

Hierarchical Bayesian modeling for comparing nonlinear functions and estimating heritability of growth curve parameters in llamas

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ABSTRACT

Genetic modeling of growth curve parameters in llamas is fundamental for breeding programs; however, previous studies have relied predominantly on two-stage frequentist approaches or conventional MCMC algorithms (Gibbs/Metropolis-Hastings), which present limitations regarding computational efficiency and simultaneous incorporation of multiple information sources. The objective of this study was to compare nonlinear functions (Brody, Gompertz, and von Bertalanffy) and jointly estimate growth curve parameters (asymptotic weight, A ; scaling parameter, B ; and maturation rate, k), variance components, and heritabilities in young llamas through hierarchical Bayesian modeling implemented with the No-U-Turn Sampler (NUTS) algorithm via Stan/brms. We analyzed 11,409 monthly weight records from birth to 365 days of age from 1000 llamas (456 males and 544 females) of K'ara and Ch'accu breeds from the Quimsachata Experimental Station (Peru). A three-stage hierarchical Bayesian model was adopted: (i) normal likelihood for weights conditioned on individual curves; (ii) multivariate animal model for parameters A , B , and k , including systematic effects (sex and breed) and additive genetic effects; and (iii) normal prior distributions for standard deviations. Posterior sampling (4000 post-warmup iterations) showed adequate convergence according to the Gelman-Rubin, Geweke, and Effective sample size diagnostics. The von Bertalanffy model was selected as the most parsimonious (Watanabe-Akaike Information Criterion (WAIC) = 20104.8; Leave-One-Out Information Criterion (LOOIC) = 27588). Estimated heritabilities for A were high (0.79 - 0.87), while those associated with parameters B and k were close to zero (0.007 - 0.075). We conclude that the hierarchical Bayesian approach with NUTS/brms is computationally efficient and statistically robust for analyzing growth curves in llamas, evidencing high genetic potential for adult weight selection, in contrast to the low heritability of curve shape parameters. This study represents the first application of the NUTS algorithm in hierarchical growth models for South American camelids.

1. Introduction

In South American camelid production, animal growth is generally assessed using body weight measurements recorded at standardized

ages, including birth, weaning, one year of age, and adulthood. Breeder selection frequently relies on information obtained during early developmental stages; however, it is well recognized that weights at different ages exhibit high and positive genetic correlations [1–3]. Consequently,

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selection for increased growth rate may result in undesired increases in adult body weight, thereby raising dam maintenance costs, a phenomenon that has been widely documented in beef cattle [4,5] and rabbits [6]. Therefore, the use of early predictors of adult weight, obtained through individual growth curves, represents a strategic alternative for breeding programs. The nonlinear functions commonly employed to describe growth curves, such as Brody, Gompertz, and von Bertalanffy, allow direct biological interpretation of their parameters by associating them with economically relevant traits, including asymptotic weight, maturation rate, and initial developmental conditions [7–10]. In llamas, previous studies have applied these functions to characterize growth [7, 8]; using traditional methodological approaches that present significant limitations.

Conventional genetic analysis of growth curves is typically performed in two stages: first, curve parameters are estimated individually for each animal, and subsequently these estimates are analyzed as separate traits to obtain (co)variance components. However, this approach has important limitations, since pedigree information is not incorporated during curve fitting, reducing precision for animals with few records, and parameter estimation errors are not propagated into the (co)variance analysis, which may lead to biased inferences [1, 11–13]. As an alternative, hierarchical Bayesian models enable the joint estimation of curve parameters, (co)variance components, and genetic and environmental effects, thereby overcoming the limitations of traditional approaches. This framework was initially proposed by Varona et al. [14] for lactation curves and was later adapted for growth curves in beef cattle [1,13,15] and poultry [11,12,16]. By simultaneously integrating individual records, pedigree information, and systematic effects, this approach provides greater precision and robustness in parameter estimation, including full posterior distributions for heritabilities and robust handling of animals with fewer records through shrinkage and information sharing. In this study, the hierarchical structure integrates two levels of information: individual longitudinal weight records (level 1) and additive genetic and systematic environmental effects modeled through a linear mixed model (level 2).

Applications of hierarchical Bayesian models to growth curve analysis remain scarce, particularly when using modern computational implementations such as the NUTS (No-U-Turn Sampler) algorithm via Stan/brms, which provides greater sampling efficiency than the Gibbs or Metropolis–Hastings methods adopted in earlier studies [17,18]. This efficiency advantage is explained by the fact that NUTS avoids the random walk behavior and sensitivity to correlated parameters that affect gradient-free methods, by taking steps informed by first-order gradient information of the log-posterior, allowing it to navigate complex posterior geometries more rapidly [19]. Although hierarchical Bayesian approaches have been applied to nonlinear growth modeling in other livestock species, none have incorporated NUTS, and no studies to date have reported such an approach in llamas for the joint estimation of growth curves, genetic parameters, and model fit. Therefore, the objective of the present study was to implement a hierarchical Bayesian framework using NUTS algorithm to compare nonlinear growth functions and jointly estimate posterior distributions of curve parameters, variance components, and heritabilities in young llamas.

2. Materials and methods

2.1. Location and data

Longitudinal body weight records used in this study were provided by the Instituto Nacional de Innovación Agraria (INIA), collected at the Centro Experimental de Quimsachata, located in the Santa Lucía district, Lampa, Puno, Peru (4025 m a.s.l.; 15°45'38.9" S, 70°34'18.9" W). Mean annual temperature ranged from 5 to 18 °C, with approximately 700 mm of annual precipitation. Animals were managed under extensive grazing systems with natural pastures supplemented as needed with cultivated forages and mineral mixtures, and standard sanitary protocols including

regular deworming and vaccination. Reproductive management involved routine monitoring during gestation and parturition. From the original dataset, only animals with at least nine monthly body weight records from birth to one year of age (573 animals with 12 records, 275 with 11, 140 with 10, and 12 with 9) and properly connected pedigree information were retained. Also, records with negative or zero body weights, or values below 6 kg or above 60 kg were removed. After data editing, the final dataset comprised 11,409 monthly records from 1000 young llamas (456 males and 544 females), belonging to two types, K'ara (673 animals) and Ch'accu (327 animals), born between 2009 and 2017. The pedigree used for the genetic analyses comprised 2158 animals, including 541 founders, 272 sires and 1004 dams, and reached a maximum depth of eight traced generations. Individual body weights were measured using a digital scale. Descriptive statistics of body weight are presented in Table 1.

2.2. Models

A Bayesian analysis was conducted based on the hierarchical model (Hierarchical Bayesian Model. HBM) proposed by Varona et al. [14], Blasco et al. [6] and Forni et al. [1] to describe each animal's growth curve. Individual growth trajectories were described by a nonlinear function $f(t_{ij}; \theta)$, where $\theta_i = (A_i, B_i, k_i)$ represent the function parameters; assuming that each parameter of this function was considered influenced by genetic and systematic environmental effects; which were modeled through a linear mixed model. In the first stage of the model, three distinct nonlinear models were employed for weight fitting as shown in Table 2.

Detailed biological interpretations of these nonlinear growth models can be found in Freitas [23]. The fitting error variance (σ_e^2) is considered equal for all animals at all ages. Thus, the following distribution was adopted for the weight-age data (y_{ij}) in this first stage:

Table 1

Distribution of weights (kg) according to age (months), sex, and breed of Peruvian llamas.

Breed type	Age	Males		Females	
		n	Mean ± SD	n	Mean ± SD
K'ara	0	302	9.74 ± 1.52	371	9.75 ± 1.54
	1	301	15.94 ± 2.85	371	15.63 ± 2.80
	2	301	21.34 ± 3.78	362	21.3 ± 3.71
	3	283	25.74 ± 4.40	343	25.56 ± 4.23
	4	291	28.69 ± 5.22	362	28.56 ± 4.83
	5	294	31.12 ± 5.56	361	30.94 ± 5.64
	6	276	33.46 ± 5.66	337	33.35 ± 5.93
	7	275	34.70 ± 6.12	344	35.03 ± 5.98
	8	263	35.37 ± 6.35	340	35.49 ± 6.28
	9	286	36.27 ± 6.37	345	36.36 ± 6.17
	10	269	37.43 ± 6.00	334	38.07 ± 5.88
	11	255	39.42 ± 6.00	321	39.93 ± 6.25
	12	41	41.95 ± 7.30	28	40.46 ± 6.54
Total		3437		4219	
Ch'accu	0	154	9.25 ± 1.51	173	9.5 ± 1.69
	1	153	14.71 ± 2.68	171	15.11 ± 2.52
	2	152	19.82 ± 3.33	172	19.74 ± 3.61
	3	142	23.55 ± 3.88	166	23.95 ± 4.40
	4	149	26.51 ± 5.06	167	26.47 ± 5.35
	5	149	27.91 ± 5.16	170	28.6 ± 5.67
	6	142	30.34 ± 5.41	160	30.96 ± 6.10
	7	139	31.22 ± 5.64	160	32.3 ± 6.32
	8	143	31.74 ± 5.85	158	32.74 ± 6.51
	9	147	32.56 ± 6.20	163	33.6 ± 6.16
	10	141	33.93 ± 5.93	163	34.78 ± 6.08
	11	139	35.92 ± 5.95	151	37.29 ± 6.21
	12	16	39.56 ± 8.12	13	35.85 ± 5.40
Total		1766		1987	

n: total number of weight records for a given age. Source: From the author (2026).

Table 2

Equations of nonlinear models used to describe the growth curve of young llamas.

Model	Formula	References
Brody	$y_{ij} = A_i(1 - B_i e^{-k_i t_{ij}}) + \varepsilon_{ij}$	Brody [20]
von Bertalanffy	$y_{ij} = A_i(1 - B_i e^{-k_i t_{ij}})^3 + \varepsilon_{ij}$	von Bertalanffy [21]
Gompertz	$y_{ij} = A_i e^{-B_i e^{-k_i t_{ij}}} + \varepsilon_{ij}$	Laird [22]

y_{ij} : the observed body weight of individual i ($i = 1, \dots, n$) at measurement time j ($j = 1, \dots, n_i$) for animal i ; A_i : the asymptotic body weight of animal i ; B_i : scaling parameter related to the initial body weight of animal i ; k_i : the maturation rate of animal i ; t_{ij} : the age of animal i in months, at time j ; and ε_{ij} : the random residual term.

$$f(y_{ij} | \theta_i, \sigma_\varepsilon^2) \sim N\{f(t_{ij}; \theta_i), \sigma_\varepsilon^2\} \quad [1]$$

In the second stage of the HBM, the variation of growth curves among individuals is attributed to additive genetic effects and systematic environmental effects; which are modeled through a multivariate animal model jointly applied to the growth curve parameter. Considering θ_{pi} as the value of parameter $p \in \{A, B, k\}$ for animal i , the following linear structure was assumed for each parameter:

$$\theta_{pi} = \mathbf{X}_i \boldsymbol{\beta}_p + \mathbf{Z}_i \mathbf{u}_{pi} + \mathbf{e}_{pi} \quad [2]$$

where $\boldsymbol{\beta}_p$ is the vector of systematic environmental effects (sex and breed) associated with parameter p ; $\mathbf{u}_{pi}$ represents the additive genetic effect of animal i for parameter p ; $\mathbf{X}_i$ and $\mathbf{Z}_i$ are the corresponding rows of the incidence matrices for systematic environmental and additive genetic effects, respectively. The vectors of additive genetic effects for each parameter are assumed distributed according to $\mathbf{u}_p | \mathbf{G}, \mathbf{A} \sim MVN(0, \mathbf{G} \otimes \mathbf{A})$; where $\mathbf{G}$ is the 3×3 matrix of additive genetic (co)variances among parameters A , B , and k , and $\mathbf{A}$ is the relationship matrix between individuals. Similarly, the residual effects are assumed distributed according to $\mathbf{e}_p | \mathbf{R} \sim MVN(0, \mathbf{R} \otimes \mathbf{I})$, where $\mathbf{R}$ is the 3×3 matrix of residual (co)variances among parameters A , B , and k , and $\mathbf{I}$ is an identity matrix.

2.3. Inference

The third stage of the hierarchical structure of the HBM consists of describing the *a priori* distributions of all parameters considered in the first and second stages.

Prior distributions. For the vectors of systematic environmental effects $\boldsymbol{\beta}_p$ (sex and breed) and additive genetic effects $\mathbf{u}_p$ with $p \in \{A, B, k\}$, multivariate normal distributions were adopted as described in Forni et al. [1]:

$$f(\boldsymbol{\beta}_p | m, \mathbf{V}) \propto |\mathbf{V}|^{-1/2} \exp \left[-\frac{1}{2} (\boldsymbol{\beta}_p - m)' \mathbf{V}^{-1} (\boldsymbol{\beta}_p - m) \right] \quad [3]$$

$$f(\mathbf{u}_p | \mathbf{G}, \mathbf{A}) \propto (\mathbf{G})^{-N_A/2} |\mathbf{A}|^{-1} \exp \left[-\frac{1}{2} \mathbf{u}_p' (\mathbf{G} \otimes \mathbf{A})^{-1} \mathbf{u}_p \right] \quad [4]$$

where m and $\mathbf{V}$ represent, respectively, the means and (co)variances *a priori* of the systematic environmental effects ($\boldsymbol{\beta}_p$); N_A denotes the number of animals in the relationship matrix ($\mathbf{A}$). Informative normal priors were adopted: $N(36.7, 1)$ for parameter A , $N(1.24, 0.15)$ for parameter B , and $N(0.38, 0.03)$ for parameter k , all with lower bound zero. The residual standard deviation σ_ε received a $N(5, 1)$ prior with lower bound zero.

The density of the growth curve parameters (θ_p) given the systematic environmental and additive genetic effects, was a multivariate normal distribution:

$$f(\theta_p | \boldsymbol{\beta}_p, \mathbf{u}_p, \mathbf{R}) = |\mathbf{R}|^{-N/2} \exp \left[-\frac{1}{2} (\theta_p - \mathbf{X} \boldsymbol{\beta}_p - \mathbf{Z} \mathbf{u}_p)' (\mathbf{R} \otimes \mathbf{I})^{-1} (\theta_p - \mathbf{X} \boldsymbol{\beta}_p - \mathbf{Z} \mathbf{u}_p) \right] \quad [5]$$

Informative normal priors were assumed for the standard deviations of the additive genetic effects and residual effects associated with growth curve parameters ($p \in \{A, B, k\}$), based on posterior estimates from the initial model fit. Following the standard parameterization of the brms package [17] for nonlinear models with random effects, Normal distributions with lower bound zero were adopted, given by:

$$f(\sigma_{u_p} | \mu_u, s_u) \propto \exp \left[-\frac{1}{2} \frac{(\sigma_{u_p} - \mu_u)^2}{s_u^2} \right] \quad [7]$$

$$f(\sigma_{e_p} | \mu_e, s_e) \propto \exp \left[-\frac{1}{2} \frac{(\sigma_{e_p} - \mu_e)^2}{s_e^2} \right] \quad [8]$$

$$f(\sigma_\varepsilon | \mu_\varepsilon, s_\varepsilon) \propto \exp \left[-\frac{1}{2} \frac{(\sigma_\varepsilon - \mu_\varepsilon)^2}{s_\varepsilon^2} \right] \quad [9]$$

with $\sigma_{u_p}, \sigma_{e_p}, \sigma_\varepsilon \geq 0$; $p \in \{A, B, k\}$

where μ_u and s_u represent the mean and standard deviation of the Normal prior for the genetic standard deviations of curve parameters; μ_e and s_e represent the mean and standard deviation of the Normal prior for the residual standard deviations of curve parameters; and μ_ε and s_ε represent the mean and standard deviation of the Normal prior for the fitting error standard deviation, whose values are detailed in [Supplementary Material](#).

Likelihood function (conditional density function of the data). Conditional independence between observations of different individuals is assumed. Thus, the joint distribution of the observation vector $\mathbf{y}$, conditioned on the growth curve parameters, is given by the product of independent normal distributions:

$$f(\mathbf{y} | \boldsymbol{\theta}, \sigma_\varepsilon^2) = \prod_{i=1}^N \prod_{j=1}^{n_i} \frac{1}{\sqrt{2\pi\sigma_\varepsilon^2}} \exp \left\{ -\frac{[y_{ij} - f(t_{ij}; \theta_i)]^2}{2\sigma_\varepsilon^2} \right\} \quad [10]$$

where N is the number of individuals with records; n_i is the number of weight observations of individual i ; $f(t_{ij}; \theta_i)$ represents the nonlinear function corresponding to the considered growth model.

Considering independence between prior densities, and applying Bayes' theorem, the joint posterior distribution of model parameters can be expressed as:

$$f(\boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{R}, \sigma_\varepsilon^2 | \mathbf{y}) \propto f(\mathbf{y} | \boldsymbol{\theta}, \sigma_\varepsilon^2) \times \prod_{p \in \{A, B, k\}} [f(\theta_p | \boldsymbol{\beta}_p, \mathbf{u}_p) f(\mathbf{u}_p | \mathbf{G}, \mathbf{A}) f(\boldsymbol{\beta}_p) f(\mathbf{G})] f(\mathbf{R}) f(\sigma_\varepsilon^2) \quad [11]$$

where $f(\mathbf{y} | \boldsymbol{\theta}, \sigma_\varepsilon^2)$ corresponds to the likelihood function; $f(\theta_p | \boldsymbol{\beta}_p, \mathbf{u}_p)$ corresponds to the density of growth curve parameters; $f(\mathbf{u}_p | \mathbf{G}, \mathbf{A})$ represents the prior distribution of additive genetic effects structured by the relationship matrix $\mathbf{A}$; $f(\boldsymbol{\beta}_p)$ denotes the prior distribution of systematic environmental effects; $f(\mathbf{G})$ and $f(\mathbf{R})$ represent the prior distributions of the additive genetic and residual (co)variance matrices, respectively, following the parameterization described in equations [7], [8] and [9]; and $f(\sigma_\varepsilon^2)$ represents the Normal prior for the fitting error variance.

Mixed model equations system. In the hierarchical Bayesian approach the individual latent growth curve parameters θ_p ($p \in \{A, B, k\}$) were modeled jointly through a multivariate animal model, estimating the full 3×3 additive genetic (co)variance matrix $\mathbf{G}$ and residual (co)variance matrix $\mathbf{R}$, corresponding to the three growth-curve parameters analyzed (A , B , and k). Although inference was performed via MCMC sampling, the linear structure of the second hierarchical stage is

equivalent to the following multivariate mixed model equations system:

$$\begin{bmatrix} \mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z} \\ \mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z + (G \otimes A)^{-1}} \end{bmatrix} \begin{bmatrix} \beta_p \\ u_p \end{bmatrix} = \begin{bmatrix} \mathbf{X'R^{-1}\theta_p} \\ \mathbf{Z'R^{-1}\theta_p} \end{bmatrix} \quad [12]$$

with $p \in \{A, B, k\}$. Where θ_p is the vector containing the latent values of parameter p for all animals; β_p is the vector of systematic environmental effects (sex and breed for each parameter); u_p is the vector of additive genetic effects structured by the relationship matrix A ; X and Z are the incidence matrices for systematic environmental and random effects, respectively; and $\sigma^2_{u_p}$ corresponds to the additive genetic variance.

with $p \in \{A, B, k\}$. Where θ_p is the stacked vector of latent growth curve parameters for all animals and parameters; β_p is the vector of systematic environmental effects (sex and breed); u_p is the vector of additive genetic effects structured by the relationship matrix A ; X and Z are the incidence matrices for systematic environmental and random effects, respectively.

2.4. Statistical analyses

For each nonlinear model (Brody, von Bertalanffy, and Gompertz), four parallel Monte Carlo chains were run using HMC/NUTS, with 2000 iterations per chain, of which the first 1000 were discarded as warmup, yielding 4000 posterior samples per model for inference. The adequacy of the warmup period was evaluated using the Raftery and Lewis diagnostic [24], whose dependence factor values were close to or equal to 1 for all parameters, indicating sufficient reduction of initial dependence. Chain convergence was assessed using multiple criteria: the Gelman and Rubin statistic [25] with $\hat{R} < 1.01$, the Geweke diagnostic [26] (accepting convergence when $|Z| < 1.96$, and visual inspection of trace plots. Sampling efficiency was evaluated through the effective sample size (ESS, [27], ensuring $ESS > 400$ for all parameters of interest. Autocorrelation between successive samples was also examined and considered acceptable when approaching zero after a few lags. Overall, these diagnostics confirmed adequate mixing and convergence, allowing robust comparisons between the three fitted growth models.

Model comparison and goodness of fit. Model comparison and goodness of fit were assessed for the three nonlinear models (Brody, von Bertalanffy, and Gompertz) using information-theoretic and cross-validation criteria. Specifically, the Deviance Information Criterion (DIC; [28]), the Watanabe–Akaike Information Criterion (WAIC; [29]), and leave-one-out cross-validation (LOOIC; [30]) were computed. LOOIC also provided an estimate of out-of-sample predictive accuracy. Models with lower DIC LOOIC and WAIC values, indicating adequate regularization, were considered preferable. Although DIC is commonly used for Bayesian model comparison, it may underestimate the penalization for effective parameters in complex hierarchical structures [27]. For this reason, model selection among the three candidate growth functions was primarily guided by the WAIC and LOOIC criteria, which provide a more statistically robust penalization for the hierarchical parameters involved in the present multivariate animal model framework; accordingly, the von Bertalanffy model was prioritized as the base model on this statistical basis.

Sampling algorithms. Parameter estimation was performed using the No-U-Turn Sampler (NUTS; [19]), an adaptive extension of Hamiltonian Monte Carlo (HMC; [31]), implemented in the Stan inference engine via the brms package [17]) in conjunction with cmdstanr [32]. NUTS automatically tunes the integration step size and mass matrix, eliminating the need for manual specification of proposal parameters required by Metropolis–Hastings or Gibbs samplers, and enabling efficient sampling in high-dimensional hierarchical models with complex geometry. Informative normal prior distributions, based on posterior estimates from the initial model fit, were assigned to growth curve parameters, genetic and residual standard deviations, and fitting error standard deviation, all constrained to positive values to ensure

biological plausibility during sampling. All analyses were conducted in the R environment [33] using brms and cmdstanr, which allow just-in-time compilation of Stan models and parallel execution of chains.

3. Results

Convergence diagnostics for the three nonlinear models (Brody, Gompertz, and von Bertalanffy) fitted to body weight records of young llamas indicated adequate convergence and robust inference (Tables 3–5). Gelman–Rubin statistics ($\hat{R}$) were consistently close to 1.00 across most parameters, with values generally below the recommended threshold of 1.01. Dependence factors from the Raftery–Lewis diagnostic ranged from 1.12 to 13.5 (means: 3.28 for Brody, 2.31 for Gompertz, and 2.27 for von Bertalanffy), indicating low to moderate chain dependence and generally adequate MCMC sampling efficiency across models. Geweke $|Z|$ statistics were generally low, with most values remaining within the conventional convergence threshold of ± 1.96 , although a few parameters exceeded this criterion. Effective sample size (ESS) ratios showed a consistent pattern among models, with genetic variance components exhibiting the lowest ratios, whereas the systematic environmental effects and residual variance displayed higher efficiencies. Visual inspection of trace plots and posterior densities (Figs. 1 and 2) further confirmed stable chains and well-behaved unimodal distributions, with no evidence of multimodality or divergence.

Table 6 summarizes model comparisons based on Bayesian information criteria. The von Bertalanffy model achieved the best overall performance, presenting the lowest LOOIC (27588.0) and WAIC (20104.8), indicating superior predictive ability and a favorable balance between goodness of fit and model complexity. The Brody model showed intermediate LOOIC (29050.8) and WAIC (21550.0) values, whereas the Gompertz model exhibited the highest values for both criteria (LOOIC = 34065.4; WAIC = 26766.2), indicating poorer predictive performance. In contrast, the Brody model yielded the lowest DIC (3132891), followed by Gompertz (3973300) and von Bertalanffy (4179381). The discrepancy among criteria likely reflects the different penalization strategies used by DIC and the fully Bayesian predictive criteria (LOOIC and WAIC), with the latter generally preferred for

Table 3
Convergence diagnostics of Brody growth curve model fitted to body weight records of young llamas, including sex and breed effects.

Parameter	effects	$\hat{R}$	DF	Geweke $ Z $	ESS ratio
Systematic environmental effects					
A	Intercept	1.00	2.29	0.366	0.232
	sex	1.00	2.35	−0.528	0.178
	breed	1.00	2.88	−0.910	0.165
B	Intercept	1.00	2.00	1.112	0.284
	sex	1.00	1.71	−1.141	0.251
	breed	1.00	1.88	−1.272	0.263
k	Intercept	1.00	1.47	−0.087	0.271
	sex	1.00	1.76	1.510	0.599
	breed	1.00	1.71	0.667	0.603
Random effects					
A	σ_{aA}	1.00	2.00	−1.230	0.154
	σ_{eA}	1.00	3.24	−1.354	0.027
B	σ_{aB}	1.00	1.88	−2.361	0.232
	σ_{eB}	1.01	4.71	−2.654	0.047
k	σ_{aK}	1.00	4.35	0.504	0.128
	σ_{eK}	1.03	4.71	−0.320	0.019
	σ_ϵ	1.15	13.50	8.221	0.001

$\hat{R}$: Gelman–Rubin potential scale reduction factor; DF: Dependence Factor values from the Raftery and Lewis diagnostic; Geweke $|Z|$: Absolute value of Geweke’s Z diagnostic for MCMC convergence; ESS ratio: Ratio of effective sample size to total sample size. A: asymptotic body weight; B: integration constant; k: maturation rate.

Table 4

Convergence diagnostics of Gompertz growth curve model fitted to body weight records of young llamas, including sex and breed effects.

Parameter	effects	$\hat{R}$	DF	Geweke Z	ESS ratio
Systematic environmental effects					
A	Intercept	1.00	1.35	0.791	0.181
	sex	1.00	2.00	0.347	0.164
	breed	1.00	2.00	−0.864	0.114
B	Intercept	1.00	1.24	2.056	0.259
	sex	1.00	1.47	−0.185	0.249
	breed	1.00	1.35	−2.430	0.223
k	Intercept	1.01	1.35	0.800	0.438
	sex	1.00	1.12	−0.172	0.587
	breed	1.00	1.59	−1.171	0.613
Random effects					
A	σ_{aA}	1.02	1.35	−0.976	0.126
	σ_{eA}	1.22	1.47	−1.557	0.002
B	σ_{aB}	1.00	1.24	−2.173	0.239
	σ_{eB}	1.08	3.94	−3.226	0.009
k	σ_{ak}	1.01	1.41	−1.136	0.066
	σ_{ek}	1.06	2.47	2.465	0.015
	σ_e	1.16	11.6	4.466	0.001

$\hat{R}$: Gelman-Rubin potential scale reduction factor; DF: Dependence Factor values from the Raftery and Lewis diagnostic; Geweke |Z|: Absolute value of Geweke's Z diagnostic for MCMC convergence; ESS ratio: Ratio of effective sample size to total sample size. A: asymptotic body weight; B: integration constant; k: maturation rate.

Table 5

Convergence diagnostics of von Bertalanffy growth curve model fitted to body weight records of young llamas, including sex and breed effects.

Parameter	effects	$\hat{R}$	DF	Geweke Z	ESS ratio
Systematic environmental effects					
A	Intercept	1.00	1.47	0.366	0.170
	sex	1.00	1.88	1.085	0.124
	breed	1.00	1.88	−0.788	0.132
B	Intercept	1.00	1.59	−0.201	0.243
	sex	1.00	1.71	1.265	0.202
	breed	1.00	1.24	−0.296	0.228
k	Intercept	1.01	1.35	−1.172	0.285
	sex	1.00	2.71	0.122	0.616
	breed	1.00	1.35	1.269	0.567
Random effects					
A	σ_{aA}	1.00	1.76	0.779	0.147
	σ_{eA}	1.15	1.82	2.322	0.003
B	σ_{aB}	1.00	1.29	2.311	0.310
	σ_{eB}	1.05	4.24	−0.339	0.014
k	σ_{ak}	1.00	1.76	−0.419	0.087
	σ_{ek}	1.01	2.29	2.051	0.038
	σ_e	1.79	7.94	−0.948	0.001

$\hat{R}$: Gelman-Rubin potential scale reduction factor; DF: Dependence Factor values from the Raftery and Lewis diagnostic; Geweke |Z|: Absolute value of Geweke's Z diagnostic for MCMC convergence; ESS ratio: Ratio of effective sample size to total sample size. A: asymptotic body weight; B: integration constant; k: maturation rate.

hierarchical Bayesian models.

Table 7 presents posterior heritability estimates for growth curve parameters under the three nonlinear models (Brody, Gompertz, and von Bertalanffy). Heritability estimates for parameter A (asymptotic weight) were high and consistent across models, with values of 0.867, 0.791, and 0.814 for the Brody, Gompertz, and von Bertalanffy models, respectively, and relatively narrow 95% highest posterior density (HPD) intervals. In contrast, parameters B (scaling parameter) and k (maturation rate) exhibited low heritabilities, although with some variation among models. Parameter B ranged from 0.007 to 0.075, whereas parameter k ranged from 0.016 to 0.027. The corresponding standard

errors were small, and the 95% HPD intervals remained concentrated at low values, indicating a limited additive genetic contribution to these growth curve parameters.

Table 8 summarizes the posterior genetic, residual, and phenotypic correlations among growth curve parameters (A, B, and k) for the three nonlinear models. Across models, parameter A showed strong positive genetic and phenotypic correlations with B, whereas correlations between A and k and between B and k were consistently negative. Residual correlations exhibited greater variability among models but generally followed similar patterns, with particularly strong negative associations between B and k. Overall, the three growth functions yielded qualitatively consistent correlation structures.

Table 9 summarizes Bayesian posterior estimates of growth curve parameters for the three nonlinear models (Brody, Gompertz, and von Bertalanffy). Estimates of asymptotic weight differed moderately between models, with posterior means of 41.678 kg (Brody), 38.788 kg (Gompertz), and 39.479 kg (von Bertalanffy), all with relatively narrow 95% HPD intervals. Parameter B exhibited greater variation across models (0.763, 1.359, and 0.369, respectively), reflecting structural differences among growth functions. Maturation rate was estimated at 0.233, 0.394, and 0.339, respectively, indicating a faster approach to the asymptote under the Gompertz model. In all cases, posterior modes were virtually identical to posterior means and medians, suggesting well-behaved and approximately symmetric posterior distributions.

4. Discussion

Integrated diagnostics across the three nonlinear models confirmed adequate convergence and reliable inference, with $\hat{R}$ values consistently below 1.01. Dependence factors showed limited variability among models (means: 3.28 for Brody, 2.31 for Gompertz, and 2.27 for von Bertalanffy), reflecting the inherent complexity of hierarchical nonlinear frameworks, as previously reported for growth curve in beef cattle [1,13,15] and poultry [11,12,16]. Furthermore, most Geweke statistics remained within the conventional convergence threshold, supporting overall chain stability. The consistently lower ESS ratios observed for genetic variance components agree with previous reports in pedigree-based animal models, where variance components typically exhibit higher autocorrelation due to positivity constraints and interactions between fixed and random effects [1,34,35]. Overall, the consistency of diagnostics across models supports the robustness of the inferential process achieved using NUTS via Stan/brms. Compared with earlier studies relying on Metropolis–Hastings or Gibbs sampling (e.g., Forni et al., [1]; Silva et al., [15]; Lázaro et al., [11]; Gotuzzo et al., [12]), NUTS provides more efficient exploration of high-dimensional hierarchical parameter spaces, such as the present model including pedigree structure.

The Bayesian model comparison reveals that the von Bertalanffy model presents the best overall performance, with the lowest WAIC and LOOIC values. WAIC, considered more robust than DIC for hierarchical models [28,29], adequately penalizes model complexity, favoring von Bertalanffy over Gompertz, which exhibited substantially higher LOOIC and WAIC values. The Brody model showed intermediate predictive performance according to both criteria. LOOIC provides an estimate of out-of-sample predictive performance, with lower values indicating better expected prediction for new observations. Although the Brody model presented the lowest DIC, its higher WAIC and LOOIC values indicate inferior predictive performance relative to the von Bertalanffy model. In hierarchical Bayesian models, discrepancies among information criteria are not uncommon because they rely on different measures of model fit and complexity [29]. The superiority of the von Bertalanffy model aligns with previous studies in ruminants, where this function frequently provides better fit for post-natal growth data [1,22].

The high heritabilities for A, consistently above 0.79 across the three models, indicate strong additive genetic control over this trait in young

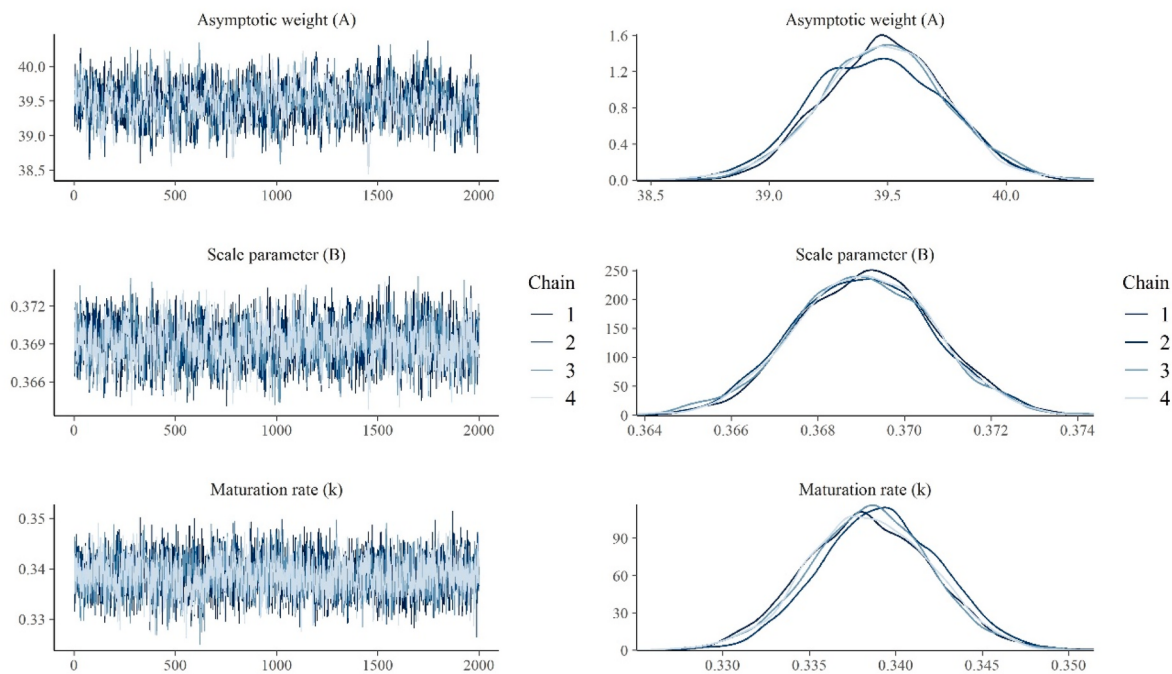


Fig. 1. Trace plots and posterior densities of asymptotic weight (A), scale parameter (B), and maturation rate (k) from the von Bertalanffy growth model.

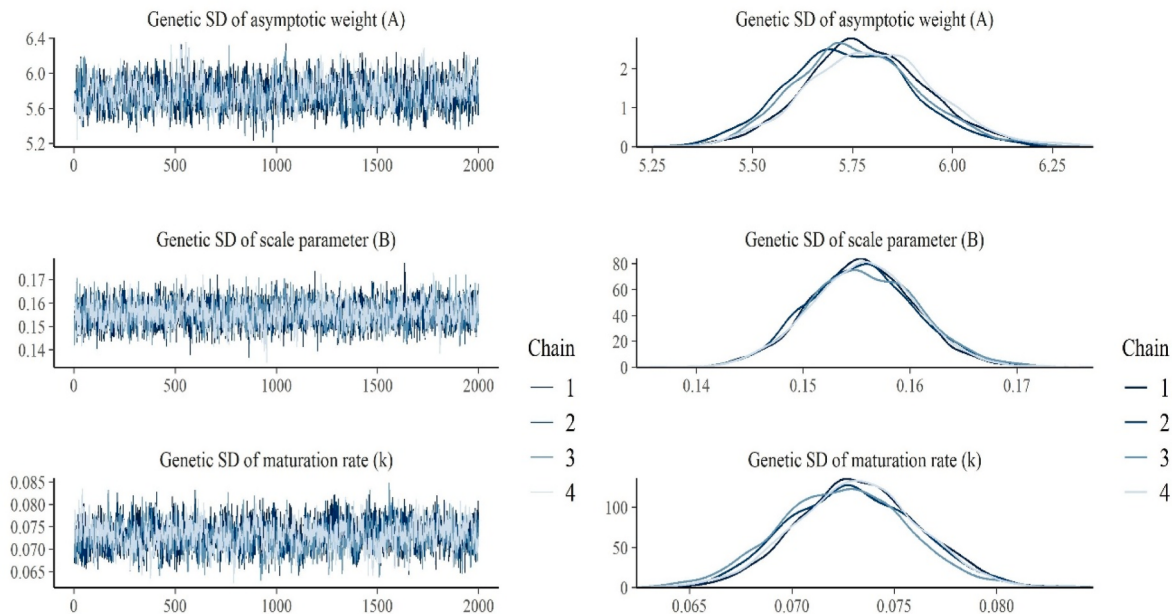


Fig. 2. Trace plots and posterior densities of Genetic SD of asymptotic weight (A) Genetic SD of scale parameter (B) Genetic SD of maturation rate (k) from the von Bertalanffy growth model.

Table 6
Bayesian model comparison of growth curve models fitted to body weight data of young llamas using LOOIC, WAIC, and DIC.

models	LOOIC	WAIC	DIC
Gompertz	34065.40	26766.2	3973300
vonBertalanffy	27588.00	20104.8	4179381
Brody	29050.80	21550.0	3132891

LOOIC: Leave-One-Out Information Criterion; WAIC: Widely Applicable Information Criterion; DIC: Deviance Information Criterion.

llamas, suggesting that a high response to selection can be expected based on growth curve parameter A. These values are higher than those reported in young llamas by Canaza-Cayo et al. [7] who found heritability of 0.10 for parameter A in the von Gompertz model. Using the same methodology as in the present study, Forni et al. [1], applying the von Bertalanffy growth model, reported a heritability estimate of 0.52 for adult weight in beef cattle, which is lower than the values observed here for young llamas. The higher heritability observed in llamas may reflect lower environmental influence in extensive high-altitude systems or greater genetic uniformity in the studied populations. The negligible heritability estimates for parameters B and k suggest that these traits are

Table 7

Posterior mean estimates of additive genetic variance (σ_a^2), residual variance (σ_e^2), phenotypic variance (σ_p^2), and heritability (h^2) for growth curve parameters (A , B , and k) in young llamas fitted using the Brody, Gompertz, and von Bertalanffy models.

Model	Parameter	σ_a^2	σ_e^2	σ_p^2	h^2	SE	95% HPD CI
Brody	A	44.628	6.841	51.468	0.867	0.010	0.847 – 0.886
	B	0.002	0.199	0.200	0.009	0.003	0.005 – 0.018
	k	0.003	0.199	0.202	0.016	0.005	0.008 – 0.031
Gompertz	A	33.344	8.786	42.130	0.791	0.012	0.768 – 0.814
	B	0.024	0.331	0.355	0.075	0.024	0.042 – 0.126
	k	0.005	0.319	0.324	0.019	0.007	0.010 – 0.034
von Bertalanffy	A	35.664	8.141	43.805	0.814	0.011	0.792 – 0.835
	B	0.001	0.177	0.178	0.007	0.003	0.004 – 0.013
	k	0.004	0.178	0.182	0.027	0.010	0.014 – 0.049

SE: Standard error; 95% HPD CI: Lower and upper limits of the 95% Highest Posterior Density interval.

Table 8

Posterior mean estimates of genetic (r_g), residual (r_e), and phenotypic (r_p) correlations among growth curve parameters (A , B , and k) in llamas fitted using the Brody, Gompertz, and von Bertalanffy models.

Trait 1	Trait 2	r_g	SD	95% HPD CI	r_e	SD	95% HPD CI	r_p	SD	95% HPD CI
Brody model										
A	B	0.86	0.02	0.83 – 0.89	−0.01	0.12	−0.26 – 0.20	0.70	0.02	0.66 – 0.74
A	k	−0.48	0.03	−0.55 to −0.41	−0.34	0.08	−0.46 to −0.16	−0.46	0.03	−0.51 to −0.39
B	k	−0.65	0.04	−0.71 to −0.58	−0.88	0.06	−0.97 to −0.76	−0.69	0.03	−0.75 to −0.64
Gompertz model										
A	B	0.80	0.02	0.77 – 0.84	0.52	0.09	0.31 – 0.68	0.71	0.02	0.66 – 0.75
A	k	−0.26	0.04	−0.34 to −0.17	−0.65	0.04	−0.72 to −0.57	−0.36	0.03	−0.42 to −0.29
B	k	−0.32	0.05	−0.41 to −0.23	−0.90	0.06	−0.98 to −0.77	−0.52	0.04	−0.59 to −0.44
von Bertalanffy model										
A	B	0.81	0.02	0.77– 0.84	0.36	0.10	0.15 – 0.54	0.69	0.02	0.65 – 0.73
A	k	−0.33	0.04	−0.41 to −0.25	−0.58	0.04	−0.65 to −0.49	−0.39	0.03	−0.45 to −0.33
B	k	−0.42	0.04	−0.50 to −0.34	−0.90	0.05	−0.98 to −0.77	−0.56	0.04	−0.63 to −0.49

SD: standard deviation; 95% HPD CI: Lower and upper limits of the 95% Highest Posterior Density interval.

Table 9

Bayesian posterior summaries of parameters (A , B , and k) for growth curve models fitted to body weight data.

Model	Parameter	Mean	SD	Median	Mode	95% HPD CI
Brody	A	41.678	0.309	41.674	41.688	41.106 - 42.325
	B	0.763	0.002	0.763	0.763	0.759 - 0.767
	k	0.233	0.003	0.233	0.233	0.227 - 0.239
Gompertz	A	38.788	0.264	38.786	38.795	38.278 - 39.318
	B	1.359	0.008	1.359	1.359	1.345 - 1.374
	k	0.394	0.004	0.394	0.394	0.386 - 0.402
von Bertalanffy	A	39.479	0.264	39.478	39.480	38.971 - 39.997
	B	0.369	0.002	0.369	0.369	0.366 - 0.372
	k	0.339	0.004	0.339	0.338	0.332 - 0.346

HPD (LL) 2.5%: Lower limit of the 95% Highest Posterior Density (HPD) interval; HPD (UL) 97.5%: Upper limit of the 95% Highest Posterior Density (HPD) interval.

predominantly influenced by environmental factors in llamas. This pattern is consistent with the findings of Canaza-Cayo et al. [7], who reported low heritability for maturation rate in young llamas, and with Forni et al. [1], who also found values close to zero for these parameters. The consistency of this result across the three models reinforces its robustness and suggests that, unlike asymptotic weight, the shape of the growth curve in llamas is not highly susceptible to direct genetic selection. The pedigree structure used in this study, with a maximum depth of eight traced generations, provided substantial genealogical information and likely contributed to the stability of the genetic parameter estimates. Despite the observed inferential robustness, some methodological limitations must be considered. In particular, the first-stage model assumed homogeneous residual variance across ages, whereas growth data may exhibit age-dependent heteroscedasticity. This assumption facilitated estimation of the complex multivariate hierarchical model and contributed to stable MCMC convergence, but future studies should evaluate more flexible residual structures that allow residual variance to vary with age. Incorporating explicit variance functions, such as splines or power-of-the-mean models, represents a

logical next step to accommodate this natural increase in variance. Moreover, although the brms package allowed the incorporation of both the genetic and residual (co)variance matrices in a multivariate framework, the estimated heritabilities were consistently higher than those generally reported in the literature for ruminants. Given that convergence diagnostics (R-hat, ESS) and prior specification were adequate, this discrepancy could be attributed to particularities of the studied population (e.g., pedigree structure not fully capturing the relatedness among individuals, limited sample size, or unmodeled shared environmental effects). Regarding unmodeled shared environmental effects, maternal effects were not included, as doing so would have increased model parameterization and compromised convergence stability. Consequently, part of the additive genetic variance estimated for parameter A may include maternal contributions not explicitly separated by the model. Regarding sample-related particularities, the pedigree spanned a maximum depth of eight traced generations but included only 541 founders, resulting in a comparatively narrow genetic base relative to the number of records. This pedigree structure, combined with the presence of two llama types (K'ara and Ch'ac'u) within the same

relationship matrix, may have inflated the additive genetic variance component relative to populations with broader founder representation or more balanced family structures. Therefore, the presented results should be interpreted with caution, potentially reflecting both structural model limitations and particularities of the studied population. Additionally, informative priors were adopted for the growth curve parameters and their (co)variance components because the hierarchical model was fitted using longitudinal records limited to the first year of life, whereas parameter *A* represents mature body weight attained later in life, an approach consistent with previous Bayesian growth curve studies [1,6,11,12,15]. Although Bayesian inference depends on prior specification, the sensitivity of the posterior estimates to alternative prior distributions was not formally evaluated in the present study. Such an analysis would help determine the robustness of the proposed methodology and whether similar biological conclusions are maintained under different prior specifications [27,34].

Regarding computational requirements, the Bayesian hierarchical nonlinear model required approximately 2 h of computation using Stan through the brms package on a laptop equipped with an Intel Core i9 processor, 64 GB of RAM, and 24 logical cores. Sampling parameters, particularly adapt_delta, were adjusted to achieve adequate convergence diagnostics. Although the approach is computationally more demanding than conventional nonlinear methods, the availability of the code as supplementary material facilitates reproducibility, while further studies are needed to evaluate its scalability for larger datasets.

Parameter estimates revealed systematic differences between nonlinear functions. The higher *A* obtained with the Brody model (41.68 kg), compared with Gompertz (38.79 kg) and von Bertalanffy (39.48 kg), is expected, as the Brody function assumes a more gradual approach to the asymptote. In contrast, the Gompertz model, which produced the lowest *A* estimate, tends to slightly underestimate final body weight relative to fully sigmoidal growth functions such as von Bertalanffy. In addition to differences in asymptotic weight, parameter *B* from the von Bertalanffy model, representing the proportion of adult weight to be gained after birth, was estimated at 0.355. This implies that young llamas are born with approximately 26.8% of their potential adult weight, reflecting a substantial prenatal contribution to final body size. This result is consistent with those reported by Maquera [36], who obtained asymptotic weight estimates ranging from 34.9 to 40.6 kg using the NLIN procedure in SAS. However, these values (37.9–40.2 kg) are lower than those reported by Canaza-Cayo et al. [7,37] and Apaza and Quispe [18], for young llamas (46.7–67.5 kg), likely reflecting differences in modeling strategy. Those authors applied a conventional two-stage approach, whereas the present study used a hierarchical Bayesian framework that jointly estimates individual and population-level parameters, allowing uncertainty in growth curve estimation to be properly propagated and potentially leading to more conservative asymptotic weight estimates. Given that llamas reach adult weight at 4–5 years of age, but animals were only monitored until 365 days, estimates of asymptotic weight involve extreme extrapolation beyond the observed data. Therefore, *A* should be interpreted as a mathematical parameter within the fitted growth curve, not as a true biological adult weight, and breeding values based on *A* must be considered with caution. The maturation rate estimates obtained in the present study were comparable to those reported by Wurzinger et al. [38] in Bolivian llamas, but exceeded values previously reported in Peru by other authors [7,18,36,37]. This difference may be associated with variations in nutritional management, environmental conditions, or age range evaluated, since rate parameters are highly sensitive to non-genetic factors. The higher rate observed in our work suggests more accelerated growth, possibly related to improvements in management or accumulated genetic selection in the studied population.

5. Conclusion

The hierarchical Bayesian methodology, implemented through the

NUTS algorithm via Stan/brms, demonstrated computational robustness and allowed identification of the von Bertalanffy model as the most adequate for describing growth in young llamas. The results revealed high genetic potential for selection of asymptotic weight, but low heritability for characteristics related to curve shape, with direct implications for genetic breeding programs of this species.

CRedit authorship contribution statement

Ali William Canaza-Cayo: Writing – original draft, Formal analysis, Conceptualization. **Ruben Herberht Mamani-Cato:** Writing – review & editing, Methodology, Formal analysis. **Francisco Halley Rodríguez-Huancá:** Writing – review & editing, Resources. **Roxana Churata-Huacani:** Writing – review & editing, Methodology, Formal analysis. **Oscar Efraín Cardenas Minaya:** Writing – review & editing, Validation. **Ferdynand Marcos Huacani-Pacori:** Writing – review & editing, Validation. **Maribel Calsin-Cari:** Writing – review & editing, Resources. **Júlio Sílvio de Sousa Bueno Filho:** Writing – review & editing, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data (Here, only “Supplementary data” should appear; please delete “Appendix A”)

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.repbre.2026.08.002>.

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