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Growth curves of meat-producing mammals by von Bertalanffy's model

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Abstract – The objective of this work was to evaluate how the parameterization and the application of different allometric values affect the obtention of the most adequate fit of von Bertalanffy's model, in the description of the growth curve of meat-producing mammals (bovine, pigs, rabbits, and sheep). Among the nonlinear models, von Bertalanffy's has been very often applied in several areas, with different parameterizations. This model has been commonly used with an allometric value of m = 2/3; however, for mammals, it is believed that this value can be m = 3/4. The analyzed data referring to the mass of meat-producing mammals according to their age were obtained from research institutions and from the literature. The results showed that von Bertalanffy's model, with the allometric value of m = 3/4 and the used parameterization, provided better adjustments to quality evaluators. Besides, the model softened the overestimation of parameter a, giving a direct interpretation of parameter b, with the lowest values for curvature measurements, mainly for the parametric ones, and provided more reliable adjustments. Von Bertalanffy's model can be used in the description of the growth curves of meat-producing mammals.

Index terms: allometry, modeling, nonlinear model, parameterization, regression.

Curvas de crescimento de mamíferos produtores de carne pelo modelo de von Bertalanffy

Resumo – O objetivo desde trabalho foi avaliar como a parametrização e a aplicação de diferentes valores alométricos afetam a obtenção do ajuste mais adequado do modelo de von Bertalanffy, na descrição da curva de crescimento de mamíferos produtores de carne (bovinos, porcos, coelhos e ovelhas). Entre os modelos não lineares, o de von Bertalanffy tem sido frequentemente aplicado em diversas áreas, com diferentes parametrizações. Em geral, esse modelo tem sido utilizado com um valor alométrico de m = 2/3; no entanto, para mamíferos, acredita-se que o valor possa ser m = 3/4. Os dados analisados quanto à massa dos mamíferos de corte de acordo com a sua idade foram obtidos de instituições de pesquisa e da literatura. Os resultados mostraram que o modelo de von Bertalanffy, com o valor alométrico de m = 3/4 e com a parametrização utilizada, forneceu melhores ajustes aos avaliadores de qualidade. Além disso, o modelo suavizou a superestimativa do parâmetro a, o que possibilitou interpretação direta ao parâmetro b, com menores valores das medidas de curvatura, principalmente as paramétricas, e forneceu ajustes mais confiáveis. O modelo de von Bertalanffy pode ser utilizado na descrição da curva de crescimento de mamíferos produtores de carne.

Termos para indexação: alometria, modelagem, modelo não linear, parametrização, regressão.

Introduction

The demand for meat-producing animals increases with the augment of population. These animals are frequently subject to researches that seek to optimize and to understand the productive process. Among the most studied meat-producing animals are the mammals because of their great economic and nutritional importance. According to IBGE (2018), in the second quarter of 2018, the production of cattle and pigs increased, in comparison to the same quarter of the previous year, which confirms the growth in the sector.

The study of growth curves of these animals by nonlinear models is very attractive, as they are flexible and summarize the characteristics of the species development in a few parameters with biological interpretation. In practice, this knowledge allows of the adoption of strategies to enhance or mitigate certain characteristics of the animals under study (Freitas, 2005; Cassiano & Sáfadi, 2015; Souza et al., 2017).

Curves of animal mass growth over time are shaped in S, which is also known as sigmoid or sigmoidal curves (von Bertalanffy, 1957). Several authors have reaffirmed that the body growth of most animal species can be described by a sigmoid curve and, therefore, fit by nonlinear models which are widely used for a large number of regression applications (Freitas, 2005; Silva et al., 2011; Carneiro et al., 2014; Teleken et al., 2017; Rodrigues et al., 2018).

Animal development is related to metabolic rate, which directly influences mass, shape, size, and other body traits (von Bertalanffy, 1957). These body variations of an individual throughout their ontogeny can be measured by allometry, using an allometric coefficient "m" (Freitas & Carregaro, 2013).

Allometry provides a quantitative description of the relationship between a part and the whole, and it is important for aggregating all information into a single value. For animal growth, there is a set of theories in the literature that suggest the value m = 2/3, and others that suggest m = 3/4; however, there is no consensus on this measurement (Shi et al., 2014). In his study, von Bertalanffy (1957) states that the allometric value m = 2/3 is suitable for the growth of fish and crustaceans, and suggests m = 3/4 for mammal growth.

Among the nonlinear models most used in the literature, that proposed by von Bertalanffy (1957) has a great applicability, and is one of the most suitable for describing the growth of several animal breeds, especially in situations in which growth is not symmetrical in relation to the inflection point. However, the most commonly used parameterization does not have a direct interpretation for all parameters, which may confuse the authors, making the use of nonlinear regression more complicated.

The application of a reparameterization can facilitate the interpretations of the model, mainly for people who work in the practice. The use of reparameterization is common in nonlinear regression models, so that the parameters are rearranged to show interpretations more convenient with the study area in question (Zeviani et al., 2012; Fernandes et al., 2015).

The objective of this work was to evaluate how the parameterization of von Bertalanffy's model and the application of different allometric values affect the obtention of the most adequate fit of von Bertalanffy's model, for the description of the growth curve of meat-producing mammals (bovine, pigs, rabbits, and sheep).

Materials and Methods

Data on mass according to age of meat-producing mammals were obtained from research institutions and the literature, and are described as follows for bovine, rabbits, sheep and pigs.

For bovine animals, mass data (kg) were obtained for Angus breed cattle of the period 2013–2017 from the Santa Éster farm of Casa Branca Agropastoril Ltda., located in the municipality of Silvianópolis, in the state of Minas Gerais, Brazil. The method of cross-data collection was used, recording the body mass of 203 Angus males from the birth up to 46.5 months of age.

For rabbits, data on the mass (g) of 10 males and females of the breed New Zealand were collected in the second half of 2016, obtained by weighing from the 38^{th} day of birth to the 100^{th} day, in Instituto Federal Goiano (IFG), in the municipality of Rio Verde, in the state of Goiás, Brazil.

Sheep data on mass (kg) were collected in the report by Falcão et al. (2015) on 31 males of Ile de France breed, confined from the birth to the slaughter, at 120 days of age.

Pig data on mass (kg) were collected from the study by Oliveira et al. (2007) on males of the

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progeny Camborough 22 and AGPIC 412 TG, in good management and nutrition.

The rate of change of the animal mass as a function of time can be expressed by the following differential equation:

$$\frac{dP}{dt} = \alpha P^m + \beta P^n,$$

in which: P represents the mass of the animal as a function of time t; α and β are constants of anabolism and catabolism, respectively; and m and n are exponents that indicate the last proportional values to some potency of the body mass P (von Bertalanffy, 1957). Also, according to this author, by means of physiological facts, the exponent n equal to 1 can be used without any considerable loss.

Then, by substituting n = 1 and developing the differential equation, the general model is obtained as follows:

$$P(t) = P_\infty \left\{ 1 + \left[\left(\left(\frac{P_0}{P_\infty} \right)^{1-m} - 1 \right) \exp\left(-\beta(1-m)t\right) \right] \right\}^{\frac{1}{1-m}}$$

With this generalization, we have that P(t) is the mass of the animal as a function of time t; β is the catabolism constant; m is the allometric value; P_0 is the initial mass; and P_∞ is the the asymptotic mass of the animal, obtained by $P_\infty = \lim_{t\to\infty} P(t)$.

The allometric coefficient m is directly related to the development pattern of the animal, and the correct use of this value allows of better estimates for the study on the growth curves. However, there is much discussion in the literature on the value of the more adequate metabolic rate, or allometric coefficient, to describe the body growth. There are theories suggesting the value m = 2/3, and others suggesting m = 3/4; however, the authors have not yet reached a consensus (West et al., 2002; Ohnishi et al., 2014).

Developing the general model gives the following expression:

$$y_i = a\left\{1 + \left[(m-1)\exp\left(-k(x_i - b)\right)\right]\right\}^{\frac{1}{1-m}}$$

in which:

$$a = P_\infty = \lim_{t\to\infty} P(t);\ k = \beta(1-m),\ \text{and}\ b = \left[\frac{\ln\left(\frac{m-1}{\frac{P_0}{P_\infty}^{1-m} - 1}\right)}{\beta(1-m)}\right]$$

The model of von Bertalanffy shows three parametrizations, for i = 1, 2, ..., t, in which: y_i is the i^th observation of the dependent variable; x_i is the i^th observation of the independent variable; a is the asymptotic value, that is, the expected value for the maximum growth of the object under study, where $x_i \rightarrow \infty$; b is associated with the abscissa of the inflection point; is an index of maturity, or precocity, and is associated with growth, and the greater its value, the lesser the time necessary for the object under study to reach the asymptotic value a; ε_j is the random error associated with the i^th observation, which is assumed to be independent and identically distributed, following a normal distribution of zero mean and constant variance, that is, $\varepsilon_i \sim N(0, I\,\sigma^2)$ (Table 1).

Model 1 shows the parameterization of the model of von Bertalanffy, usually found in the literature, for the fitting of growth curves with the allometric value of m = 2/3. Although it is widely used, this parameterization does not provide a direct interpretation for parameter b, and the abscissa of the inflection point is given by transformation 1/k × ln(3b). That is, in this parameterization the estimate of b is not directly the abscissa of the inflection point.

Model 2 still considers the allometric value m = 2/3; however, it is a reparameterization of model 1, so that parameter b has a direct interpretation as the abscissa of the inflection point.

Model 3 uses the allometric value of von Bertalanffy (1957), and West et al. (2002) state that it is the allometry

Table 1. Parameterizations of von Bertalanffy's model (1957).

Model 1	$y_i = a \times (1 - b \times \exp(-kx_i) + \varepsilon_i$
Model 2	$y_i = a \times \left(1 - \frac{\exp\left(k \times (b - x_i)\right)}{3}\right)^3 + \varepsilon_i$
Model 3	$y_i = a \times \left(1 - \frac{\exp\left(k \times (b - x_i)\right)}{4}\right)^4 + \varepsilon_i$

Equation terms: x_i is the i^th observation of the independent variable; a is the asymptotic value, that is, the expected value for the maximum growth of the object under study; b is associated with the abscissa of the inflection point; k is an index of maturity or precocity; ε_i is the random error associated with the i^th observation.

suitable for the description of mammalian growth m = 3/4; in this parameterization, all parameters have a direct and practical interpretation similar to Model 2.

The parameters of all models were estimated for the description of growth curves of the four meat-producing mammals, in each of the three parameterizations studied (Table 1). The estimates of these parameters were obtained by the iterative method of Gauss-Newton implemented in the *nls( )* function of the software R (R Core Team, 2017). The significance of the parameters ($\theta_i \neq 0$) was checked by the t-test, at 5% probability. Initially, all assumptions about the errors (ε) were considered as met. From the error vector of this fit, the analysis of residuals was performed based on statistical tests. The statistical tests of Shapiro-Wilk, Durbin-Watson and Breusch-Pagan were applied to check normality, independence, and residual homoscedasticity, respectively. If any of the assumptions were not met, the deviation were corrected or incorporated into the parameter estimation process.

In order to evaluate the fit quality of the models, the nonlinearity of Bates and Watts curvatures, described by Souza et al. (2010), were obtained using the *rms×curv( )* function of the R software. Concomitantly to the nonlinearity measures, the quality evaluators – coefficient of determination (R^2) and corrected Akaike's information criterion (AICc) – were used as follows:

$$R^2 = 1 - \frac{SSR}{SST} \text{ and } AICc = AIC + \left(\frac{2p(p+1)}{n-p-1}\right),$$

in which: SSR is the square sum of residuals; SST is the total square sum; n is the sample size; p is the number of parameters; and AIC is the Akaike's information criterion (below)

$$AIC = n\ln\left(\frac{SQR}{n}\right) + 2p$$

in which: ln is the natural logarithm operator. These evaluators were obtained using the functions *Rsq()* and *AICc()* of the AICcmodavg package, in the software R.

Results and Discussion

At first, the parameters of the three models were estimated for each mammalian species (Table 1) and the residuals were analyzed with the Shapiro-Wilk (SW), Breusch-Pagan (BP) and Durbin-Watson (DW) tests, considering 5% significance level.

It was observed that the tests were nonsignificant for all mammals, except for pig data. For the other species this fact indicates that there are no problems of violation of residual assumptions, and that the residuals showed normality, constant variances, evidencing that they were independent.

For the pig data, the DW test was significant, indicating that the residuals showed dependence, so a new fit was made by the generalized least squares method, incorporating into the model a first order autoregressive parameter (ϕ) [AR(1)]. This was made because, according to Nascimento et al. (2011) and Muniz et al. (2017), it is necessary to model this autocorrelation, and to incorporate it into the model, to obtain adjustments that produce more accurate predictions, and that allow of the analysis of measured series in few temporal observations, thus guaranteeing a greater precision in the estimates and a better quality of fit.

Based on the fit of the three parameterizations of von Bertalanffy's model, all parameters were significant, by the t-test, at 5% probability (Table 2).

The practical interpretation of the parameters is very important for the understanding of growth studies (Freitas, 2005). Based on the estimates of parameter a by the models (Table 2), it is possible to observe that the mass estimations by Model 3 were more consistent with the real values, whose maximum observed were 599.5 kg (bovines), 154.8 kg (pigs), 2,258.3 g (rabbits), and 36.9 kg (sheep).

Models 1 and 2 overestimated the final mass of the meat-producing mammals, as verified by Silva et al. (2011) in the study on cows, Falcão et al. (2015) in the study on sheep, and Jacob et al. (2015) in the study on rabbits, using the model of von Bertalanffy.

Therefore, it can be concluded that Model 3 provided a minimization of overestimation of parameter a, and also showed a smaller amplitude of the standard error.

Lopes et al. (2016) state that, for bovine growth, Brody's model was the one that most approached the adult mass, observed with the estimate of parameter a. However, Silva et al. (2011) and Santana et al. (2016) showed that, in addition to the Brody's model, that of von Bertalanffy also showed adequate results to describe cattle growth curves. Thus, the relationship between the asymptotic estimation of the model and the real values is explicit, and models that overestimate the adult mass are usually discarded in practice.

In the parameterization used in Model 1, which is one of the most found in the literature, b is a location parameter that maintains the sigmoidal shape of the model, and is associated with the abscissa of the inflection point of the curve, but it has not a direct, practical interpretation (Silveira et al., 2011; Teixeira Neto et al., 2016). However, some authors, such as Mischan & Pinho (2014) and Louzada et al. (2014), present mathematical transformations which can find the abscissa value of the inflection point, through the estimation of Model 1.

Thus, a great advantage of the parameterization of Models 2 and 3 is related to parameter b, since its estimates are interpreted directly as the abscissa of the inflection point, that is, it indicates the age at which the growth of the animal slows down. For instance, for pigs, it is expected that up to approximately 121 days their growth will be more accentuated and, after this period, it will decrease until stabilization (Table 2).

According to Teleken et al. (2017), von Bertalanffy's model was the most suitable, among others, for the description of the growth of New Zealand rabbits. Jacob et al. (2015) also state that this model described well the growth of rabbits of the Soviet Chinchilla and White Giant breeds, however, their estimates overestimated the asymptotic parameter, and did not give a direct interpretation for parameter b.

Values of the coefficient of determination (R^2) were higher than 0.99, indicating a satisfactory fit. Regarding the corrected Akaike's information criterion (AICc), Model 3 showed smaller values, and the lower AICc value suggests that the model is the most adequate to describe the data. Therefore, the goodness-of-fit shows the superiority of Model 3 to describe the growth curve of meat-producing mammals (Table 3).

The measures of intrinsic (C^l) and parametric ($C^θ$) nonlinearity for each parameterization of the model are also presented (Table 3). As commented by Souza et al. (2010), Zeviani et al. (2012), and Fernandes et al. (2015), lower-nonlinearity values of measures indicate a better fit of the models, since more reliable estimates are obtained.

The present study shows that the values of the intrinsic curvature (C^l) remain practically constant in the three parameterizations, for all scenarios, and only for pigs it has a more pronounced decrease for Model 3. This change in the measure of intrinsic nonlinearity may be a result of the change in the allometric value, since it did not change for Models 2 and 3.

The parametric nonlinearity measure changes, according to the parameterization and the allometric

Table 2. Estimates with standard error (SE) for the parameters of the three forms of von Bertalanffy's model[1] (1957), in the description of growth curve of meat-producing mammals.

Mammal	Parameter[2]	Model 1	SE	Model 2	SE	Model 3	SE
Bovine	a	658.20	(25.52)	658.20	(25.52)	652.60	(24.02)
	b	0.5978	(0.0365)	6.605	(0.5433)	7.127	(0.5504)
	k	0.0884	(0.0092)	0.0884	(0.0092)	0.0935	(0.0094)
Rabbit	a	2588.00	(68.07)	2588.00	(68.07)	2561.00	(64.26)
	b	1.252	(0.0934)	40.20	(0.4919)	41.34	(0.5102)
	k	0.03291	(0.0019)	0.03291	(0.0019)	0.0346	(0.002)
Sheep	a	47.9336	(2.6283)	47.9336	(2.6283)	46.6372	(2.294)
	b	0.5485	(0.0117)	32.2988	(2.7776)	34.157	(2.6287)
	k	0.0154	(0.0013)	0.0154	(0.0013)	0.0167	(0.0013)
Pig	a	259.0049	(13.9763)	259.0049	(13.9763)	242.9691	(10.4726)
	b	0.9264	(0.0311)	121.0277	(5.0752)	121.0709	(4.0281)
	k	0.0084	(0.0005)	0.0084	(0.0005)	0.0096	(0.0005)
	ϕ	0.9425	-	0.9425	-	0.9396	-

[1]Model 1, von Bertalanffy's model with m = 2/3, without direct interpretation of b; Model 2, von Bertalanffy's model with m = 2/3, with direct interpretation of b; Model 3, von Bertalanffy's model with m = 3/4, with direct interpretation of b. [2]Parameters: a is the asymptotic value, that is, the expected value for the maximum growth of the object under study; b is associated with the abscissa of the inflection point; k is the index of maturity or precocity; ϕ is a first-order autoregressive parameter.

value used (Table 3), provided worse results for Model 1, and better results for Model 3. This fact evidenced that for the description of growth characteristics of the group of animals under study, the parameterization and the value of m = 3/4 of great importance to obtain better fits.

In practice, it is common to neglect the models with a practical or biological interpretation for parameter b, as in the studies of Silva et al. (2011), Silveira et al. (2011), Cassiano & Sáfadi (2015), Jacob et al. (2015), and Rodrigues et al. (2018). Nevertheless, if the parameterization of Model 3 is used, considering the correct allometry, a better fit can be achieved in these studies.

For all meat-producing species, it is possible to identify the sigmoidal shape in the development of the animals (Figure 1); however, this shape is more remarkable in the data of pigs, as they show a greater number of mass measurements in the study interval.

In the graphical adjustment, the three parameterizations (Figure 1) did not change practically. It is noticed that the adjustment lines for the three

Tabela 3. Goodness-of-fit test for the three parameterizations of von Bertalanffy's model (1957), in the description of the growth curves of meat-producing mammals.

Mammal	Criteria(1)	Model 1	Model 2	Model 3
Bovine	R^2	0.9938	0.9938	0.9938
	AICc	93.4718	93.4718	93.3386
	C^{ι}	0.1106	0.1106	0.1109
	C^{θ}	0.9623	0.8797	0.8141
Rabbit	R^2	0.9974	0.9974	0.9974
	AICc	121.8681	121.8681	121.8064
	C^{ι}	0.0284	0.0284	0.0284
	C^{θ}	0.8958	0.6756	0.6030
Sheep	R^2	0.9978	0.9978	0.9979
	AICc	31.1405	31.1405	30.6398
	C^{ι}	0.0445	0.0445	0.0446
	C^{θ}	2.0296	1.4957	1.2771
Pig	R^2	0.9978	0.9979	0.9984
	AICc	74.5154	73.5078	67.8611
	C^{ι}	0.0402	0.0402	0.0301
	C^{θ}	1.7030	0.9408	0.6432

(1)R^2, coefficient of determination; AICc, corrected Akaike's information criterion; C^{ι} measurement of intrinsic nonlinearity; and C^{θ} measurement of parametric nonlinearity.

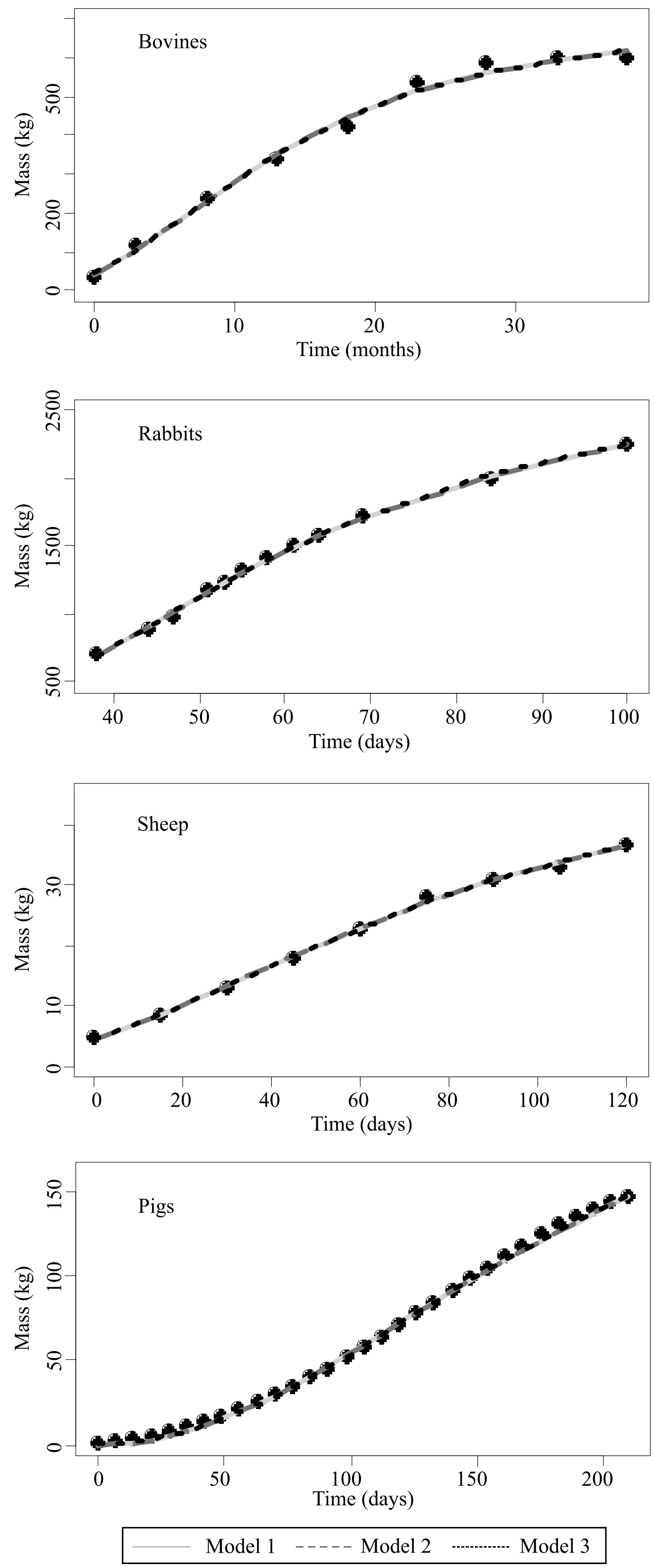

Figure 1. Adjustment of the three parameterizations of von Bertalanffy's (1957) models in the description of the growth curves of meat-producing mammals.

forms of von Bertalanffy's model are overlapped, therefore, in the present study, the graphical analysis of the models was not taken into account to select the best model. The fact evidenced the superiority of Model 3 for R^2 and AICc, and the considerable reduction of the parametric nonlinearity, therefore making the parameter estimates more reliable.

Conclusions

1. The most adequate data of meat-producing mammals (bovines, pigs, rabbits, and sheep) are the allometric value of m = 3/4, as well as the results in lower values of the corrected Akaike's information criterion and higher values of the coefficient of determination.
2. Model 3 of von Bertalanffy minimizes the overestimation of parameter a, and its parameterization gives a direct interpretation for parameter b, besides the lowest values for curvature measurements, mainly the parametric ones, providing more reliable adjustments; therefore, this model can be used in the description of the growth curve of meat-producing mammals.

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