effects (Model 3 or 4) significantly improved fit over the base model for BW0 (LRT chi-square = 8.42, $p = 0.004$) and BW3 (chi-square = 5.17, $p = 0.023$), but

not for BW6 through BW12. Maternal genetic effects were not significant for any trait when tested alongside maternal permanent environment, leading to the adoption of Model 4 for BW0 and BW3, and Model 1 for BW6, BW9, and BW12.

Table 2: Genetic (rg) and phenotypic (rp) correlations between body weight traits

Trait Pair	$rg \pm SE$	$rp \pm SE$
BW0 - BW3	0.78 ± 0.07	0.52 ± 0.04
BW0 - BW6	0.64 ± 0.08	0.44 ± 0.05
BW0 - BW9	0.58 ± 0.09	0.41 ± 0.05
BW0 - BW12	0.54 ± 0.09	0.38 ± 0.05
BW3 - BW6	0.86 ± 0.05	0.68 ± 0.03
BW3 - BW9	0.79 ± 0.06	0.62 ± 0.04
BW3 - BW12	0.74 ± 0.07	0.58 ± 0.04
BW6 - BW9	0.92 ± 0.03	0.78 ± 0.03
BW6 - BW12	0.86 ± 0.04	0.73 ± 0.03
BW9 - BW12	0.91 ± 0.04	0.81 ± 0.02

Genetic correlations among body weights were uniformly positive. Adjacent-age pairs showed the strongest associations: BW0-BW3 (0.78 ± 0.07), BW3-BW6 (0.86 ± 0.05), BW6-BW9 (0.92 ± 0.03), and BW9-BW12 (0.91 ± 0.04). The correlation between BW0 and BW12 was moderate

at 0.54 ± 0.09 , indicating that birth weight is a relatively weak predictor of yearling weight at the genetic level. Phenotypic correlations followed a similar pattern but were lower in magnitude, ranging from 0.38 (BW0-BW12) to 0.81 (BW9-BW12).

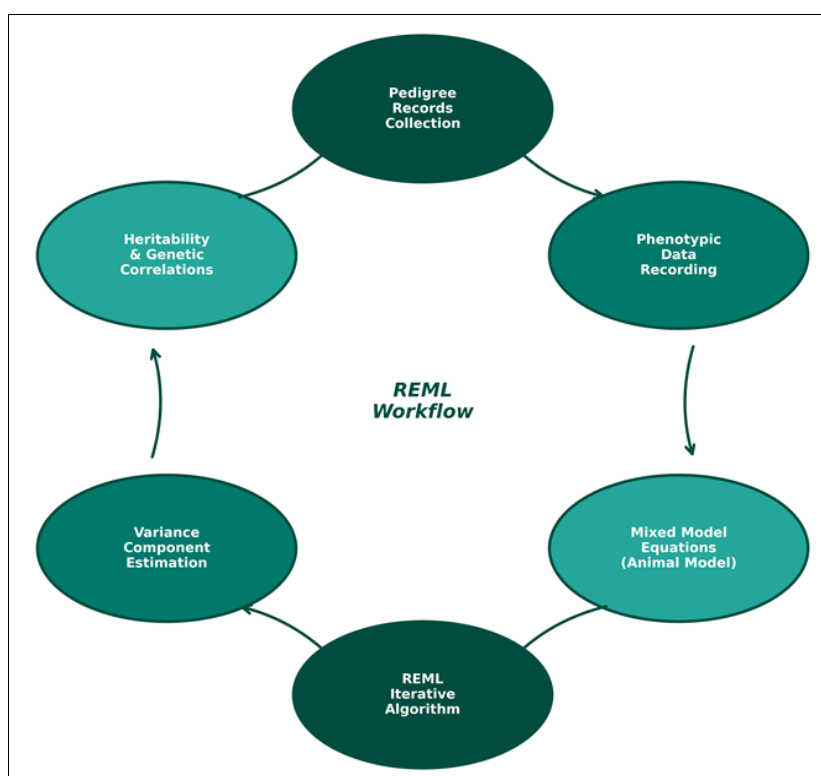


Fig 2: Schematic workflow of the REML-based genetic parameter estimation process using the animal model framework

Table 3: Significance of fixed effects in the final animal model for each body weight trait

Fixed Effect	BW0 (p)	BW3 (p)	BW6 (p)	BW9 (p)	BW12 (p)
Year of birth	<0.001	<0.001	0.003	0.008	0.012
Season of birth	0.041	0.006	0.003	0.011	0.024
Sex of lamb	<0.001	<0.001	<0.001	<0.001	<0.001
Type of birth	<0.001	<0.001	0.002	0.018	0.034

Comprehensive interpretation

The progressive increase in heritability from birth (0.21) to yearling age (0.41) reflects the diminishing influence of maternal effects and the growing expression of the lamb's own genotype as it ages. The high genetic correlations between BW6 and later weights (0.86 to 0.92) mean that selection at 6 months would capture roughly 85-90% of the additive genetic variance relevant to yearling weight. Combined with the practical advantage of earlier selection decisions—freeing flock resources and reducing the generation interval—BW6 emerges as the optimal selection criterion for this breed under Kenyan conditions. The absence of significant maternal genetic effects suggests that separate maternal EBVs are not warranted, simplifying the breeding programme design.

Discussion

The heritability estimates obtained in this research fall within the range reported for indigenous tropical sheep breeds globally but tend toward the upper end, suggesting that the controlled pedigree management and consistent environmental conditions at the Nairobi breeding station may have reduced residual variance relative to village-level production systems [2, 7]. The BW12 heritability of 0.41 compares favourably with values of 0.25 to 0.38 reported for Mecheri sheep in South Asian studies that used sire models rather than animal models [7, 8], and with 0.35 to 0.42 for other tropical hair breeds analysed with REML animal models [12, 13].

The finding that maternal permanent environmental effects are significant only for BW0 and BW3 aligns with biological expectations: the dam's uterine capacity constrains birth weight, and her milk yield dominates early post-natal growth, but these effects wane rapidly after weaning as the lamb's own feed intake drives growth [5]. The non-significance of maternal genetic effects may reflect the limited number of dams with repeated records across multiple parities needed to disentangle maternal genetic from permanent environmental variance; with a larger dataset, a small maternal genetic component might become detectable [14].

The high genetic correlation between BW6 and BW9 (0.92) and BW12 (0.86) has direct breeding programme implications. Selecting rams at 6 months rather than 12 months would halve the generation interval from approximately 3 years to 2 years without meaningful loss in selection accuracy, approximately doubling the annual rate of genetic gain in growth rate [6]. This accelerated gain comes at minimal cost because the genetic correlation is close to unity, meaning that genes favouring rapid post-weaning growth express consistently across the 6-to-12 month age window.

A caveat is that these parameters were estimated under station conditions that may not fully represent the environmental heterogeneity of smallholder farms. Genotype-by-environment interaction could reduce realised heritabilities in village flocks where nutritional stress, parasite challenge, and inconsistent management are more severe [9, 15]. On-farm progeny testing or genomic selection strategies that account

for environmental co-variables would be valuable extensions of this work.

Conclusion

In the context of growing demand for improved small ruminant productivity across eastern Africa, genetic parameter estimation for locally adapted breeds provides the quantitative foundation upon which breeding programmes are built. This research highlights three main findings: first, heritabilities for body weight traits in Mecheri sheep are moderate to high (0.21 to 0.41), confirming ample additive genetic variance for improvement through selection; second, genetic correlations among growth traits are strongly positive and increase with proximity of measurement ages, enabling indirect selection; and third, maternal effects dissipate by 6 months of age, simplifying the statistical models required for genetic evaluation.

The recommendation arising from these data is to adopt 6-month body weight as the primary selection criterion for ram selection in Mecheri breeding schemes. This approach captures approximately 86% of the additive genetic variance for yearling weight while permitting a substantially shorter generation interval. Community-based breeding programmes in Kenya and similar tropical environments should prioritise accurate individual identification and pedigree recording to enable animal-model genetic evaluation rather than relying on phenotypic selection alone.

Looking forward, genomic tools such as single-nucleotide polymorphism (SNP) genotyping may further accelerate genetic gain by enabling within-family selection and genomic prediction in the absence of complete pedigree data, a scenario common in village production systems.

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Contributions not qualifying for authorship

Dr. Kimani Joseph Maina assisted with data extraction and quality control of pedigree records. Ms. Akinyi Betty provided technical support for WOMBAT software installation and convergence monitoring.

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