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Comparison of different nonlinear functions to describe Nelore cattle growth[1]

S. Forni,* M. Piles,† A. Blasco,‡ L. Varona,§ H. N. Oliveira,# R. B. Lôbo, ‖
and L. G. Albuquerque*[2]

*Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista "Julio de Mesquita Filho,"
Jaboticabal, São Paulo, 14884900, Brazil; †Institute of Agro-Food Research and Technology,
Unidad de Cunicultura, Caldes de Montbui, 68140, Spain; ‡Departamento de Ciencia Animal, Universidad
Politécnica de Valencia, 46071, Spain; §Centre University of Lleida-Institute of Agro-Food Research
and Technology, Lleida, 25198, Spain; #Faculdade de Medicina Veterinária e Zootecnia, Universidade Estadual
Paulista "Julio de Mesquita Filho," Botucatu, São Paulo, 18618000, Brazil; and ‖Faculdade de Medicina,
University of São Paulo, Ribeirão Preto, São Paulo, 14049900, Brazil

ABSTRACT: This work aims to compare different nonlinear functions for describing the growth curves of Nelore females. The growth curve parameters, their (co)variance components, and environmental and genetic effects were estimated jointly through a Bayesian hierarchical model. In the first stage of the hierarchy, 4 nonlinear functions were compared: Brody, Von Bertalanffy, Gompertz, and logistic. The analyses were carried out using 3 different data sets to check goodness of fit while having animals with few records. Three different assumptions about SD of fitting errors were considered: constancy throughout the trajectory, linear increasing until 3 yr of age and constancy thereafter, and variation following the nonlinear function applied in the first stage of the hierarchy. Comparisons of the overall goodness of fit were based on Akaike information criterion, the Bayesian information criterion, and the deviance information criterion. Goodness of fit at different points of the growth curve was compared applying the Gelfand's check function. The posterior means of adult BW ranged from 531.78 to 586.89 kg. Greater estimates of adult BW were observed when the fitting error variance was considered constant along the trajectory. The models were not suitable to describe the SD of fitting errors at the beginning of the growth curve. All functions provided less accurate predictions at the beginning of growth, and predictions were more accurate after 48 mo of age. The prediction of adult BW using nonlinear functions can be accurate when growth curve parameters and their (co)variance components are estimated jointly. The hierarchical model used in the present study can be applied to the prediction of mature BW in herds in which a portion of the animals are culled before adult age. Gompertz, Von Bertalanffy, and Brody functions were adequate to establish mean growth patterns and to predict the adult BW of Nelore females. The Brody model was more accurate in predicting the birth weight of these animals and presented the best overall goodness of fit.

Key words: Bayesian analysis, beef cattle, growth curve, longitudinal data, model choice, nonlinear function

INTRODUCTION

Several studies suggest the Brody function as the most appropriate to describe beef cattle growth, because of its goodness of fit, computational simplicity, interpretability of parameters, and model convergence, even if data are missing (Bullock et al., 1993; Kaps et al., 2000; Arango and Van Vleck, 2002). However, other studies reported that other functions better fitted cattle data. DeNise and Brinks (1985) and Beltran et al. (1992) reported the Richard function as the best to fit cattle growth records. Mazzini et al. (2003) reported that Brody and Richards functions presented less convergence rate and were inadequate for the description of Hereford growth. Oliveira et al. (2000) and Santoro et al. (2005) concluded that the Von Bertalanffy and a modified logistic function, respectively, were the best to model Zebu cattle data.

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Table 1. Summary of the different data sets analyzed to compare growth functions

Item	DS4[1]	DS3[2]	DS2[3]
No. of records	21,232	25,069	28,625
No. of animals	830	1,041	1,260
No. of contemporary groups	108	119	131
No. of sires	105	137	153
No. of dams	632	768	883
No. of animals in the relationship matrix	3,014	3,552	4,079

[1]Data for females weighed at least once after 4 yr of age.
[2]Data for females weighed at least once after 3 yr of age.
[3]Data for females weighed at least once after 2 yr of age.

In most comparisons of nonlinear functions, a 2-step analysis was performed. The growth function parameters were predicted for each animal, and as a second step, environmental effects and (co)variance components were estimated. The adjustment errors from the first step were ignored, and information on relatives was not considered when the curve parameters were estimated. Also, not all information was used, and animals with few records could not be included in the analysis. Model goodness of fit is generally evaluated using the variance of fitting errors, the mean square error, and the coefficient of determination. These criteria are more influenced by adjustments at the end of the curve due to a scale effect. In the present work, these problems were avoided. Functions were compared under a nested Bayesian model that allowed estimation of the joint posterior distribution of curve parameters, (co)variance components, and environmental and genetic effects. Functions were compared using different criteria that permit comparisons of both the overall predictive ability and predictive ability at different points of the curve using cross-validation.

MATERIALS AND METHODS

Animals were raised in different commercial herds, and special conditions or treatments were not needed to collect the records. Therefore, animal care committee approval for the specific study was not required.

Data

The data set used for fitting growth curves was provided by Associação Nacional de Criadores e Pesquisadores (Ribeirão Preto, São Paulo, Brazil), which has been running the Nelore Breeding Program since 1987 (Lôbo et al., 2005). Animals from 5 different herds, all located in the southeast of Brazil, were evaluated. The animals were weighed every 90 d from birth to 540 d of age, and those remaining in the herd for reproduction continued to be weighed at 90-d intervals. Births mainly occurred in spring and summer, and the animals were weaned on average at 210 d of age. Only records from the following individuals were included in the analysis: animals reared on pasture without supplemental feeding, animals weighing at least 20 kg at birth, animals

that did not have a foster dam, animals whose BW records were within the range of the mean of all animals at the same age ± 3 SD, animals that did not receive special veterinary treatment, and animals born from cows aged 2 to 18 yr at calving and belonging to a contemporary group with at least 3 animals. The contemporary groups were defined nesting the variables: herd, management group (animals in the same pasture paddock), season and year of birth, and first or greater-parity cow.

The analysis was carried out using 3 different data files, which included data from animals that were or were not weighed close to maturity. The smallest data set (DS4) contained records from animals weighed at least once after 4 yr of age; 95% maturity is expected to be reached at this point (Garnero et al., 2005). The second data set (DS3) had records from the same animals as in the previous data set (DS4), plus data from those animals culled before 4 yr of age but that had at least 1 record after 3 yr of age. The largest data set (DS2) included records from all animals weighed at least once after 2 yr of age. Thus, model goodness of fit was evaluated in different scenarios, increasing the number of individuals that were not weighed close to maturity due to selection decisions. Because of the small number of males that met the conditions set for each data file, only females were evaluated. A summary of the data sets is shown in Table 1.

Models

A Bayesian hierarchical model as described by Varona et al. (1997), Blasco et al. (2003), and Forni et al. (2007) was employed to describe the growth curve of each animal. It was assumed that individual trajectories followed a nonlinear function, and each parameter of this function was influenced by genetic and environmental effects described in a linear model. Four nonlinear functions frequently used for the description of growth curves in beef cattle (Oliveira et al., 2000; Arango and Van Vleck, 2002) were applied in the first stage of the hierarchy: Brody, Von Bertalanffy, logistic, and Gompertz. These nonlinear functions are detailed in Table 2. The conditional distributions of data given the Brody and logistic functions are described in the Appendix. The conditional distributions of data given

Table 2. Nonlinear functions applied to describe the growth curves

Model	Function[1]
Brody (Brody, 1945)	$y_{ij} = a_i\left[1 - b_i\exp\left(-k_it_j\right)\right] + \varepsilon_{ij}$
Von Bertalanffy (Von Bertalanffy, 1957)	$y_{ij} = a_i\left[1 - b_i\exp\left(-k_it_j\right)\right]^3 + \varepsilon_{ij}$
Logistic (Nelder, 1961)	$y_{ij} = a_i\left[1 + \exp\left(-k_it_j\right)\right]^{-M_i} + \varepsilon_{ij}$
Gompertz (Laird, 1965)	$y_{ij} = a_i\exp^{\left(-b_i\right)\exp\left\{^{\left(-k_it_j\right)}\right\}} + \varepsilon_{ij}$

[1]y_{ij} represents the BW of animal i at age j; a_i, b_i, k_i, and M_i are the parameters of each animal; ε_{ij} is the fitting error.

other functions were presented in Blasco et al. (2003) and Forni et al. (2007).

Fitting errors were considered to be independent between individuals and normally distributed, and 3 different assumptions about SD of fitting errors were compared. Initially, the SD were considered constant throughout the growth trajectory. Then, linear variation until 3 yr and constancy thereafter was considered. The third assumption was that the SD of fitting errors varied following the same nonlinear function employed to describe the data, as proposed by Blasco et al. (2003).

In the second stage of the hierarchy, an animal model was employed describing the genetic and environmental effects on parameters of the growth functions. In addition to the additive genetic effects, effects of contemporary group, age of dam at calving (in years), and maternal permanent environment were included. At this stage, residual effects were also considered to be independent between individuals and normally distributed. However, in view of the biological meaning of parameters, the residual covariance between parameters of the same individual was considered to differ from zero [i.e., the residual (co)variance matrix (**R**) had a block diagonal structure].

Inference

The joint posterior distribution of growth curve parameters, (co)variance components, and environmental and genetic effects was estimated using a hierarchical Bayesian model. The prior distribution $N\left(0, A\otimes G_0\right)$ was assumed for genetic effects. Prior distributions for the nuisance parameters, (co)variance matrices, and parameters of fitting errors models were flat with limits that guaranteed proper posterior distributions. A detailed description of fully conditional distributions for hierarchical multistage models is given in Sorensen and Gianola (2002). The fully conditional posterior distributions of all unknowns of the Gompertz model were described by Blasco et al. (2003) and of the Von Bertalanffy model by Forni et al. (2007). Few modifications are required to obtain conditional distributions using

other functions, and a brief description is provided in the Appendix.

Samples of the parameter a of all functions and of the parameter b of the Brody function were drawn from normal distributions; see Eq. [6] and [7] in the Appendix. However, the conditional posterior distributions of parameter b of other functions and of parameters k and M do not have a closed form. The fully conditional posterior distribution of fitting error variance was proportional to a scaled inverted χ^2 distribution, and the distributions of the parameters of models used to describe its variation along the trajectory also do not have a closed form. The fully conditional posterior distributions of the (co)variance matrices were proportional to inverted Wishart distributions, and the conditional posterior distribution for each location parameter was a normal distribution defined by the coefficients and the right-hand side of the mixed model equations. Here, the system of mixed model equations was built considering each parameter of the growth function as a record; see Forni et al. (2007) for details.

Gibbs sampling (Casella and George, 1992; Sorensen and Gianola, 2002) was used to identify samples from known distributions, and the Metropolis-Hastings algorithm (Chib and Greenberg, 1995; Sorensen and Gianola, 2002) was applied in other cases. Normal distributions centered on the values sampled in the immediately previous iteration were used as proposal distributions. Markov chains of 550,000 samples were carried out with sampling intervals of 50. The last 10,000 samples of each chain were used to estimate the features of marginal distributions. The burn-in period was greater than that indicated by the Raftery and Lewis (1992) test. Lack of convergence in each chain was tested using the criterion of Geweke (1992) and the Gelman and Rubin (1992) test. Autocorrelations between samples and Monte Carlo errors (Geyer, 1992) of means, modes, and medians of the marginal distributions were calculated.

Goodness of Fit

Both the overall predictive power and goodness of fit at different points were evaluated using predictive densities. The observed values y_{ij} were compared with the

densities of their predictions Y_{ij}, which were obtained using all other data y_{-ij}. The estimation of the density of Y_{ij} given y_{-ij} requires the distributions of parameters in the absence of y_{ij}. Estimation of such distributions would be computationally infeasible, because it would require repeating the sampling process of the growth curve parameters and their (co)variance components to predict each data point. Therefore, the predictive densities were estimated using the importance sampling procedure described by Gelman et al. (1995). The sampling distribution used was the same as that detailed by Forni et al. (2007).

Overall goodness of fit was evaluated using different criteria. Maximum likelihood principles of model comparison invariably lead to choosing the greatest possible dimension. Thus, criteria belonging to the family of penalized maximum likelihood methods were applied. These criteria are based on the recommendation of choosing the model for which the likelihood of the data minus a penalty for the model dimension obtains the maximum value. An easy-to-compute penalized maximum likelihood criterion often employed in statistics is the Akaike information criterion (**AIC**) proposed in Akaike (1974). The argument underlying the AIC is that if 2 models favor the data equally well, the more parsimonious should be chosen. Such evidence can be reached through minimizing the expression:

$$\text{AIC} = -2\left\{\log\left[\text{p}\left(\mathbf{y} \mid \boldsymbol{\theta}_i, M_i\right)\right]\right\} + 2k_i, \qquad [1]$$

where $\boldsymbol{\theta}_i$ stands for the parameters and k_i for the dimensions of the ith model (M_i).

Studying the asymptotic behavior of the Bayesian estimators under a special class of priors, Schwarz (1978) proposed the Bayesian information criterion (**BIC**). In a general statistical context, BIC recommends choosing the model that maximizes the expression:

$$\text{BIC} = \log\left[\text{p}\left(\mathbf{y} \mid \boldsymbol{\theta}_i, M_i\right)\right] - \frac{1}{2}k_i \log\left(n\right). \qquad [2]$$

The BIC differs from AIC only in the fact that the dimension is multiplied by 0.5 log(n); this implies that the former leans more toward lower dimensional models, and for large numbers of observations, the procedures differ markedly from each other, as noted by Schwarz (1978). Because models were compared within a Markov chain Monte Carlo framework, the distribution of the data conditionally to the posterior means of the parameters given a model, $\left[\text{p}\left(y \mid \hat{\theta}_i, M_i\right)\right]$, was used to compute the BIC and AIC. It is important to note that these criteria are valid large-sample criteria beyond the Bayesian context, because they do not depend on the prior distributions.

The models were also compared using strictly Bayesian measures of fit. Considering the problem of compar-

ing complex hierarchical models in which the number of parameters is not clearly defined, Spiegelhalter et al. (2002) proposed the deviance information criterion (**DIC**) for comparing models:

$$\text{DIC} = 2\bar{\text{D}} - \text{D}\left(\bar{\theta}_i\right), \qquad [3a]$$

where

$$\bar{\text{D}} = -2\int \log\left[\text{p}\left(y \mid \theta_i, M_i\right)\right] \text{p}\left(\theta_i \mid y, M_i\right) d\theta_i, \qquad [3b]$$

and

$$\text{D}\left(\bar{\theta}_i\right) = -2\log\left[\text{p}\left(y \mid \hat{\theta}_i, M_i\right)\right]. \qquad [3c]$$

The authors defined a measure for the effective number of parameters in a model as the difference between the posterior mean of the deviance [3b] and the deviance at the posterior means of the parameters of interest [3c]. Models with a smaller DIC should be favored, because this indicates a better fit and a smaller degree of complexity.

The goodness of fit at different points along the growth curve was compared using the check function (g) proposed by Gelfand et al. (1992), with g = 1 if $Y_{ij} < y_{ij}$ and g = 0 if $Y_{ij} \geq y_{ij}$. The expected value $\text{E}(\text{g} \mid y_{-ij})$ was calculated for each observation and indicated the probability of a predicted value being greater or lesser than the observed one. The expectations calculated for all individuals with a record at a given point j indicated the goodness of fit at this point. The closer the mean in each point is to 0.5, the better the fit. Values greater than 0.5 indicated a greater probability of obtaining predictions less than the observed values, whereas means less than 0.5 indicated a greater probability of obtaining predictions greater than the true value. Therefore, this check function allowed an evaluation of goodness of fit at different points along the growth curve in a probabilistic setting. The mean of the probabilities at all points of the trajectory was also accounted as an overall fit criterion. Details about the implementation of the Gelfand's check function were described in Forni et al. (2007).

RESULTS AND DISCUSSION

Although the letters used to represent the parameters are the same in all functions, they do not have the same mathematical meaning. Comparisons of estimates from different functions might be wrong. Biological associations are possible: a represents the asymptotic BW and is the only parameter comparable across models, b is a parameter related to the initial conditions, k is related to the maturation rate, and M determines the point when the acceleration phase of growth ends. The posterior means of adult BW (parameter a) ranged

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Table 3. Posterior means and SD of Nelore asymptotic BW (kg) considering SD of fitting errors constant (cst), increasing linearly until 3 yr of age (lin), or following a nonlinear function (exp)

	Asymptotic BW (kg)					
	DS4[1]		DS3[2]		DS2[3]	
Model	Means	SD	Means	SD	Means	SD
Gompertz (cst)	544.84	34.21	550.84	60.07	542.35	39.60
Gompertz (lin)	537.07	39.44	532.75	41.92	532.52	43.07
Gompertz (exp)	541.49	41.02	538.81	44.09	531.78	43.26
Von Bertalanffy (cst)	552.57	44.20	564.37	61.04	551.61	41.76
Von Bertalanffy (lin)	542.23	39.58	539.18	42.09	540.09	43.81
Von Bertalanffy (exp)	541.18	39.50	538.96	42.01	539.49	45.31
Brody (cst)	580.52	46.29	583.25	38.56	586.89	47.15
Brody (lin)	562.47	44.35	562.16	47.17	565.22	56.34
Brody (exp)	560.66	44.92	560.49	48.55	564.64	55.75
Logistic (cst)	548.63	42.36	541.23	42.50	542.36	49.65
Logistic (lin)	532.47	38.71	527.30	41.78	526.56	42.88
Logistic (exp)	535.80	40.32	531.84	46.61	532.17	44.88

[1]Data for females weighed at least once after 4 yr of age.

[2]Data for females weighed at least once after 3 yr of age.

[3]Data for females weighed at least once after 2 yr of age.

from 531.78 to 586.89 kg (Table 3). The estimates were greater than those found in the literature for Nelore cattle (Carrijo and Duarte, 1999; Garnero et al., 2005; Santoro et al., 2005). However, in most studies, parameter convergence was achieved for a markedly smaller number of animals than that evaluated here, and BW records were limited to 18 or 24 mo of age. Thus, most estimates of adult BW presented in the literature can be considered extrapolations. Only Garnero et al. (2005) reported estimates of parameter *a* obtained for a data set of Nelore females weighed after 2 yr of age. Their estimates are similar to those obtained in the present study, ranging from 501.11 to 552.77 kg, although they are not adjusted for genetic and environmental effects.

The differences between our estimates and those from other studies can also be due to differences in populations sampled. Rosa et al. (2000) evaluated the adult BW of Nelore cows considering BW obtained in autumn and winter from animals with a minimum age of 3.5 yr and reported mature BW ranging from 330 to 585 kg, with a mean of 485 kg. Extracting from the present data set the records of animals with a minimum age of 3.5 yr, the BW ranged from 384 to 762 kg (mean of 539.03 kg).

Comparisons of asymptotic BW obtained with different functions using the same fitting error model showed that the Brody model provided greater estimates. These results are similar to those reported by Oliveira et al. (2000) and Garnero et al. (2005) in studies on growth of Zebu females. Considering the same growth function, greater adult BW were estimated when the fitting error variance was considered constant along the trajectory. According to Varona et al. (1997), different approaches to model the growth curve fitting error variance can result in differences in parameter estimates. Here, highly similar estimates of adult BW were obtained using either linear or exponential models to describe the vari-

ance of fitting errors. The differences between adult BW estimates obtained in different data sets reflect both the amount of information provided by the data and selection effects. Culling is the main reason for not having mature BW records in DS2 and DS3. Thus, different functions can work differently to predict adult BW in light of selection.

Table 4 presents estimates from the overall goodness-of-fit criteria in the different data sets. The Gelfand's function means indicated closely similar fits for all functions. Differences in AIC greater than 2 indicate differences in goodness of fit, according to Burnham and Anderson (1998). Both AIC and BIC indicated that goodness of fit improved when the fitting error variance was not considered to be constant along the trajectory. Also, differences favoring exponential models against the linear model were observed with all growth functions apart from the Gompertz. Mazzini et al. (2003), studying growth curves of Hereford cattle, also reported better fit of growth functions when heterogeneity in fitting error variance was assumed.

Differences between growth functions were not observed when the fitting error SD were considered constant along the curve. Numerous studies comparing nonlinear functions to describe cattle growth assumed homogeneous fitting error variance and did not report differences between models (Oliveira et al., 2000; Behr et al., 2001; Mazzini et al., 2003; Garnero et al., 2005). Here, the disadvantage of increasing the number of parameters to account for heterogeneity of fitting error variance was overcome by better overall fit. The Brody function with the same exponential model describing fitting error SD presented decreased values of AIC and BIC than the other functions for all data sets. According to these criteria, more accurate predictions can be expected applying the Brody function. Similar results were reported by Garnero et al. (2005).

Table 4. Akaike information criterion (AIC), Bayesian information criterion (BIC), means of Gelfand's check function (G), and deviance information criterion (DIC) of different nonlinear functions considering SD of fitting errors constant (cst), increasing linearly until 3 yr of age (lin), or following a nonlinear function (exp)

Item	AIC	BIC	DIC	G
DS4[1]				
Gompertz (cst)	226,831	−113,870	228,661	0.4974
Gompertz (lin)	199,652	−100,301	203,023	0.4967
Gompertz (exp)	200,922	−100,956	204,352	0.4963
Von Bertalanffy (cst)	226,582	−113,744	228,534	0.4981
Von Bertalanffy (lin)	214,449	−107,699	184,452	0.4965
Von Bertalanffy (exp)	197,971	−99,481	201,525	0.4978
Brody (cst)	226,604	−113,756	227,878	0.4946
Brody (lin)	214,768	−107,987	179,076	0.5005
Brody (exp)	192,738	−96,864	195,935	0.4974
Logistic (cst)	226,989	−114,039	228,923	0.4911
Logistic (lin)	214,441	−107,695	204,979	0.4979
Logistic (exp)	205,394	−101,394	210,345	0.4975
DS3[2]				
Gompertz (cst)	264,529	−132,726	267,154	0.4953
Gompertz (lin)	234,578	−117,772	238,789	0.4964
Gompertz (exp)	236,115	−118,561	240,258	0.4957
Von Bertalanffy (cst)	264,427	−132,717	266,483	0.4961
Von Bertalanffy (lin)	249,449	−125,207	219,277	0.4961
Von Bertalanffy (exp)	234,642	−116,894	236,695	0.4971
Brody (cst)	265,532	−132,792	264,641	0.4983
Brody (lin)	244,044	−122,620	214,124	0.5003
Brody (exp)	225,920	−112,989	230,145	0.4977
Logistic (cst)	265,889	−132,849	267,385	0.4894
Logistic (lin)	255,957	−124,986	244,876	0.4974
Logistic (exp)	240,867	−119,063	250,044	0.4968
DS2[3]				
Gompertz (cst)	298,920	−149,928	302,057	0.4964
Gompertz (lin)	266,684	−133,370	271,576	0.4957
Gompertz (exp)	266,720	−133,390	271,660	0.4973
Von Bertalanffy (cst)	298,882	−149,468	301,654	0.4971
Von Bertalanffy (lin)	281,325	−140,691	251,436	0.4957
Von Bertalanffy (exp)	264,280	−132,170	269,164	0.4964
Brody (cst)	300,015	−150,035	299,654	0.4983
Brody (lin)	274,184	−137,120	245,944	0.4995
Brody (exp)	256,396	−128,228	261,270	0.4979
Logistic (cst)	300,888	−150,983	302,334	0.4896
Logistic (lin)	283,044	−141,550	260,410	0.4967
Logistic (exp)	270,870	−135,987	282,435	0.4963

[1]Data for females weighed at least once after 4 yr of age.
[2]Data for females weighed at least once after 3 yr of age.
[3]Data for females weighed at least once after 2 yr of age.

Spiegelhalter et al. (2002) suggested that models differing in up to 2 units of DIC can be considered similar, whereas differences of 3 to 7 units indicate less evidence of similar fit. These differences represent variations on a logarithmic scale; therefore, even small numbers are associated with large values of deviance. Estimates of DIC indicated a better fit of functions when fitting error variance was considered to be heterogeneous. In contrast to AIC and BIC, differences favoring the linear model over the exponential models were observed, except for the Gompertz function. Akaike information criterion and BIC penalize more parameterized models purely based on a fixed number of parameters; the penalty imposed by DIC depends on prior information about the parameters and the information provided by the data. The different functions presented a similar fit when the SD of the fitting error was considered to be constant. On the other hand, differences between functions were observed when assuming linear or exponential variation. The Brody function represented the data better, whereas the worst fit was obtained with the logistic function in all data sets.

The mean values obtained from Gelfand's check function for the 3 data sets are shown in Figures 1, 2, and 3. All growth functions presented similar prediction patterns at the same stages of growth. They under- or overestimated the BW to a greater or lesser extent. All functions provided less accurate predictions at the beginning of the growth curve, and predictions were more accurate after 48 mo of age. The Brody function provided more accurate estimates of birth weights; this was also observed by Garnero et al. (2005). The probability of overestimating birth weights was greater with other functions than with the Brody function. The greatest
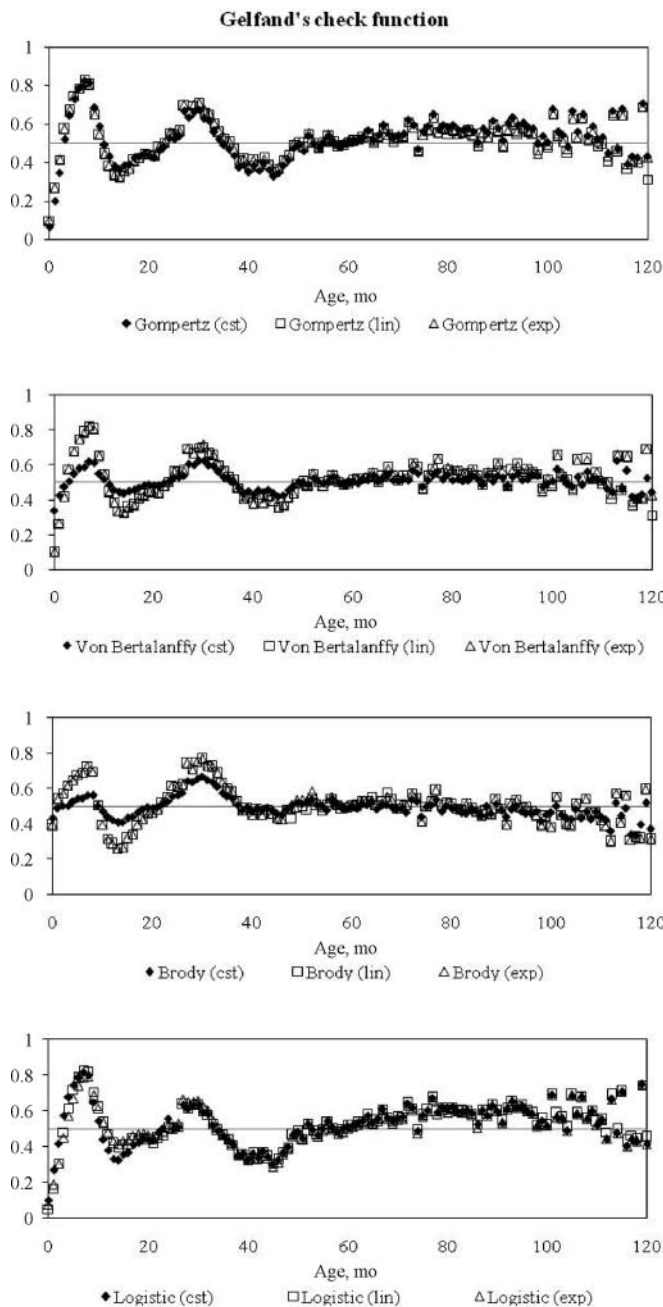
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Figure 1. Mean expectations of Gelfand's check function analyzing data for females weighed at least once after 4 yr of age with different nonlinear models, considering SD of fitting errors constant (cst), increasing linearly until 3 yr of age (lin), or following a nonlinear function (exp).

Figure 2. Mean expectations of Gelfand's check function analyzing data for females weighed at least once after 3 yr of age with different nonlinear models, considering SD of fitting errors constant (cst), increasing linearly until 3 yr of age (lin), or following a nonlinear function (exp).

probabilities were observed using the logistic function. These results support the hypothesis that cattle are more mature at birth compared with other species, as if they had already passed the phase of growth acceleration (Arango and Van Vleck, 2002). Hence, a non-sigmoidal function would be more adequate to describe the growth in this species.

The different models showed a high probability of over- or underestimating BW until about 48 mo of age. Afterward, the check function expectations remained closer to 0.5. The poor fit during the initial phase of growth was not surprising, because of the wider rela-
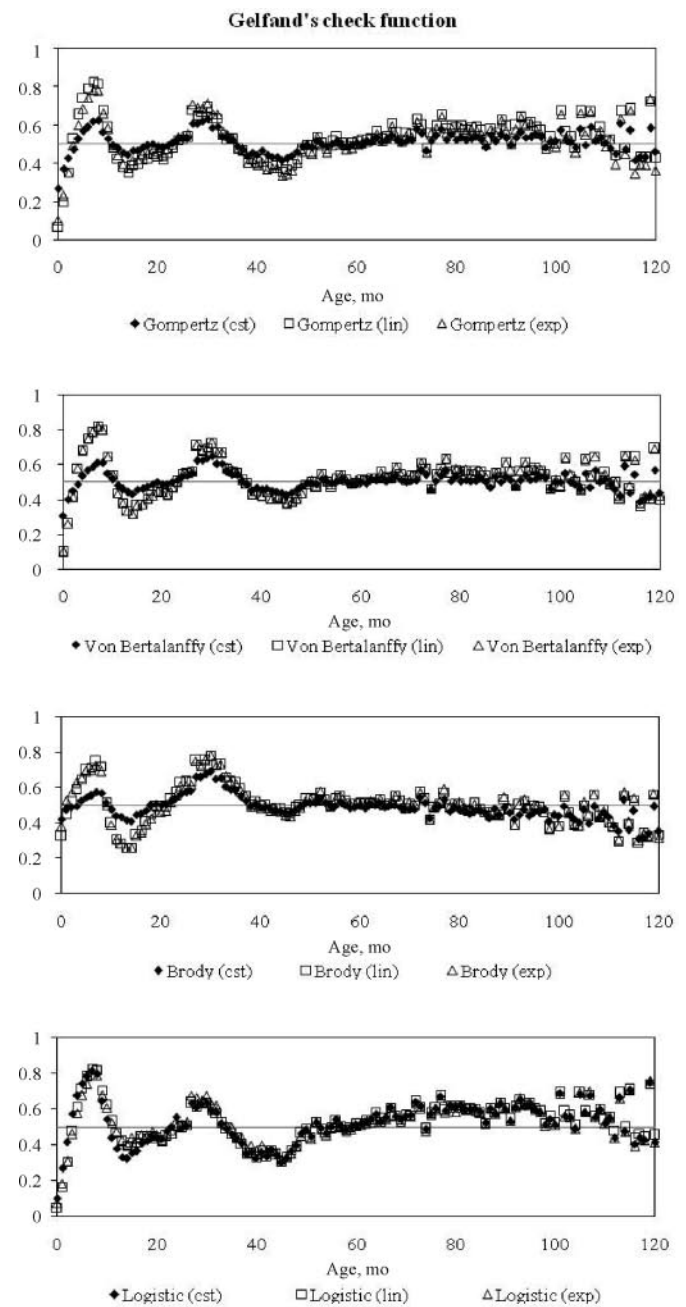
tive variation of records at the beginning of the growth curves. Before maturity, the models presented alternating good and poor performance. However, models in which the fitting error variance was considered to be constant provided more accurate predictions of initial BW. The models used to describe the fitting error did not adequately represent the variance of this parameter at the beginning of the curve. This lack of fit was not observed in the analysis of the overall fitting criteria, which are more influenced by the predictive power in the final part of the curve due to a scale effect. The analysis of the Gelfand's check function demonstrated
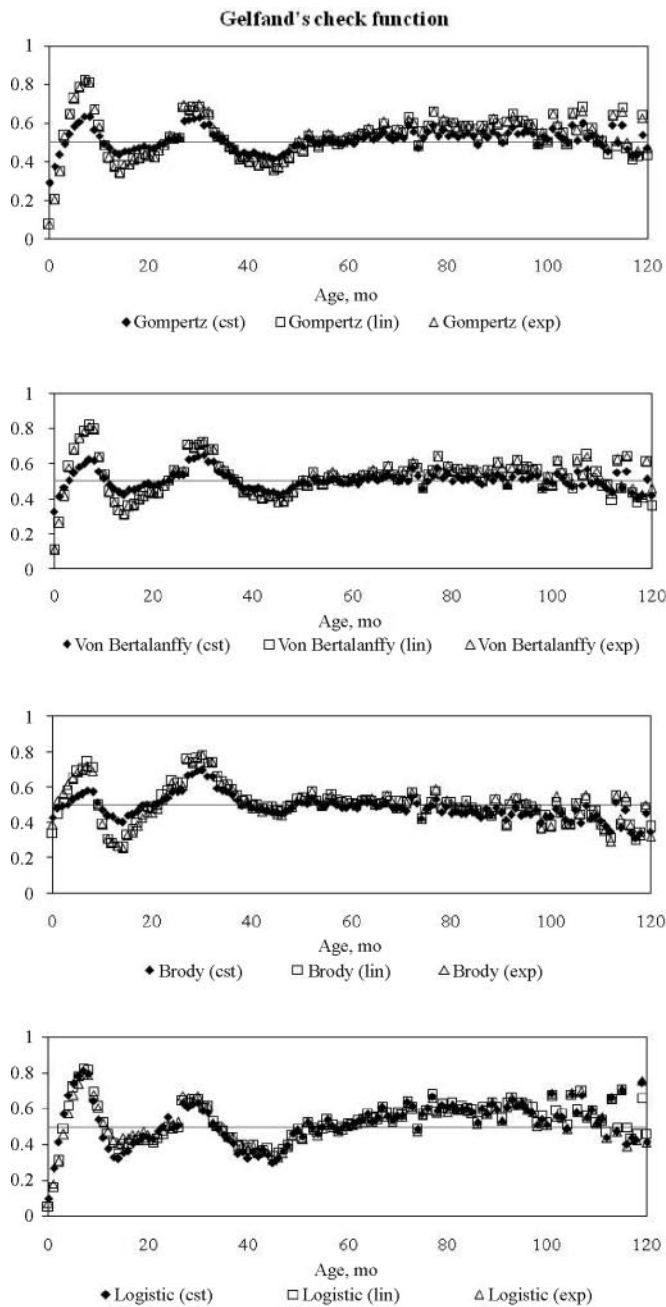
Figure 3. Mean expectations of Gelfand's check function analyzing data for females weighed at least once after 2 yr of age with different nonlinear models, considering SD of fitting errors constant (cst), increasing linearly until 3 yr of age (lin), or following a nonlinear function (exp).

that it is possible to detect pointed errors and choose a function based on the goodness of fit at different parts of the growth curve. Usually, Nelore animals are slaughtered close to 36 mo of age. Until this point, none of the models presented clear advantages against others.

High probabilities of predicting BW correctly after 4 yr of age were observed using all functions. The expectations between 48 and 100 mo of age ranged from 0.48 to 0.56. The greatest discrepancy in values from 0.5 was observed with the logistic function, which showed a marked tendency to underestimate BW after 60 mo of age (Figures 1, 2, and 3).

Gompertz, Von Bertalanffy, and Brody functions accurately predicted adult BW, and biologically unacceptable estimates were not observed. Models that correctly describe the increase in fitting error variance at the beginning of the growth curve require further studies. Albuquerque and Meyer (2001), in a phenotypic analysis of growth data from Nelore animals up to 630 d of age, found that a linear logarithmic function provided a better fit of error variance than the assumption of homogeneity. Mazzini et al. (2003) reported a better fit of nonlinear functions to growth data of Hereford cattle by weighting records by their inverse variance in classes of 40 d of age.

Optimum size for beef cattle has been debated among researchers and breeders. Selection programs have placed emphasis on growth, favoring faster growing animals, but also have led to an increase in mature size that may not necessarily be advantageous. Beef cattle have a low rate of reproduction and high maternal cost per animal slaughtered. Mature BW, predicted by parameter a of growth curves, could be included in selection indexes with its corresponding economic value. This parameter could be accurately predicted by combining individual BW with information derived from relatives in hierarchical models.

The Gompertz, Von Bertalanffy, and Brody functions are all adequate to establish mean growth patterns and to predict the adult BW of Nelore females. The Brody model is more accurate in predicting the birth weight of these animals and has better overall fit. The prediction of adult BW using nonlinear functions can be accurate when growth curve parameters and their (co)variance components are estimated jointly. The hierarchical model used in the present study can be applied to the prediction of mature BW in herds where a portion of the animals are culled before they reach adult age.

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APPENDIX

Assuming independence among individuals, the conditional distribution of data $\mathbf{y}$, given the curve parameters, is a product of normal distributions. Considering the Brody function:

$$f\left(\mathbf{y} \mid \boldsymbol{\theta}, \sigma_\varepsilon^2\right) = \prod_{i=1}^{N} \prod_{j=1}^{n_i} \frac{1}{\sqrt{2\pi}\sigma_\varepsilon}$$
$$\exp\left\{\frac{-\left[y_{ij} - a_i\left(1 - b_i \exp{-k_i t_j}\right)\right]^2}{2\sigma_\varepsilon^2}\right\}, \quad [4a]$$

and considering the logistic function:

$$f\left(\mathbf{y} \mid \boldsymbol{\theta}, \sigma_\varepsilon^2\right) = \prod_{i=1}^{N} \prod_{j=1}^{n_i} \frac{1}{\sqrt{2\pi}\sigma_\varepsilon}$$
$$\exp\left\{\frac{-\left[y_{ij} - a_i\left(1 + \exp{-k_i t_j}\right)^{-M_i}\right]^2}{2\sigma_\varepsilon^2}\right\}, \quad [4b]$$

where $\boldsymbol{\theta}$ represents the vector with the growth function parameters, σ_ε^2 is the fitting error variance, N is the number of individuals with data, and n_i is the number of BW recorded on each individual i.

The density of the growth curve parameters, given the genetic and environmental effects, is a multivariate normal distribution:

$$f(\theta \mid \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}) =$$
$$\left|\mathbf{R}\right|^{-N/2} \exp\left[-\frac{1}{2}\left(\boldsymbol{\theta} - \mathbf{X}\boldsymbol{\beta} - \mathbf{Z}\mathbf{u} - \mathbf{W}\mathbf{c}\right)^{`} \left(\mathbf{R} \otimes \mathbf{I}\right)^{-1}\left(\boldsymbol{\theta} - \mathbf{X}\boldsymbol{\beta} - \mathbf{Z}\mathbf{u} - \mathbf{W}\mathbf{c}\right)\right], \quad [5]$$

where $\boldsymbol{\beta}$ represents the systematic effects; $\mathbf{u}$ is the vector of additive genetic effects; $\mathbf{G}$ is the genetic (co)variance matrix; $\mathbf{c}$ is the vector of maternal permanent environmental effects; $\mathbf{P}$ is the maternal effects (co)variance matrix; $\mathbf{R}$ is the residual (co)variance matrix; $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are incidence matrices; and $\mathbf{I}$ is an identity matrix.

The fully conditional distributions of growth function parameters are products of the likelihood [4] and the prior distribution [5]. Supposing $\bar{a}_i$, $\bar{b}_i$, $\bar{k}_i$, and $\bar{M}_i$ are the means of parameters given the genetic and environmental effects and r^{aa}, r^{bb}, r^{kk}, r^{MM}, r^{ab}, r^{ak}, r^{aM}, r^{bk}, and r^{kM} are elements of the inverse of the residual (co)variance matrix ($\mathbf{R}$), the fully conditional distribution of parameter a in the Brody function can be written as:

$$f\left(a_i \mid b_i, k_i, \ \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}, \sigma_\varepsilon^2, \mathbf{y}\right)$$
$$\propto f\left(a_i \mid b_i, \ k_i, \sigma_\varepsilon^2, \ \mathbf{y}_i\right) f\left(a_i \mid b_i, \ k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right),$$

where

$$f\left(a_i \mid b_i, k_i, \sigma_\varepsilon^2, \mathbf{y}_i\right)$$

$$\sim \mathrm{N}\left(\frac{\sum_{j=1}^{n_i}\left\{y_{ij}\left[1 - b_i \exp(-k_i t_{ij})\right]\right\}}{\sum_{j=1}^{n_i}\left[1 - b_i \exp(-k_i t_{ij})\right]^2}, \frac{\sigma_\varepsilon^2}{\sum_{j=1}^{n_i}\left[1 - b_i \exp(-k_i t_{ij})\right]^2}\right),$$

$$[6a]$$

and

$$f\left(a_i \mid b_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right)$$
$$\sim \mathrm{N}\left[\bar{a}_i - (b_i - \bar{b}_i)\frac{r^{ab}}{r^{aa}} - (k_i - \bar{k}_i)\frac{r^{ak}}{r^{aa}}, \frac{1}{r^{aa}}\right]. \qquad [6b]$$

The fully conditional distribution of parameter b is:

$$f\left(b_i \mid a_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}, \sigma_\varepsilon^2, \mathbf{y}\right)$$
$$\propto f\left(b_i \mid a_i, k_i, \sigma_\varepsilon^2, \mathbf{y}_i\right) f\left(b_i \mid a_i, k_i, \mathbf{b}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right),$$

where

$$f\left(b_i \mid a_i, k_i, \sigma_\varepsilon^2, \mathbf{y}_i\right)$$

$$\sim \mathrm{N}\left(\frac{\sum_{j=1}^{n_i}\left\{-\left[y_{ij} - a_i\right]\left[a_i \exp(-k_i t_{ij})\right]\right\}}{\sum_{j=1}^{n_i}\left[-a_i \exp(-k_i t_{ij})\right]^2}, \frac{\sigma_\varepsilon^2}{\sum_{j=1}^{n_i}\left[-a_i \exp(-k_i t_{ij})\right]^2}\right),$$

$$[7a]$$

and

$$f\left(b_i \mid a_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right)$$
$$\sim \mathrm{N}\left[\bar{b}_i - (a_i - \bar{a}_i)\frac{r^{ab}}{r^{bb}} - (k_i - \bar{k}_i)\frac{r^{bk}}{r^{bb}}, \frac{1}{r^{bb}}\right]. \qquad [7b]$$

The fully conditional distribution of parameter k is:

$$f\left(k_i \mid a_i, b_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}, \sigma_\varepsilon^2, \mathbf{y}\right)$$
$$\propto f\left(k_i \mid a_i, b_i, \sigma_\varepsilon^2, \mathbf{y}_i\right) f\left(k_i \mid a_i, b_i, \mathbf{b}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right),$$

where

$$f\left(k_i \mid b_i, k_i, \sigma_\varepsilon^2, \mathbf{y}_i\right)$$

$$\propto \prod_{j=1}^{n_i} \exp\left(-\frac{\left\{y_{ij} - a_i\left[1 - b_i \exp(-k_i t_{ij})\right]\right\}^2}{2\sigma_\varepsilon^2}\right), \qquad [8a]$$

and

$$f\left(k_i \mid a_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right)$$
$$\sim \mathrm{N}\left[\bar{k}_i - (a_i - \bar{a}_i)\frac{r^{ak}}{r^{kk}} - (b_i - \bar{b}_i)\frac{r^{bk}}{r^{kk}}, \frac{1}{r^{kk}}\right]. \qquad [8b]$$

The fully conditional distribution of parameter a in the logistic function is:

$$f\left(a_i \mid k_i, M_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}, \sigma_\varepsilon^2, \mathbf{y}\right)$$
$$\propto f\left(a_i \mid k_i, M_i, \sigma_\varepsilon^2, \mathbf{y}_i\right) f\left(a_i \mid k_i, M_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right),$$

where

$$f\left(a_i \mid k_i, M_i, \sigma_\varepsilon^2, \mathbf{y}_i\right)$$

$$\sim \mathrm{N}\left(\frac{\sum_{j=1}^{n_i} y_{ij}\left[1 + \exp(-k_i t_{ij})\right]^{-M_i}}{\sum_{j=1}^{n_i}\left\{\left[1 + \exp(-k_i t_{ij})\right]^{-M_i}\right\}^2}, \frac{\sigma_\varepsilon^2}{\sum_{j=1}^{n_i}\left\{\left[1 + \exp(-k_i t_{ij})\right]^{-M_i}\right\}^2}\right),$$

$$[9a]$$

and

$$f\left(a_i \mid k_i, M_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right)$$
$$\sim \mathrm{N}\left[\bar{a}_i - \left(k_i - \bar{k}_i\right)\frac{r^{ak}}{r^{aa}} - \left(M_i - \bar{M}_i\right)\frac{r^{aM}}{r_{aa}}, \frac{1}{r^{aa}}\right]. \qquad [9b]$$

Finally, the fully conditional distribution of parameter M is:

$$f\left(M_i \mid a_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \ \mathbf{R}, \sigma_\varepsilon^2, \mathbf{y}\right)$$
$$\propto f\left(M_i \mid a_i, k_i, \sigma_\varepsilon^2, \mathbf{y}_i\right) f\left(M_i \mid a_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right),$$

where

$$f\left(M_i \mid a_i, k_i, \sigma_\varepsilon^2, \mathbf{y}_i\right)$$

$$\propto \prod_{j=1}^{n_i} \exp\left(-\frac{\left\{y_{ij} - a_i\left[1 + \exp(-k_i t_{ij})\right]^{-M_i}\right\}^2}{2\sigma_\varepsilon^2}\right), \quad [10a]$$

and

$$f\left(M_i \mid a_i, k_i, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{c}, \mathbf{P}, \mathbf{R}\right)$$

$$\sim \mathrm{N}\left[\bar{M}_i - \left(a_i - \bar{a}_i\right)\frac{r^{aM}}{r^{MM}} - \left(k_i - \bar{k}_i\right)\frac{r^{kM}}{r^{MM}}, \frac{1}{r^{MM}}\right]. \quad [10b]$$

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