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Genetic parameters and age-dependent genetic variation of growth and body conformation traits in Xinjiang Huaxi cattle

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Abstract

Background

Growth performance and body conformation traits are important selection objectives in beef cattle breeding. However, genetic parameters describing developmental patterns remain limited in newly established breeds such as Huaxi cattle.

Results

The estimated genetic variation differed among body conformation traits. Skeletal traits showed relatively high heritability, including body height (0.58), hip height (0.50), and cannon circumference (0.47), whereas body weight and body length showed lower estimates (0.18 and 0.17, respectively). The lower heritability of body weight was mainly associated with larger residual variation. In the longitudinal analysis, body weight heritability changed with age and reached the highest value at 12 months (0.46). Genetic correlations among body weights from 3 to 24 months were consistently high (>0.98), whereas birth weight showed weak genetic relationships with later growth stages. Maternal effects were additionally evaluated for birth and three-month weights, and maternal permanent environmental effects were identified as an important source of variation for three-month body weight.

Conclusions

This study characterizes genetic variation in body conformation and longitudinal growth patterns in Huaxi cattle. Post-weaning body weights showed strong genetic relationships across ages, whereas birth weight represented a relatively distinct genetic stage. These results characterize the genetic variation underlying body conformation and longitudinal growth in Xinjiang Huaxi cattle and provide reference information for genetic evaluation of this population.

Keywords: Huaxi cattle; genetic parameters; body conformation; body weight; random regression; heritability

Background

Genetic improvement through selective breeding relies on accurate estimates of genetic parameters to support effective selection decisions[(1)]. However, for recently established breeds, systematic evaluations of genetic variation underlying economically important traits are often limited. Huaxi cattle, a newly recognized specialized beef breed in China, represent such a population. Although previous genomic studies have characterized its genetic background [(2)], comprehensive estimates of genetic parameters for body conformation and longitudinal growth remain insufficient. Existing studies have focused on body weight at discrete ages, leaving two questions unanswered: how body dimensions covary genetically, and how the genetic control of growth unfolds continuously from birth to maturity. These parameters are essential for establishing quantitative strategies for genetic evaluation and selection.

Restricted maximum likelihood (REML) and Bayesian approaches are widely used for estimating genetic parameters in livestock. REML provides reliable estimates of variance components in animal models, whereas Bayesian methods are particularly useful for complex longitudinal analyses involving multiple random effects and covariance structures [(3)]. Random regression models are useful for analysing repeated measurements and longitudinal phenotypes in animal breeding. Body conformation traits in beef cattle generally carry moderate to high heritability. A factor analysis of 20 body measurements in Simmental cattle identified a common skeletal genetic factor with moderate heritability, suggesting that height and girth measures share substantial additive genetic control [(4)]. In Polish Simmental populations, chest girth heritability ranged from 0.27 to 0.69,

confirming that even within a breed, parameter estimates can vary widely depending on population structure and measurement protocol [5]. Work on Nellore cattle found that visual scores for conformation and muscularity have heritabilities of 0.15–0.28 and growth trait heritabilities of 0.13–0.44, with frame size genetically correlated with yearling weight at 0.82 [6, 7]. These studies demonstrate that body type carries ample additive genetic variation for selection, though the exact figures depend on breed, age, and environment.

For repeated body weight records collected throughout development, random regression models (RRM) provide a flexible framework for describing age-dependent changes in genetic variation. Unlike conventional multi-trait models that analyze each age as an independent trait, RRM model genetic effects as continuous functions of age using orthogonal polynomials, with Legendre polynomials being widely applied in livestock growth studies. Previous studies have demonstrated the applicability of random regression approaches for modeling growth-related traits in beef cattle. These studies showed that genetic parameters may vary with age and that appropriate modeling of longitudinal records can improve the characterization of growth trajectories [8]. In Pirenaica beef cattle, random regression models have also been used to characterize maternal genetic effects across dam ages, highlighting the importance of accounting for age-dependent genetic variation [9]. A review of maternal effect estimation in beef cattle cautioned that the apparent antagonism between direct and maternal genetic effects can partly reflect data structure rather than biology, and recommended that at least 35% of dams carry their own phenotypic records for reliable estimation [10]. On the polynomial-order question, eigenvalues of the coefficient covariance matrix provide a simple diagnostic: a near-zero eigenvalue signals that the corresponding term captures negligible genetic signal and can be dropped with minimal loss of genetic information.

Several recent studies have focused on genetic improvement and genomic evaluation in Huaxi cattle and related beef cattle populations. Ahmad et al. developed a selection index integrating production traits in Huaxi cattle, providing initial information for breeding strategy optimization [11]. Random regression approaches have been used in beef cattle to characterize longitudinal growth patterns and to model body weight as a continuous trajectory rather than as independent age-specific traits [12]. In addition, genomic mating strategies

and genomic prediction methods have been explored in Huaxi cattle and multi-breed cattle populations, providing opportunities for improving selection efficiency [13]. Ma et al. compared BayesR and GBLUP models in a multi-breed population including Huaxi cattle and reported improved prediction accuracy for growth and carcass traits using Bayesian approaches [14]. However, systematic evaluations of genetic parameters for body conformation traits and longitudinal growth patterns remain limited in Huaxi cattle. In particular, how genetic control of body weight changes throughout development and how different growth stages are genetically related have not been fully characterized in this breed. Therefore, this study aimed to characterize genetic variation in body conformation traits and longitudinal growth patterns in a Huaxi cattle nucleus herd. Late-growth body conformation traits were evaluated using animal models, whereas longitudinal body weight records from birth to 24 months were analyzed using a random regression model to estimate age-dependent changes in genetic variation and relationships among growth stages.

Materials and Methods

Animal Data and Quality Control

Data were collected from the Huaxi cattle nucleus herd at a large-scale breeding farm in Xinjiang, China, from 2016 to 2024. The farm is a nationally accredited Huaxi cattle core breeding facility with over 2000 breeding cows under year-round calving. Animals were housed in confinement with seasonal grazing, and feed rations were adjusted by growth stage with water and mineral blocks available ad libitum. Two overlapping datasets were extracted from this herd. Part 1 consisted of late-growth body conformation records, including 885 quality-controlled records from 613 animals measured between 18 and 30 months of age. Part 2 consisted of longitudinal body weight records, including 4,641 quality-controlled records from 865 animals collected at scheduled ages of birth, 3, 6, 12, 18, and 24 months. The Part 2 records spanned 0.03 to 29.95 months, because 23 measurements fell more than half a month after the scheduled 24-month age and were retained. Seven conformation traits were measured: Body weight, Body height, Body length, Hip height, Cannon circumference, Chest girth, and Abdominal girth, abbreviated as BW, BH, BL, HH, CC, CG, and AG

respectively. BW was recorded with a calibrated electronic platform scale to 0.5 kg precision; linear traits were measured with a measuring stick and flexible tape to 0.1 cm precision. All measurements were taken by uniformly trained technicians with instruments calibrated before each session, and actual measurement age spanned 18 to 30 months (mean 22.1, SD 2.8 months) owing to herd management logistics. Descriptive statistics are presented in Table 1. Coefficients of variation ranged from 5.3% for CC to 12.4% for BW, and AG showed higher variability than CG. Quality control removed records outside biological limits for late-growth cattle within the 18–30-month measurement window (Table 1). After additionally removing statistical outliers ($|z| > 4.0$), the final Part 1 dataset contained 885 records from 613 animals. For animals with more than one measurement within the 18–30-month window, all available QC-passed records were retained to maximize the use of available information. The animal additive genetic effect was modeled using the numerator relationship matrix. A separate permanent environmental effect was not fitted for Part 1 because the average number of records per animal was limited (1.44 records per animal), preventing reliable estimation of a repeatability model. Therefore, a parsimonious animal model was applied to estimate genetic parameters for late-growth conformation traits. Potential non-genetic covariance among repeated records should be considered when interpreting the variance component estimates.

Table 1 Descriptive statistics of body conformation traits.

Trait	Abbr	Unit	N	Mean	SD	Min	Max	CV (%)
Body height	BH	cm	885	137.9	7.6	117.0	167.0	5.5
Hip height	HH	cm	885	144.2	7.8	122.0	170.0	5.4
Cannon circumference	CC	cm	884	20.9	1.1	17.0	25.0	5.3
Chest girth	CG	cm	885	197.1	12.8	153.0	240.0	6.5
Abdominal girth	AG	cm	879	228.7	15.8	175.0	260.0	6.9
Body weight	BW	kg	885	540.7	66.9	378.0	788.0	12.4
Body length	BL	cm	885	168.8	10.8	125.0	215.0	6.4

Note: CV = SD / Mean × 100%. Descriptive statistics are record-level summaries based on available QC-passed records for each trait. For animals with more than one measurement within the 18–30-month window, all available records were retained in the main

analysis. Additive genetic relationships among animals were modeled through the numerator relationship matrix. Because a separate permanent environmental effect was not fitted for Part 1, the estimates should be interpreted as record-level genetic parameter estimates for late-growth conformation traits.

The raw Part 2 dataset contained 4773 records from 871 animals. Over 90% of records fell within ±0.5 months of the scheduled ages. Age in months was computed as days of age divided by 30.44. Table 2 summarizes BW by scheduled age. Mean weight increased from 41.2 kg at birth to 568.5 kg at 24 months; the coefficient of variation declined from 18.7% at birth to 7.3% at 24 months.

Table 2 Descriptive statistics of BW by scheduled measurement age.

Age (month)	N	Mean (kg)	SD (kg)	Min (kg)	Max (kg)	CV (%)
0	839	41.2	7.7	22	58	18.7
3	850	118.6	21.5	62	178	18.1
6	898	227.3	35.8	118	318	15.7
12	814	368.4	42.1	210	498	11.4
18	658	476.2	52.6	265	628	11.0
24	574	568.5	41.3	435	698	7.3

Note: Age in months = days of age / 30.44. Birth group includes records within 0–1 month of age. N represents records within ±1.5 months of the scheduled age; owing to boundary placement, the sum across ages may differ slightly from the total post-QC count (4,641).

The pedigree was exported from the farm's breeding information system and verified for completeness prior to all analyses. It comprised 2676 individuals spanning four generations, including 870 founders with unknown parents, 79 sires, and 1500 dams. A one-to-one mapping linked original ear-tag identifiers to integer codes. For Part 2, a pruned pedigree of 1649 individuals was constructed by tracing all known ancestors of the 865 phenotyped animals. Quality control was carried out in three steps, as summarized in Table 3. The first step checked for missing entries in key fields, specifically animal ID, age, and BW; no such records were found. The second step applied age-stratified biological outlier screening. The predefined acceptable ranges for each age group were 15-70 kg at birth, 60-180 kg at 3 months, 100-300 kg at 6 months, 150-500 kg at 12 months, 200-650 kg at 18 months, and 250-920 kg at 24 months. In total, 120 records falling outside these bounds were removed. The third step excluded animals with fewer than three records, because reliable

estimation of individual growth trajectories requires at least three time points. This step removed 6 animals and 12 records. After quality control, the final dataset contained 4641 records from 865 animals.

Table 3 Data quality control pipeline.

QC step	Rec. removed	Remaining rec	Remaining animals
Raw data	—	4773	871
Remove missing key fields	0	4773	871
Remove biological outliers	120	4653	871
Remove animals with < 3 records	12	4641	865
Final analytical dataset	—	4641	865

Statistical Models

Fixed effects were selected based on preliminary Wald and likelihood-ratio tests together with their biological relevance to growth and body conformation traits. The final models included birth year, birth season, production type, pen, and parity or reproductive status as fixed effects. Parity information was available in both datasets. In Part 1, parity was included as a binary factor (nulliparous vs. parous females), with deviation from mean measurement age fitted as a linear covariate. In Part 2, parity was also coded as a binary variable; however, variation occurred only at 24 months because records from birth to 18 months were from nulliparous animals. Therefore, parity in Part 2 should be interpreted as a reproductive-status adjustment at the late growth stage rather than a general parity effect across the trajectory. Sex was not included because the analyzed records with parity information were obtained from female breeding animals, and no castrated males or steers were available for evaluation. Fixed-effect collinearity was examined during model fitting. Pen and production type showed near collinearity because most pens contained animals from a single production type. Rank-deficient columns were automatically removed during model fitting and did not affect the estimation of variance components. Each conformation trait was first analyzed under a univariate animal model. For BW, model sensitivity was assessed by excluding the pen effect.

$$y=Xb+Za+e$$

where y is the vector of phenotypic observations; b contains the fixed effects described above; a ~ N(0, $A\sigma^2_a$) is the vector of additive genetic effects, with A the numerator relationship matrix; e ~ N(0, $I\sigma^2_e$) is the residual vector; and X and Z are the corresponding incidence matrices. Standard errors of variance components were obtained from the inverse average information matrix generated during the AI-REML procedure. Standard errors of heritability estimates and genetic correlations were calculated using the delta method based on the full variance–covariance matrix of the estimated components. Genetic correlation confidence intervals were obtained using Fisher z transformation and back-transformation to maintain the range of (-1, 1). Maternal effects on birth weight and 3-month weight were evaluated by extending the single-trait model with maternal genetic and/or maternal permanent environmental effects. The maternal genetic effect was fitted as an additional random effect using the numerator relationship matrix of the dam. Genetic correlations among body conformation traits were estimated using bivariate animal models for all 21 trait combinations. The additive covariance structure was specified as $G_0 \otimes A$, where G_0 represents the genetic variance-covariance matrix and A represents the pedigree relationship matrix. Genetic correlations were derived from the estimated additive covariance and variance components, with standard errors calculated using the delta method based on the full variance-covariance matrix of the estimated components. The longitudinal BW trajectory was analyzed using a Bayesian random regression model with Legendre orthogonal polynomials. The fixed regression included five Legendre coefficients to describe the population mean growth curve, whereas the random regression included three coefficients ($\varphi_0(t)$, $\varphi_1(t)$, and $\varphi_2(t)$) to model individual deviations from the population mean trajectory. The observation for animal i at measurement j was modeled as:

$$y_{ij}=x'_{ij}\beta+\sum_{k=0}^{4}\phi_k(t_{ij})\gamma_k+\sum_{k=0}^{2}\phi_k(t_{ij})\alpha_{ik}+e_{ij}$$

where $x'_{ij}\beta$ represents fixed effects (birth year, birth season, production type, pen, and parity); $\varphi k(tij)$ is the k-th Legendre polynomial; γ_k are fixed regression coefficients; α_{ik} are random regression coefficients for animal i. The vector of animal-specific random regression coefficients was assumed to follow $\alpha \sim N(0, K_a \otimes A)$, where K_a represents the additive genetic covariance matrix of random regression coefficients and A

represents the numerator relationship matrix. Genetic parameters were derived from K_a. Residual variance was modeled as heterogeneous across six age classes, with breakpoints at 1, 2, 4.5, 7.5, 15, 21, and 31 months. These non-integer breakpoints ensured that the six key evaluation ages (0, 3, 6, 12, 18, and 24 months) were located within residual variance classes rather than at class boundaries. The six classes contained approximately 839, 833, 850, 825, 695, and 599 records, respectively. A permanent environmental effect was not included in the final random regression model because the available data structure did not support reliable simultaneous estimation of additive genetic, permanent environmental, maternal genetic, and maternal permanent environmental random regression effects. Therefore, a parsimonious additive genetic random regression model was adopted. Maternal genetic and maternal permanent environmental effects were not included in the trajectory model. The potential influence of these omitted effects on age-specific genetic parameter estimates, particularly at early ages, is considered in the Discussion.

Variance Component Estimation and Genetic Parameters

Convergence was declared when the relative change in variance components was below 10^{-7} and the norm of the AI-REML gradient was below 10^{-6} within 10 iterations. Sensitivity of the BW heritability estimate was assessed by refitting the model without the pen effect. For Part 2, the random regression model was fitted using the MCMCglmm package (Hadfield, 2010) in R. Weakly informative inverse-Wishart priors were assigned for the additive genetic covariance matrix (K_a) and residual covariance matrix (R): $K_a \sim IW(V = diag(3)\times100, \nu = 3)$ and $R \sim IW(V = diag(6)\times100, \nu = 6)$. The MCMC chain was run for 500,000 iterations, with the first 100,000 iterations discarded as burn-in and a thinning interval of 400, resulting in 1,000 posterior samples. Convergence was assessed using trace plots and effective sample size (ESS), with ESS values >300 considered adequate for all parameters. Model comparison was performed using the Deviance Information Criterion (DIC; Spiegelhalter et al., 2002). Eigen-decomposition of K_a from the K = 3 model revealed a near-zero third eigenvalue, representing only 0.0023% of total variance, indicating that the quadratic term carried limited independent genetic signal. To formally assess whether this term improved model fit, a reduced K = 2

model was also fitted, with the prior adjusted to $K_a \sim IW(V = diag(2)\times 1000, \nu = 2)$ and identical MCMC settings.For each MCMC posterior sample, age-specific heritability was calculated as:

$$h^{2(s)}(t)=\frac{\phi'(t)K_a^{(s)}\phi(t)}{\phi'(t)K_a^{(s)}\phi(t)+\sigma_{e,r}^{2(s)}}$$

where $K_a^{(s)}$is the additive genetic covariance matrix of the random regression coefficients in posterior sample s, and $(\sigma_{e,r}^2)^{(s)}$ is the residual variance for the age class r containing age t in the same posterior sample. For each MCMC posterior sample, the additive genetic variance at age t was calculated as $V_a(t) = \phi'(t)K_a\phi(t)$, where $\phi(t) = [\phi_0(t), \phi_1(t), \phi_2(t)]'$ is the vector of Legendre basis function values at age t and K_a is the additive genetic covariance matrix of the random regression coefficients. The corresponding phenotypic variance was calculated as $V_p(t) = V_a(t) + V_e(t)$, where $V_e(t)$ denotes the residual variance for the age class containing age t. Age-specific heritability was calculated as $h^2(t) = V_a(t)/V_p(t)$ for each posterior sample and summarized as the posterior mean and 95% HPD credible interval. Genetic correlations between ages ti and tj were calculated for each posterior sample as $r_g(ti, tj) = Cov_a(ti, tj) / [V_a(ti)\times V_a(tj)]^{\wedge}1/2$, where $Cov_a(ti, tj) = \phi'(ti)Ka\phi(tj)$. Posterior means, posterior standard deviations, and 95% equal-tail credible intervals for age-specific genetic correlations were calculated from 1,000 posterior samples. Data processing and visualization were performed in R 4.5.2 (R Core Team, 2025). For Part 1, pedigree processing and variance component estimation were conducted using the sommer package v4.3 (Covarrubias-Pazaran, 2016), with the pedigree relationship matrix constructed using AGHmatrix (Amadeu et al., 2023). AI-REML models were fitted using the Newton-Raphson implementation in sommer. For Part 2, Bayesian random regression analyses were performed using MCMCglmm v2.36 (Hadfield, 2010). Figures were generated using ggplot2 v3.5 (Wickham, 2016) and corrplot v0.94 (Wei & Simko, 2021).

Results

Genetic Parameters for Body Conformation Traits

Univariate AI-REML analyses of 885 late-growth conformation records from 613 animals estimated additive genetic and residual variance components for seven traits. Because some animals contributed multiple records within the measurement window, the estimates represent record-level genetic parameters under the

fitted animal model. Heritability estimates differed among the seven traits (Table 4 and Figure 1). Skeletal traits showed relatively higher estimates, with BH, HH, and CC showing heritabilities of 0.58, 0.50, and 0.47, respectively. CG showed an intermediate estimate (0.42), whereas AG, BW, and BL had lower estimates ranging from 0.17 to 0.27. Standard errors ranged from 0.040 to 0.046, and all 95% confidence intervals excluded zero. Variance component estimates showed differences in the contribution of additive genetic and residual variance among traits. BW showed the largest additive genetic variance among the seven traits (Va = 140.7 kg²), but also had a relatively large residual variance (Ve = 649.4 kg²). AG showed a similar pattern, with residual variance exceeding additive genetic variance. In contrast, BH and CC showed relatively balanced additive genetic and residual variance components.

Table 4. Genetic parameters of body conformation traits.

Trait	V_a	V_e	V_p	$h^2 \pm SE$	95% CI
BH	11.21 ± 1.00	8.21 ± 0.92	19.42	0.58 ± 0.040	[0.50, 0.66]
HH	9.87 ± 0.97	10.04 ± 1.11	19.91	0.50 ± 0.044	[0.41, 0.58]
CC	0.20 ± 0.02	0.22 ± 0.03	0.42	0.47 ± 0.044	[0.38, 0.56]
CG	27.59 ± 3.07	38.87 ± 4.27	66.46	0.42 ± 0.046	[0.33, 0.50]
AG	23.60 ± 3.65	63.07 ± 6.81	86.67	0.27 ± 0.046	[0.18, 0.36]
BW	140.70± 30.49	649.41± 67.58	790.11	0.18 ± 0.043	[0.09, 0.26]
BL	11.46 ± 2.61	56.91 ± 5.90	68.37	0.17 ± 0.043	[0.08, 0.25]

Note: V_a : additive genetic variance; V_e : residual variance; V_p : phenotypic variance = V_a + V_e. Estimates from 613 animals with 885 records. Fixed effects: birth year, birth season, pen, production type, parity, and age deviation (linear covariate). AI-REML convergence achieved within 10 iterations for all seven traits

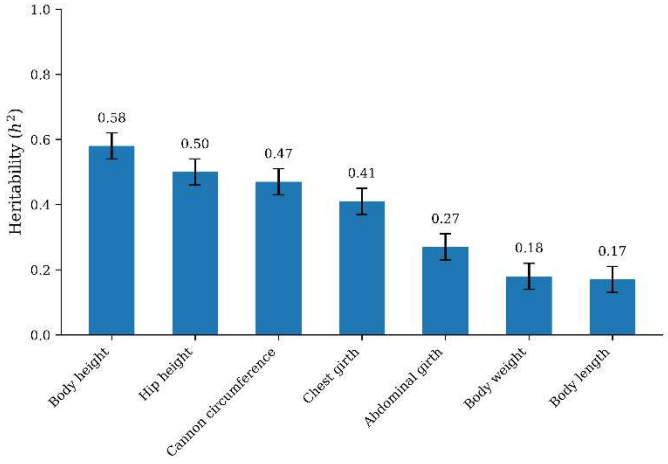


Figure 1. Heritability estimates ($h^2 \pm SE$) for seven body conformation traits in Huaxi cattle.

To quantify genetic relationships among body dimensions, all 21 bivariate animal models were fitted. The genetic correlation matrix is shown in Figure 2A, and standard errors and 95% confidence intervals for all pairs are provided in Table 5. Estimates ranged from $r_g = 0.12$ between BH and BW to $r_g = 0.75$ between CG and AG, with a mean absolute value of 0.29. The strongest association was observed between CG and AG ($r_g = 0.75$), followed by correlations among skeletal traits, including BH with HH ($r_g = 0.62$) and CG with BH ($r_g = 0.54$). In contrast, BW showed relatively weak correlations with most conformation traits, except for BL ($r_g = 0.64$). Genetic and phenotypic correlation matrices are shown in Figure 2A and Figure 2B, respectively. Phenotypic correlations were generally lower than the corresponding genetic correlations. The mean phenotypic correlation across all 21 pairs was 0.20, compared with 0.29 for genetic correlations. HH with BH showed the strongest phenotypic association ($r_p = 0.59$), followed by CG with AG ($r_p = 0.49$), while no other phenotypic correlation exceeded 0.40. Multi-trait genetic evaluation, which exploits the full additive covariance structure, can capture favourable genetic associations that are invisible in the raw phenotypic correlation matrix. Whether the relationship between BW and skeletal conformation observed at late growth is maintained throughout development is further evaluated using the longitudinal BW analysis.

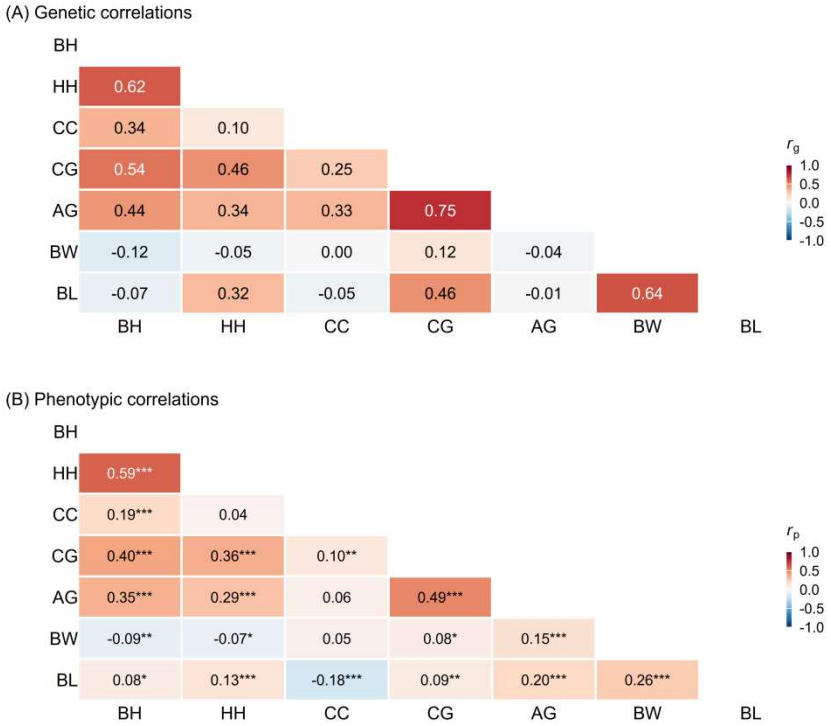


Figure 2. Genetic and phenotypic correlation matrices among body conformation traits in Xinjiang Huaxi cattle. (A) Genetic correlations estimated from bivariate animal models. Numbers indicate genetic correlation

coefficients (r_g); standard errors and 95% confidence intervals for all 21 pairs are given in Table 5 and Supplementary Table S1. (B) Phenotypic correlations derived from the same bivariate models; standard errors and 95% confidence intervals for all 21 pairs are given in Table 5 (upper triangle) and Supplementary Table S2.

Table 5. Genetic and phenotypic correlations among body conformation traits

Trait	BH	HH	CC	CG	AG	BW	BL
BH	1.00	0.59 (0.027)	0.19 (0.040)	0.40 (0.035)	0.35 (0.037)	-0.09 (0.041)	0.08 (0.041)
HH	0.62 (0.041)	1.00	0.04 (0.041) †	0.36 (0.036)	0.29 (0.039)	-0.07 (0.042) †	0.13 (0.042)
CC	0.34 (0.062)	0.10 (0.071) †	1.00	0.10 (0.042)	0.06 (0.043) †	0.05 (0.043) †	-0.18 (0.042)
CG	0.54 (0.054)	0.46 (0.061)	0.25 (0.073)	1.00	0.49 (0.035)	0.08 (0.044) †	0.09 (0.044)
AG	0.44 (0.070)	0.34 (0.078)	0.33 (0.085)	0.75 (0.058)	1.00	0.15 (0.045)	0.20 (0.044)
BW	-0.12 (0.094) †	-0.05 (0.101) †	0.00 (0.102) †	0.12 (0.108) †	-0.04 (0.131) †	1.00	0.26 (0.045)
BL	-0.07 (0.097) †	0.32 (0.101)	-0.05 (0.105) †	0.46 (0.114)	-0.01 (0.129) †	0.64 (0.131)	1.00

Note: The lower triangle gives genetic correlations (r_g) and the upper triangle gives phenotypic correlations (r_p) derived from the same bivariate models, with standard errors in parentheses. Trait order follows Figure 2A. BH, body height; HH, hip height; CC, cannon circumference; CG, chest girth; AG, abdominal girth; BW, body weight; BL, body length. † 95% confidence interval includes zero. Standard errors were obtained by the delta method from the inverse average information matrix, and confidence intervals by Fisher z transformation.

Longitudinal Genetic Analysis of BW

Whereas Part 1 evaluated body weight as a single-time-point trait, Part 2 examined age-dependent genetic variation in body weight from birth to 24 months. The Bayesian random regression model with Legendre polynomials (K = 3) was fitted to 4,641 longitudinal BW records from 865 animals. The population mean body weight trajectory showed a sigmoidal growth pattern, as illustrated in Figure 3. The mean body weight increased from 41.2 kg at birth to 368.4 kg at 12 months and 568.5 kg at 24 months, with the maximum growth rate occurring between 3 and 6 months. Individual trajectories showed increasing dispersion with age, indicating increased variability in observed body weight during growth.

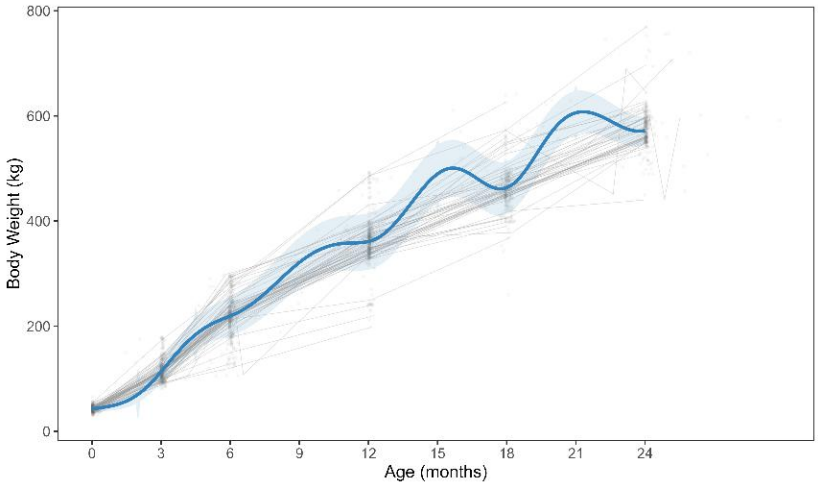


Figure 3. Observed body weight trajectories and population growth curve in Huaxi cattle. Grey lines represent individual observed body weight trajectories, the blue line represents the population mean trajectory, and the shaded region represents phenotypic variation defined as ±1 SD around the mean body weight at each age.

Age-dependent heritability of BW followed a rise-and-fall trajectory from birth to 24 months (Table 6; Figure 4). Heritability was 0.28 at birth, increased slightly to 0.31 at 3 months, remained stable at 0.28 at 6 months, and reached a local maximum of 0.46 at 12 months, coinciding with the peak of additive genetic variance in absolute terms. The highest heritability value in the continuous trajectory was 0.72 at 2 months, which was associated with low residual variance at that age rather than increased additive genetic variance. The abrupt changes at 2, 4.5, 15, and 21 months coincided with residual variance class boundaries, whereas the additive genetic component showed a smoother pattern across age. Heritability declined after 12 months, reaching 0.33 at 18 months and 0.08 at 24 months. The estimate at 24 months showed greater uncertainty due to reduced data density near the upper age boundary.

Table 6. Age-specific genetic parameters of body weight

Age (mo)	V_a (kg^2)	V_e (kg^2)	V_p (kg^2)	h^2	95% HPD CI
0	9.6	24.4	34.0	0.28	[0.21, 0.37]
3	120.7	265.7	386.4	0.31	[0.26, 0.36]
6	357.9	909.5	1267.4	0.28	[0.24, 0.33]
12	749.6	892.6	1643.0	0.46	[0.40, 0.51]
18	661.4	1338.5	2000.0	0.33	[0.28, 0.39]
24	198.3	2150.3	2349.0	0.08	[0.05, 0.15]

Note: Posterior means from 1000 MCMC samples (500000 iterations; 100000 burn-in; thinning = 400). HPD CI: highest posterior density credible interval. Heterogeneous residual variance modeled across six age classes (breakpoints at 1, 2, 4.5, 7.5, 15, 21, and 31 months).

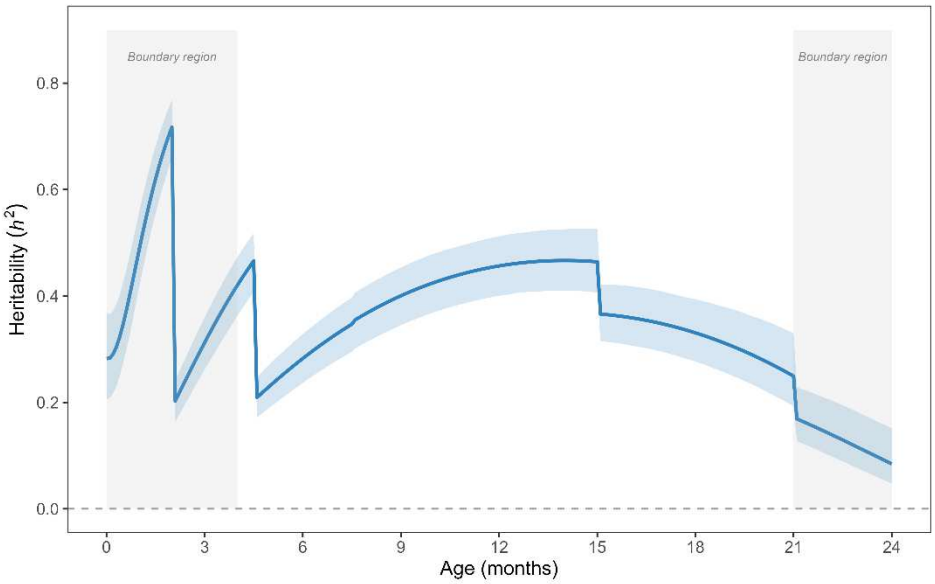


Figure 4. Age-specific heritability trajectory of body weight in Huaxi cattle. The shaded band represents the 95% HPD credible interval; grey regions indicate boundary regions where estimates may be affected by polynomial extrapolation behaviour.

The six-class heterogeneous residual variance structure revealed age-dependent changes in environmental variance. Residual class posterior means increased from 24.4 kg² at birth to 2,150.3 kg² at 24 months (Table 6), while the residual coefficient of variation remained stable at 9–14%, indicating that the increase in absolute residual variance largely reflected the increase in body weight scale rather than greater environmental heterogeneity at older ages. Genetic correlations indicated two distinct phases in the growth trajectory (Figure 5). Birth weight showed weak genetic correlations with subsequent body weights (0.07–0.24). From 3 months onward, genetic correlations among body weights were consistently high (0.985–1.000), suggesting similar genetic contributions across post-weaning growth stages.

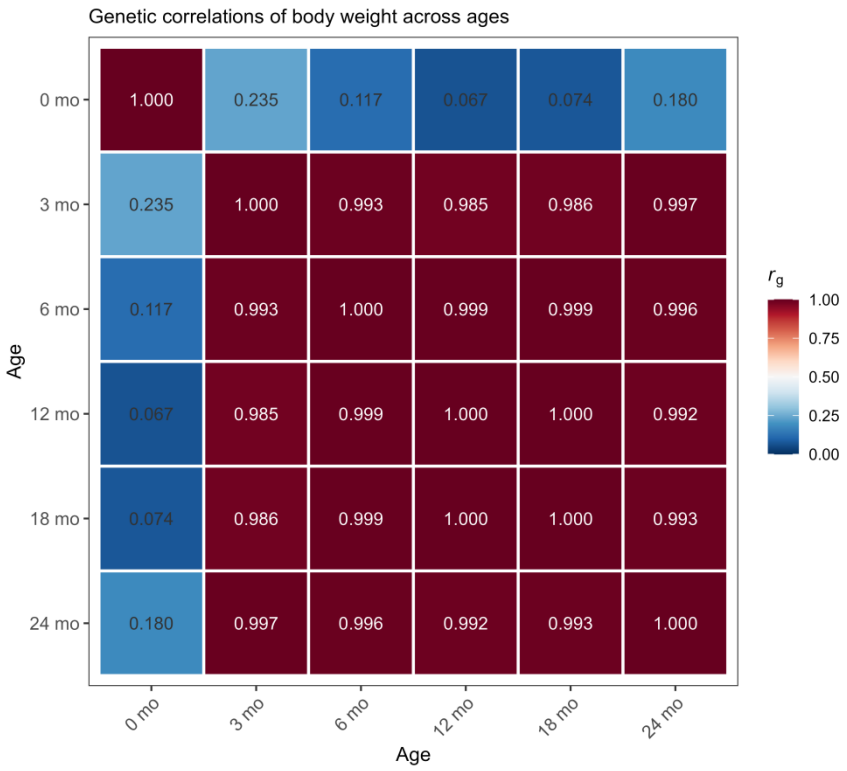


Figure 5. Age-specific genetic correlation matrix of body weight traits in Xinjiang Huaxi cattle. Posterior mean genetic correlations (r_g) among body weight traits measured at 0, 3, 6, 12, 18, and 24 months were calculated from 1,000 MCMC posterior samples of the Bayesian random regression model. The color scale ranges from 0 to 1 because all posterior mean genetic correlations were positive. Posterior standard deviations and 95% equal-tail credible intervals are provided in Supplementary Table S3.

Maternal effects were evaluated separately for birth weight (782 calves from 725 dams) and 3-month weight (790 calves from 733 dams), and the two traits showed different patterns (Supplementary Table S4). For birth weight, inclusion of a maternal genetic effect changed direct heritability from 0.580 to 0.555, while the maternal genetic variance was estimated as zero (m^2 = 0.000, SE = 0.053). For 3-month weight, maternal genetic variance also approached zero (m^2 = 0.000, SE = 0.041), whereas maternal permanent environmental effects accounted for 33.0% of phenotypic variance (c^2 = 0.330, SE = 0.161) and increased direct heritability from 0.196 to 0.250. Both results trace back to the structure of this herd: each dam contributed on average 1.08 offspring, so a dam appears essentially once in the data and her contribution cannot be separated from

the residual. Where the maternal genetic term could be fitted, adding it moved the direct heritability by no more than 0.025, so the direct estimates are not sensitive to omission of the maternal genetic term, although for 3-month weight the maternal permanent environmental effect was clearly not negligible. These single-trait estimates come from age-specific subsets of the records rather than from the Legendre function evaluated at a given age, so they are not directly comparable with the trajectory values in Table 6.

Model Validation and Sensitivity Analyses

The sensitivity of BW heritability to pen-effect specification was evaluated by refitting the model without pen as a fixed effect (Table 7). The estimated heritability changed from 0.18 in the main model to 0.15 after excluding pen, while residual variance increased from 649.4 to 684.1 kg², indicating limited impact of pen-effect specification on the BW heritability estimate.

Table 7. Sensitivity of BW heritability to alternative model specifications.

Model	Fixed effects	h^2	V_e (kg^2)
Main model	Pen fitted as fixed effect	0.18	649.4
Sensitivity model	Pen effect excluded	0.15	684.1

Note: The main model corresponds to the univariate BW model reported in Table 4. In the sensitivity model, the pen effect was excluded while other fixed effects were retained. V_e, residual variance. All models were fitted by average-information REML in sommer v4.3 (Covarrubias-Pazaran, 2016).

Eigen-decomposition of the K = 3 posterior mean K_a matrix revealed eigenvalues of 414894, 3,319, and 9.6, corresponding to variance proportions of 99.2%, 0.8%, and 0.0023%. The near-zero third eigenvalue indicated that the quadratic random regression coefficient carried negligible independent genetic variance (0.0023% of trace). The first eigenvalue, associated with the intercept term, accounted for over 99% of the total genetic variance in the random coefficients, indicating that individual variation in overall growth level dominates the genetic covariance structure, with the linear term contributing a secondary 0.8%. The K = 3 model produced a DIC of 42238 compared with 42506 for K = 2, yielding ΔDIC = 268 in favour of K = 3

(Table 8). The lower DIC indicated improved model fit for the quadratic specification compared with the linear specification. The first two eigenvalues of the Ka matrix accounted for over 99.99% of total genetic variance, indicating that the quadratic term contributed limited independent genetic variation. The improvement in DIC may therefore reflect enhanced covariance structure modeling rather than substantial additional genetic signal from the quadratic term. Both models produced similar heritability trajectories between 3 and 18 months. The K = 3 model showed slightly wider credible intervals at birth and 24 months, consistent with the known boundary behaviour of Legendre polynomials.

Table 8. Comparison of Bayesian random regression models.

Criterion	K = 3	K = 2
Random regression order	Quadratic (k = 0, 1, 2)	Linear (k = 0, 1)
Number of covariance parameters	6	3
DIC	42238	42506
ΔDIC (vs. K = 3)	—	268
Eigenvalue 1 (% of trace)	414894 (99.2%)	883600 (99.998%)
Eigenvalue 2 (% of trace)	3319 (0.8%)	19 (0.002%)
Eigenvalue 3 (% of trace)	9.6 (0.0023%)	N/A

Note: DIC: Deviance Information Criterion; lower values indicate better fit. DeltaDIC > 7 is considered meaningful. Eigenvalues are derived from the posterior mean K_a matrix; percentages refer to trace K_a. Absolute eigenvalue magnitudes differ between K = 3 and K = 2 owing to different prior specifications (IW(V = diag(3) × 100, ν = 3) vs. IW(V = diag(2) × 1000, ν = 2)); variance proportions are comparable across models.

Convergence diagnostics supported the stability of all reported estimates. All Part 1 AI-REML analyses converged successfully, with gradient norms below 10^{-6} and relative parameter changes below 10^{-7}. Pen and production type showed near collinearity, resulting in rank-deficient columns being removed during model fitting without affecting variance component estimation. For Part 2, post-burn-in MCMC samples showed Monte Carlo standard errors below 2% of posterior standard deviations, and Geweke diagnostics supported

chain stationarity. Adding a quadratic age term did not improve model fit (ΔAIC < 2 for all traits), supporting the use of a linear age covariate.

Discussion

This study characterized genetic variation in body conformation traits and longitudinal body weight in Huaxi cattle. Skeletal traits showed higher heritability than body weight, and growth trajectories revealed distinct genetic relationships between birth and post-weaning stages. Heritability estimates differed among conformation traits, with skeletal measurements showing relatively higher additive genetic variation than body weight and body length. These estimates were generally within the range reported for other beef cattle populations, with differences among studies potentially related to breed composition, measurement protocols, and environmental conditions [15], CG heritability of 0.42 lies within the range of 0.27 to 0.69 documented across Simmental populations, and yearling weight heritability in Brazilian Simmental has been reported between 0.28 and 0.42 [16]. Our BW estimate of 0.18 was lower than some previous reports, which may be associated with differences in population structure, measurement stage, environmental conditions, and sample size among studies. Factor analysis of Simmental conformation traits identified a common skeletal genetic factor, consistent with the strong genetic correlations observed among height and girth measures.

Although BW showed substantial additive genetic variance, its heritability was relatively low because residual variance accounted for a larger proportion of phenotypic variance ($V_e/V_a = 4.6$). AG showed a similar pattern, whereas BH and CC showed relatively balanced contributions from additive genetic and residual variance. These results indicate that environmental variation contributed substantially to the phenotypic variation of BW and AG. Longitudinal recording further enabled evaluation of age-dependent changes in genetic variation across the growth trajectory [17]. The genetic correlation analysis revealed distinct patterns among body conformation traits. Strong genetic associations were observed between trunk girth traits (CG and AG; $r_g = 0.75$) and between stature-related traits (BH and HH; $r_g = 0.62$). In contrast, BW showed a moderate genetic correlation with BL ($r_g = 0.64$) but weak correlations with most skeletal traits ($|r_g| < 0.13$). Similar variation in genetic relationships between body frame and BW has been reported among cattle

populations, suggesting that these associations may depend on breed background, measurement age, and environmental conditions. In Huaxi cattle, the weak genetic relationships between BW and most skeletal traits suggest that BW and skeletal conformation capture partly different aspects of growth-related variation.

Age-dependent heritability of BW showed a rise-and-fall pattern across the growth trajectory and reached the highest scheduled-age estimate at 12 months ($h^2 = 0.46$), consistent with previous RRM analyses in Nellore cattle [18]. Unlike the decline in early postnatal heritability reported in a Bos taurus × Bos indicus crossbred population[19] , BW heritability in the present study remained relatively stable from birth to 6 months (0.28–0.31). Additional models incorporating maternal genetic and maternal permanent environmental effects were fitted to evaluate whether maternal contributions influenced these early-age estimates. A maternal genetic component could not be reliably estimated for either BW0 or BW3, and its inclusion changed direct heritability estimates by less than 0.025. Therefore, the early-age heritability pattern was unlikely to be primarily driven by exclusion of maternal genetic effects. However, maternal permanent environmental effects contributed substantially to BW3, accounting for 33.0% of phenotypic variance, indicating that early postnatal records may still contain maternal environmental influences. Birth weight showed weak genetic correlations with subsequent BW records ($r_g < 0.24$), whereas BW measurements from 3 to 24 months exhibited consistently high genetic correlations (0.985–1.000), consistent with previous observations in Nellore cattle [20] These high correlations indicate that post-weaning BW measurements from 3 to 24 months were largely controlled by similar additive genetic factors in this population. Therefore, different post-weaning ages captured substantially overlapping genetic variation for growth. Further validation using larger populations and direct comparisons of breeding values will be required to confirm their applicability in genetic evaluation. One caveat is that the steep heritability decline after 12 months is almost certainly a boundary effect: Legendre polynomials produce unreliable variance estimates at the extremes of the fitted age range, compounded by declining record numbers after 18 months. For breeding programme use, the reliable estimation window is 3 to 18 months, where data density was highest and the K = 3 and K = 2 trajectories were near-identical. The high heritability of skeletal traits observed in this study is consistent with known molecular architecture:

PLAG1 and the NCAPG-LCORL locus have been confirmed as major determinants of stature in cattle [21, 22], with PLAG1 copy number variation linked to body size in Chinese cattle[23]. Quantitative trait loci for live weight and body conformation have also been identified in commercial crossbred populations [24]. These molecular findings align with the high heritability of skeletal traits observed here. All AI-REML analyses satisfied standard convergence criteria [25]. For Part 2, MCMC effective sample sizes exceeded 793, Geweke Z-scores were within ±1.3, and Monte Carlo standard errors remained below 2% of posterior standard deviations. Sensitivity analysis showed that excluding pen from the model only slightly changed the BW heritability estimate from 0.18 to 0.15, suggesting that the low-to-moderate heritability of late-growth BW was robust to this model specification. Taken together, these findings indicate that post-weaning BW records from 3 to 24 months share a highly similar genetic basis in this Huaxi cattle population. These results suggest that longitudinal BW measurements provide consistent information on genetic variation in post-weaning growth, although validation in larger populations is still required.

Our Part 1 estimate of 0.18 for age-adjusted late-growth BW was lower than some previous reports in Chinese beef cattle populations, which may reflect differences in population structure, measurement stage, management conditions, and genetic background among studies. The rise in heritability between 6 and 12 months in our Part 2 trajectory is broadly consistent with published estimates for growth traits in beef cattle [26, 27], supporting the conclusion that growth traits carry moderate heritability in Huaxi cattle. The heterogeneous residual variance structure resulted in a stable residual CV across age classes, suggesting that changes in residual variance were mainly associated with BW scale rather than increased environmental heterogeneity. Heterogeneous residual variance structures have been shown to produce substantial re-ranking in dairy test-day models. Genetic heterogeneity of residual variance has also been demonstrated in American Angus cattle [28], and heteroscedastic reaction norm models provided a better fit for growth traits in Nellore cattle than homogeneous alternatives [29]. Our finding of a stable residual CV provides empirical support for grouping residual variances by age class. These estimates provide preliminary information for genetic evaluation. The relatively high heritability of skeletal traits suggests potential genetic improvement through

selection. For BW, the high genetic correlation between 6- and 12-month measurements (r_g = 0.999) suggests that earlier records may provide information on genetic variation in growth potential in this population, although additional validation based on breeding values and larger datasets is required before practical implementation. The weak genetic association between birth and post-natal weights (r_g < 0.24) suggests limited correlated response in birth weight from selection on post-natal growth, although direct calving-ease records are required before making any inference about dystocia risk, and the architecture of a single growth trajectory replacing age-specific traits is the principal motivation for adopting random regression models in routine evaluation.

The near-zero genetic correlations between BW and most skeletal traits suggest that frame size and growth may be selected jointly with limited unfavorable correlated responses. In Nellore cattle, by contrast, frame score was genetically correlated with yearling weight at 0.82, creating a frame–muscling trade-off that was not evident in the present Huaxi nucleus herd. The genetic correlation between BW and BL (0.64) is the single exception requiring monitoring. Monitoring mature size in this Huaxi nucleus herd will be important, given that mature cow weight heritability ranges from 0.40 to 0.55 in Nellore cattle [30]. Morphometric measurements before one year of age predict growth potential in beef calves [31], supporting the early selection strategy proposed here. Feed efficiency traits carry moderate heritability and can be incorporated into multi-trait indices without sacrificing growth gains [32, 33]. Several limitations should be considered. The Part 1 sample (613 animals) may limit the precision of genetic correlation estimates (SE 0.041–0.131). Data from a single nucleus herd may not directly represent commercial production environments, as genotype-by-environment interaction for growth traits is well documented [34] and sire-by-herd effects explain significant variation in weaning weight [35]. Both analyses used pedigree-based rather than genomic relationship matrices; genomic approaches such as single-step GBLUP have been widely applied in routine genomic evaluation [36, 37], and genomic prediction methods can improve accuracy compared with pedigree-based approaches [38, 39]. BayesR has also shown improved prediction accuracy in populations including Huaxi cattle [14]. The Huaxi

genomic reference population has been expanding, and genomic approaches may further improve long-term selection in this breed.

The random regression model did not include a permanent environmental effect or separate maternal from direct genetic effects. Therefore, non-genetic covariance among repeated records may have been partially attributed to the additive genetic component, potentially affecting heritability estimates and genetic correlations between adjacent ages. Maternal genetic effects could not be resolved for either trait because of the limited dam-offspring structure in the dataset. With 1.08 offspring per dam, the available records were insufficient to separate maternal genetic contributions from residual variation. A maternal permanent environmental effect was identified for 3-month weight but not for birth weight. Incorporating maternal and permanent environmental effects into future random regression models would be valuable when larger datasets become available [11]. Part 1 involved a related data structure. Among the 885 records, 272 animals contributed two to four measurements each, with a median interval of 5.95 months between measurements. Including a permanent environmental effect resulted in boundary estimates for the additive component (Va = 0) in four of the seven traits, while the remaining traits showed inflated phenotypic variance estimates of up to 66%, which were considered biologically implausible. Restricting the analysis to one record per animal also resulted in boundary estimates for four traits, reflecting information loss rather than a true absence of additive variance. Given the average of 1.44 records per animal, these data were insufficient to reliably separate additive and permanent environmental components. Therefore, estimates in Table 4 were obtained from the more parsimonious animal model and should be interpreted as record-level parameters rather than exact partitions of additive variance. The preference for K = 3 based on DIC (ΔDIC = 268) should be interpreted cautiously because DIC has known limitations for hierarchical models. Although the magnitude of ΔDIC exceeded the commonly used threshold of 7, additional validation such as cross-validation would provide stronger support for model selection in future studies. Future genetic evaluations of Huaxi cattle could be strengthened by integrating routine body conformation recording, incorporating genomic information, and extending

longitudinal analyses with larger datasets, longer observation periods, and explicit maternal effect modeling [40].

5. Conclusion

This study estimated genetic parameters for body conformation traits and longitudinal body weight in Xinjiang Huaxi cattle. Skeletal traits showed moderate to high heritability, whereas body weight showed lower heritability and a greater contribution of residual variation. The random regression analysis revealed age-dependent changes in genetic variation for body weight, with strong genetic correlations among post-weaning weights. Maternal effects contributed to early growth variation, particularly for 3-month body weight through maternal permanent environmental effects. Overall, these results improve the understanding of genetic variation in growth and conformation traits in Huaxi cattle and provide reference information for genetic evaluation of this population.

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Authors' contributions Conceptualization: Y.Q. and Z.C. Data curation: Y.Q., W.Z., Q.Z., and B.Z. Formal analysis: Y.Q. and X.L. Methodology: Y.Q., S.J.,H.L, and Y.F. Manuscript writing: Z.C., Y.Q., and M.H. Final approval of manuscript: All authors. All authors read and approved the final manuscript.

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Data Availability The datasets generated and analysed during the current study are not publicly available due to institutional and breeding population data management policies but are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate This study was based on routine performance records collected from a Huaxi cattle nucleus herd with permission from the herd owner. No additional animal handling, experimental treatment, or invasive procedure was conducted specifically for this study. Therefore, this retrospective analysis of existing production records did not require additional animal ethics approval. All animals were managed according to routine welfare and management protocols of the farm. Consent to participate was obtained from the herd owner for the use of production records.

Consent for publication Not applicable.

Competing interests No potential conflict of interest relevant to this article was reported.

References

1. Johnsson M. Genomics in animal breeding from the perspectives of matrices and molecules. Hereditas. 2023;160(1):20.
2. Ma J, Gao X, Li J, Gao H, Wang Z, Zhang L, et al. Assessing the Genetic Background and Selection Signatures of Huaxi Cattle Using High-Density SNP Array. Animals (Basel). 2021;11(12).
3. Misztal I, Lourenco D, Legarra A. Current status of genomic evaluation. J Anim Sci. 2020;98(4).
4. Xu L, Luo H, Zhang X, Lu H, Zhang M, Ge J, et al. Factor Analysis of Genetic Parameters for Body Conformation Traits in Dual-Purpose Simmental Cattle. Animals (Basel). 2022;12(18).
5. Jarnecka O, Otwinowska-Mindur A, Ptak E, Jagusiak W. Genetic parameters of conformation traits in Polish Simmental cattle. Animal Science Papers & Reports. 2025;43(3).
6. Soares BB, Brunes LC, Baldi FS, Carmo ASD, Pereira LS, Carvalho RA, et al. Genetic parameters for visual scores, growth and carcass traits in Nellore Cattle. An Acad Bras Cienc. 2024;96(1):e20230010.
7. Barro AG, Marestone BS, Dos SE, Ferreira GA, Vero JG, Terto DK, et al. Genetic parameters for frame size and carcass traits in Nellore cattle. Trop Anim Health Prod. 2023;55(2):71.
8. Ramos PVB, de Oliveira Menezes GR, da Silva DA, Lourenco D, Santiago GG, Torres Júnior RAA, et al. Genomic analysis of feed efficiency traits in beef cattle using random regression models. J Anim Breed Genet. 2024;141(3):291–303.
9. Ruzzon A, López-Carbonell D, Hervás-Rivero C, Srihi H, Mantovani R, Altarriba J, et al. Maternal genetic effects throughout the life of the dam in Pirenaica beef cattle. a random regression model approach. Animal. 2024;18(7):101206.
10. Javier ER, Gabriel MJ, Candelario SJ, Manuel PG. Maternal effects and its importance in the genetic evaluations of preweaning live weight traits of beef cattle. A review. Trop Anim Health Prod. 2024;56(8):260.
11. Ahmad SZ, Feng Y, Zhang Q, Lu X, Zhao W, Zhang B, et al. Selection index for genetic improvement of beef performance in Huaxi cattle of Xinjiang, China. BMC genomics. 2026.
12. Vaz KM, Souza JC, Ferraz ALJ, Silveira MVD, Arruda R, Souza CF, et al. Estimates of Genetic Parameters, Growth Curve, and Environmental Effects for Nellore Cattle in the Pantanal. Vet Sci. 2024;11(7).
13. Wang Y, Zhu B, Wang J, Zhang L, Xu L, Chen Y, et al. Evaluation of genomic mating approach based on genetic algorithms for long-term selection in Huaxi cattle. BMC Genomics. 2024;25(1):1140.
14. Ma H, Li H, Ge F, Zhao H, Zhu B, Zhang L, et al. Improving Genomic Predictions in Multi-Breed Cattle Populations: A

543 Comparative Analysis of BayesR and GBLUP Models. Genes (Basel). 2024;15(2).
544 15. Bessa AFO, Duarte INH, Rola LD, Bernardes PA, Gonzaga Neto S, Lôbo RB, et al. Genetic evaluation for reproductive
545 and productive traits in Brahman cattle. Theriogenology. 2021;173:261–8.
546 16. Vanvanhossou SFU, König S. The impacts of prenatal drought and heat stress on genetic parameter estimates for birth
547 and weaning weights in Namibian Simmentaler and Simbra cattle. Journal of Animal Science. 2026;104:skag066.
548 17. Wu X-L, Wiggans GR, Norman HD, Caputo MJ, Miles AM, Van Tassell CP, et al. Updating test-day milk yield factors for
549 use in genetic evaluations and dairy production systems: A comprehensive review. Frontiers in Genetics. 2023;14:1298114.
550 18. Del Pilar Solar Diaz I, Bezerra LAF, Lôbo RB, de Araújo Neto FR, de Camargo GMF, da Cruz VAR, et al. Selection effect
551 for growth traits on energy requirements in beef Nelore steers. Trop Anim Health Prod. 2022;54(4):213.
552 19. Hunde D, Tadesse Y, Getachew T, Tadesse M. Estimation of genetic parameters for crossbred dairy cattle in the Central
553 Ethiopia. Ethiopian Journal of Agricultural Sciences. 2022;32(1):105–23.
554 20. Devi KS, Anjali V, Sudhakar K, Venkatseshaiah C. Analysing the growth curve in cross-bred cattle using random
555 regression models. The Pharma Innovation Journal. 2023;12(12S):479–84.
556 21. Abdelmanova AS, Sermyagin AA, Dotsev AV, Bardukov NV, Fornara MS, Brem G, et al. Genome-wide screening for
557 SNPs associated with stature in diverse cattle breeds. Diversity. 2022;14(8):692.
558 22. Gualdrón Duarte JL, Yuan C, Gori AS, Moreira GCM, Takeda H, Coppieters W, et al. Sequenced-based GWAS for linear
559 classification traits in Belgian Blue beef cattle reveals new coding variants in genes regulating body size in mammals. Genet
560 Sel Evol. 2023;55(1):83.
561 23. Zhang Z, Yang P, He P, Xu J, Lyu S, Liu X, et al. Distribution and association study of PLAG1 gene between copy number
562 variation and Chinese cattle populations. Anim Biotechnol. 2022;33(2):273–8.
563 24. Doyle JL, Purfield DC, Moore T, Carthy TR, Walsh SW, Veerkamp RF, et al. Identification of genomic regions that exhibit
564 sexual dimorphism for size and muscularity in cattle. J Anim Sci. 2021;99(5).
565 25. Rameez R, Jahageerdar S, Jayaraman J, Chanu TI, Bangera R, Gilmour A. Evaluation of alternative methods for
566 estimating the precision of REML-based estimates of variance components and heritability. Heredity (Edinb).
567 2022;128(4):197–208.
568 26. Halli K, Bohlouli M, Schulz L, Sundrum A, König S. Estimation of direct and maternal genetic effects and annotation of
569 potential candidate genes for weight and meat quality traits in a genotyped outdoor dual-purpose cattle breed. Transl
570 Anim Sci. 2022;6(1):txac022.
571 27. Londoño-Gil M, Cardona-Cifuentes D, Rodríguez JD, Brunes LC, Magnabosco CU, Pereira ASC, et al. Heritability and
572 genetic correlations between marbling in longissimus dorsi muscle and conventional economic traits in Nellore beef cattle.
573 Trop Anim Health Prod. 2022;54(5):274.
574 28. Amorim ST, Retallick KJ, Garcia A, Ibañez-Escriche N, Morota G. Genetic Heterogeneity of Residual Variance for Foot
575 Score Traits in American Angus Cattle. J Anim Breed Genet. 2026;143(1):68–78.
576 29. Carvalho Filho I, Silva DA, Teixeira CS, Silva TL, Mota LFM, Albuquerque LG, et al. Heteroscedastic Reaction Norm
577 Models Improve the Assessment of Genotype by Environment Interaction for Growth, Reproductive, and Visual Score Traits
578 in Nellore Cattle. Animals (Basel). 2022;12(19).
579 30. Ribeiro AMF, Sanglard LP, Snelling WM, Thallman RM, Kuehn LA, Spangler ML. Genetic parameters, heterosis, and
580 breed effects for body condition score and mature cow weight in beef cattle. J Anim Sci. 2022;100(2).
581 31. Fernandes TA, Vaz RZ, Restle J, Cerdótes L, Nuñez AJC, Costa PT, et al. Morphometric measurements of calves of beef
582 cattle from different genetic groups up to one year of age. Scientia Agricola. 2021;79(5):e20200374.
583 32. Archer J, Reverter A, Herd R, Arthur P. Phenotypic and genetic relationships for feed intake, feed efficiency, body
584 composition and cow milk yield measured postweaning and in mature beef cows. Animal Production Science.
585 2023;63(15):1473–82.
586 33. Pravia MI, Navajas EA, Aguilar I, Ravagnolo O. Evaluation of feed efficiency traits in different Hereford populations and

their effect on variance component estimation. Animal Production Science. 2022;62(17):1652–60.
34. Carvalho Filho I, Campos GS, Lourenco D, Schenkel FS, da Silva DA, Lima Silva T, et al. Genotype by environment interaction for productive and reproductive traits in beef cattle using imputed whole genome sequence. J Appl Genet. 2026;67(1):235–47.
35. Jang S, Lourenco D, Miller S. Inclusion of sire by herd interaction effect in the genomic evaluation for weaning weight of American Angus. J Anim Sci. 2022;100(3).
36. Lourenco D, Legarra A, Tsuruta S, Masuda Y, Aguilar I, Misztal I. Single-Step Genomic Evaluations from Theory to Practice: Using SNP Chips and Sequence Data in BLUPF90. Genes (Basel). 2020;11(7).
37. Nazari-Ghadikolaei A, Fikse F, Eriksson S. Single-Step Genomic Predictions for Growth and Carcass Traits in Nordic Charolais and Hereford Cattle. J Anim Breed Genet. 2026;143(2):283–95.
38. Colombi D, Bonifazi R, Sbarra F, Quaglia A, Calus MPL, Lasagna E. Multi-Breed Genomic Predictions for Average Daily Gain in Three Italian Beef Cattle Breeds. J Anim Breed Genet. 2026;143(1):119–29.
39. Hay EH. Machine Learning for the Genomic Prediction of Growth Traits in a Composite Beef Cattle Population. Animals (Basel). 2024;14(20).
40. Gianola D, Fernando RL, Schön CC. Inference about quantitative traits under selection: a Bayesian revisitation for the post-genomic era. Genet Sel Evol. 2022;54(1):78.

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