

http://www.uem.br/acta ISSN printed: 1806-2636 ISSN on-line: 1807-8672

Doi: 10.4025/actascianimsci.v39i1.31366

# Comparing non-linear mathematical models to describe growth of different animals

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**ABSTRACT.** The main objective of this study was to compare the goodness of fit of five non-linear growth models, i.e. Brody, Gompertz, Logistic, Richards and von Bertalanffy in different animals. It also aimed to evaluate the influence of the shape parameter on the growth curve. To accomplish this task, published growth data of 14 different groups of animals were used and four goodness of fit statistics were adopted: coefficient of determination ( $R^2$ ), root mean square error (RMSE), Akaike information criterion (AIC) and Bayesian information criterion (BIC). In general, the Richards growth equation provided better fits to experimental data than the other models. However, for some animals, different models exhibited better performance. It was obtained a possible interpretation for the shape parameter, in such a way that can provide useful insights to predict animal growth behavior.

Keywords: body weight gain, Richards model, goodness of fit.

# Avaliação comparativa de modelos matemáticos não lineares para descrever o crescimento animal

**RESUMO.** O principal objetivo deste estudo foi comparar a qualidade do ajuste de cinco modelos matemáticos recorrentemente utilizados na literatura para a descrição do ganho de peso animal. Ele também teve o objetivo de estudar a influência do parâmetro de forma sobre as curvas de crescimento. Os modelos de Brody, Gompertz, Logístico, von Bertalanffy e Richards, foram ajustados a dados experimentais de 14 grupos de animais diferentes. Como critério de qualidade de ajuste quatro índices estatísticos foram adotados: coeficiente de determinação ( $R^2$ ), raiz do quadrado médio do erro (RMSE) e os critérios de informação, Akaike (AIC) e Bayesian (BIC). Em geral, o modelo de Richards forneceu os melhores ajustes aos dados experimentais comparados aos demais modelos. No entanto, para alguns animais, diferentes modelos exibiram melhor desempenho. Foi possível obter uma possível interpretação para o significado do parâmetro de modo a fornecer ferramentas úteis para prever o comportamento do crescimento animal.

Palavras-chave: ganho de peso animal, modelo de Richards, qualidade de ajuste.

#### Introduction

Traditionally, mathematical models have been applied to describe growth-age relationship in animals. One important feature of these models is their ability to describe the weight gain and evaluate some interesting biological parameters, such as the mature weight, the rate of maturing and the rate of gain. These parameters are useful tools to provide estimates of the daily feed requirements or to evaluate the influence of the environmental conditions on the weight gain of the animal. Growth models are also used to predict the optimum slaughter age. Therefore, mathematical models applied for animal growth can be considered as being important control and optimization instruments for the animal production (France &

Thornley, 1984; France, Dijkstra, & Dhanoa, 1996; López et al., 2000; Vázquez, Lorenzo, Fuciños, & Franco, 2012).

An appropriate growth function should summarize the information provided experimental observations into a small set of parameters with biological meaning. Usually, these models consist of nonlinear functions and several studies including different mathematical models can be found in the literature. These models are usually applied for the evaluation of the growth kinetics of a wide range of animals, including birds (Aggrey, 2002; Sezer & Tarhan, 2005; Nahashon, Aggrey, Adefope, Amenyenu, & Wright, 2006), mammals (Curi, Nunes, & Curi, 1985; Silva, Alencar, Freitas, Packer, & Mourão, 2011; Franco et al., 2011), fishes

(Hernandez-Llamas & Ratkowsky, 2004; Santos, Mareco, & Silva, 2013), reptiles (Bardsley, Ackerman, Bukhari, Deeming, & Ferguson, 1995) and amphibians (Rodrigues et al., 2007; Mansano, Stéfani, Pereira, & Macente, 2013). Some mathematical functions commonly used in these studies include the Gompertz, Logistic, Brody, von Bertalanffy and Richards growth models (France et al., 1996).

The growth functions can be grouped into three main categories: those with a diminishing returns behavior (Brody model), those with sigmoidal shape and a fixed inflection point (Gompertz, Logistic and von Bertalanffy models) and those with a flexible inflection point (Richards model). The Logistic, Gompertz and von Bertalanffy models exhibit inflection points at about 50, 37 and 30% of the mature weight (asymptote), respectively. On the other hand, the Brody model does not exhibit an inflection point. The Richards model summarizes all the above growth functions in one function with a variable inflection point specified by the shape parameter (*m*) (Richards, 1959).

In this context, the aim of this study was to evaluate the influence of the shape parameter on growth curves and the five above mentioned models using experimental data of different animals, including mammals and birds, in order to identify the best growth model for each animal studied. The performance of the different models was compared using different goodness of fit statistics.

#### Material and methods

#### **Experimental data**

Growth data recorded for fourteen different datasets, all of them reported in the literature, were used for evaluation of the models. The raw growth data were collected from published articles by means of the GetData Graph Digitizer 2.24 software, as used by Vázquez, Lorenzo, Fuciños, and Franco (2012). The datasets are representative of the gain of body weight of mammals and birds (Table 1), with mature weights ranging from < 0.25 kg (Japanese quail) to > 1,000 kg (Holstein-Friesian bull). As usually adopted in similar studies, growth curves were based on means of weights of many individuals in order to minimize large variations that may occur in individual growth (López et al., 2000; Vázquez et al., 2012).

**Table 1.** Data sets used in this study to evaluate five different growth models.

Data set	Source			
	Calo, Mcdowell, Vanvleck, and Miller, 1973			
Holstein-Friesian bull <sup>a</sup>	Table 1. Means and standard deviations for body weight, growth rates and degree of maturity of Holstein-Friesian bulls from 6			
	months to 8 years of age.			
	Silva, Alencar, Freitas, Packer, and Mourão, 2011			
Nelore cow <sup>b</sup>	Figure 1. A) Estimation of weights based on age of Nelore females, observed and estimated by the models of Brody and von Bertalanffy.			
	Beltrán, Butts, Olson, and Koger, 1992			
Angus cow <sup>b</sup>	Figure 1. Growth curves of Lines A and K estimated with Brody model. Line least squares means for weight at fixed ages are used as reference for goodness of fit.			
Celta pig <sup>b</sup>	Franco et al., 2011			
(male and female)	Figure 2. Growth curve for males and females of the variety Barcina slaughtered at 14 months.  Goliomytis, Orfanos, Panopoulou, and Rogdakis, 2006			
Karagouniko sheep <sup>b</sup> (male and female)	Figure 1. Growth curve and absolute growth rate for body weight of the Karagouniko male sheep: estimate growth curve; observed mean; estimated absolute growth rate.			
	Figure 2. Growth curve and absolute growth rate for body weight of the Karagouniko female sheep: estimate growth curve; observed mean; estimated absolute growth rate.			
Beetal goat <sup>a</sup>	Waheed, Khan, Ali, and Sarwar, 2011			
(male and female)	Table 1. Means (kg) and standard deviations (SD) of growth traits of Beetal goats.			
,	Curi, Nunes, and Curi, 1985			
New Zealand rabbit <sup>a</sup>	Table 2. Body weight of Norkfolk rabbit.			
Californian rabbit <sup>a</sup> Norfolk rabbit <sup>a</sup>	Table 3. Body weight of Californian rabbit.			
NOTIOIK PADDIT	Table 4. Body weight of New Zealand rabbit.			
Athens-Canadian chicken <sup>a</sup>	Aggrey, 2002			
(male and female)	Table 1. Means and standard deviations for body weight at different ages in Athens-Canadian random-bred chickens.			
Guinea fowl <sup>a</sup>	Nahashon, Aggrey, Adefope, Amenyenu, and Wright, 2006			
(male and female)	Table 2. Means and standard for body weight at different ages in a random-bred pearl guinea fowl population.			
Japanese quail - white line <sup>a</sup>				
(male and female)				
Japanese quail - brown line <sup>a</sup>	Sezer and Tarhan, 2005			
(male and female) Japanese quail – wild line <sup>a</sup> (male and female)	Table 1. The results of statistical analyses for body weight of Japanese quail lines at different age (means ± standard errors).			

Experimental data reported in the literature; Experimental data taken from published figures by means of GetData Graph Digitizer 2.24.

#### Mathematical models

Five nonlinear functions frequently used for the description of growth curves in animal production studies were analyzed: Brody, von Bertalanffy, Logistic, Gompertz, and Richards. mathematical expressions associated to these functions are detailed in Table 2. In all equations presented, W stands for the body weight of the animal at age t,  $W_{\infty}$  stands for the mature weight (asymptote) and  $W_0$  stands for the birth weight. The parameter k is a constant that is directly related to the postnatal rate of maturing and can be interpreted as a maturing index, establishing the rate at which W approaches  $W_{\infty}$ . Finally, m is the shape parameter in Richards' model. It determines the proportion of the mature weight at which the inflection point occurs (Perroto, Cue, & Lee, 1992; Gbangboche, Glelekakai, Salifou, Albuquerque, & Leroy, 2008).

Table 2. Equations used to model the animal growth data.

Model	Equation	
Brody	$W(t) = W_{\infty} \left[ 1 + \left[ \left( \frac{W_0}{W_{\infty}} \right) - 1 \right] \exp(-kt) \right]$	(1)
von Bertalanffy	$W(t) = W_{\infty} \left[ 1 + \left[ \left( \frac{W_0}{W_{\infty}} \right)^{1/3} - 1 \right] \exp\left( -kt \right) \right]^3$	(2)
Logistic	$W(t) = \frac{W_{\infty}}{1 + \left[ \left( \frac{W_{\infty}}{W_0} \right) - 1 \right] \exp(-kt)}$	(3)
Gompertz	$W(t) = W_{\infty} \exp \left[ \ln \left( \frac{W_0}{W_{\infty}} \right) \exp \left( -kt \right) \right]$	(4)
Richards	$W(t) = \frac{W_{\infty} \cdot W_0}{\left[W_0^m + \left(W_{\infty}^m - W_0^m\right) \exp(-kt)\right]^{\frac{1}{m}}}$ for $m \neq 0$	(5)

Richards' model is a generalization of all growth models presented in Table 2, i.e., for m = -1, m = -1/3 and m = 1, it reduces to re-parameterized versions of Brody, von Bertalanffy and Logistic equations, respectively. In addition, it can be shown that it reduces to Gompertz model when one calculates  $\lim_{t \to 0} W(t)$ . The parameter m is the unique

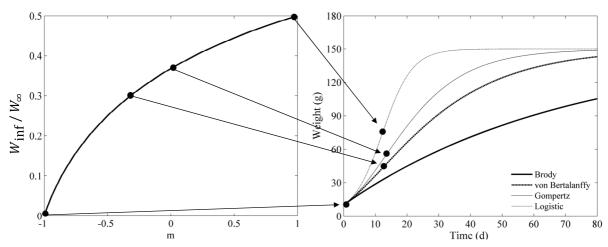
parameter which has no direct biological meaning. However, it exerts great influence on the time to an individual to reach the mature weight and on the point of inflection of the growth curve, as will be shown in the next section.

#### Influence of the shape parameter (m) on growth curves

As previously mentioned, Richards growth model encompasses all the other models, for special values of the parameter m. In order to illustrate this important feature, it is adopted a procedure to present a possible meaning to this parameter. After some algebra, it is possible to obtain a mathematical expression describing the influence of the parameter m on the relation of the weight at the inflection point  $(W_{inf})$  to the asymptotic mature weight  $(W_m)$  in equation 6:

$$\frac{W_{\text{inf}}}{W_{\infty}} = \frac{1}{\left(1 + m\right)^m} \tag{6}$$

Figure 1 presents simulations obtained with the use of equation 6 for different values of the parameter m. In all simulations performed, the values of  $W_0$  and  $W_{\infty}$  adopted were kept constant and equal to 10 g, and 150 g, respectively, and the values of k adopted were  $-0.0142 \, \mathrm{d}^{-1}$  for Brody,  $-0.0445 \, \mathrm{d}^{-1}$  for von Bertalanffy,  $-0.0739 \, \mathrm{d}^{-1}$  for Gompertz and  $-0.2143 \, \mathrm{d}^{-1}$  for Logistic model. The parameter m is the main responsible for the different shapes of the curves.



**Figure 1.** The influence of the parameter m on the inflection point of each growth curve: Brody (m = -1), von Bertalanffy (m = -1/3), Gompertz (m = 0), and Logistic (m = 1). The dots indicate the inflection points obtained for each growth model.

The weight at the inflection point is of significance because it is associated with a change in the acceleration of growth: for values of the weight lower than  $W_{\rm inf}$ , the acceleration of growth is positive and for values the weight higher than  $W_{\rm inf}$  the acceleration of growth is negative. Thus, depending on the value of m, the time to the individual reaches the mature weight is lower, as observed for the Brody growth model.

#### **Numerical method**

The fitting procedures presented in this study were performed with the 'fit function' of the Curve Fitting Tool available in the Matlab R2011a software (MathWorks, Natick, USA), using the nonlinear least squares method. The starting value of each parameter model was based on visual inspection of the plots.

#### Statistical criteria for model selection

The performance of each model was evaluated by the calculation of the root mean square error, RMSE (Equation 7), and by the coefficient of determination,  $R^2$  (Equation 8). In these expressions,  $W_{\rm exp}$  stands for the experimental data,  $W_{\rm cal}$  stands for the result fitted by the model, N represents the total number of experimental points, and K corresponds to the number of parameters of the model.

$$RMSE = \sqrt{\frac{1}{N - K} \sum_{n=1}^{N} \left[ W_{\exp}(n) - W_{cal}(n) \right]^{2}}$$
 (7)

$$R^{2} = 1 - \frac{\sum_{n=1}^{N} \left[ W_{\text{exp}}(n) - W_{cal}(n) \right]^{2}}{\sum_{n=1}^{N} \left[ W_{\text{exp}}(n) - \frac{1}{N} \sum_{n=1}^{N} W_{\text{exp}}(n) \right]^{2}}$$
(8)

In order to obtain a more complete evaluation of the performance of the models, two additional criteria based on the information theory were applied to compare the goodness of fit of the models (Burnham & Anderson, 2002): the Akaike information criterion (*AIC*) and the Bayesian information criterion (*BIC*). Equations 9 and 10 present the corresponding mathematical expressions wherein *SSE* is the sum of the squared errors.

$$AIC = N\log(SSE/N) + 2K \tag{9}$$

$$BIC = N\log(SSE/N) + K\log(N)$$
(10)

For the case in that the sample size is smaller than the number of model parameters (N/K < 40),

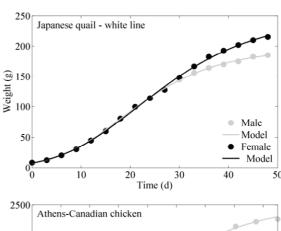
the AIC might not be accurate. Therefore the corrected AIC (AIC, in Equation 11) was used in the present study (Burnham & Anderson, 2002):

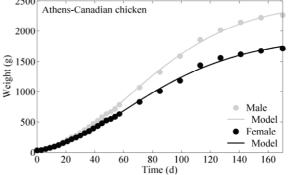
$$AIC_{c} = AIC + \frac{2K(K+1)}{N - K - 1} \tag{11}$$

#### Results and discussion

### Fit with the use of Richards growth model

The growth curves obtained from regression analyses using Richards' model are presented in Figure 2 for birds and in Figure 3 for mammals. Table 3 shows the values of the parameter *m* estimated from regression and the value of the proportion of the mature weight at which the inflection point occurs (Equation 6) for each growth curve studied.





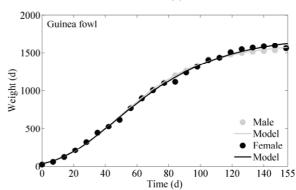


Figure 2. Birds growth kinetics fitted to the Richards' model.

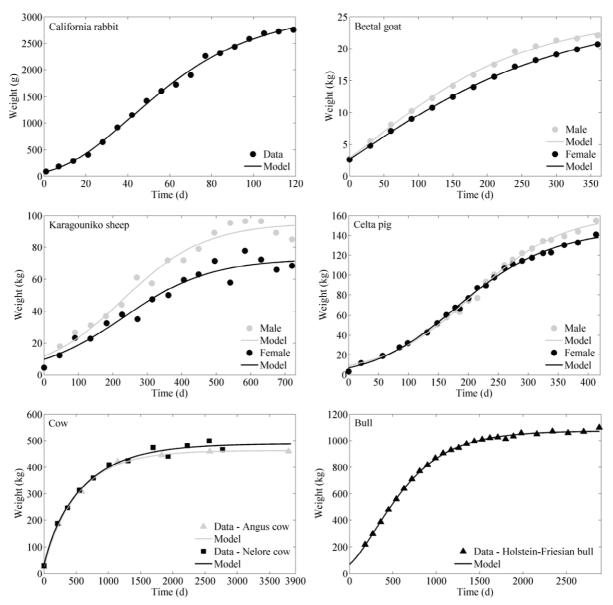


Figure 3. Mammals growth kinetics fitted to the Richards' model.

**Table 3.** Values of the parameter m estimated from regression analyses of Richards model and the relatives values of  $W_{\inf}/W_{\infty}$  estimated from Equation 6.

Animal	$m\left(W_{\mathrm{inf}} / W_{\infty}\right)$			
	Male	Female		
Athens-Canadian chicken	0.0541 (37.76%)	-0.0220 (36.38%)		
Guinea fowl	0.0798 (38.21%)	-0.0760 (35.34%)		
Japanese quail – White line	0.3549 (42.49%)	0.2321 (40.69%)		
Japanese quail – Brown line	0.6151 (45.87%)	0.1761 (39.81%)		
Japanese quail – Wild line	0.2321 (40.69%)	0.2342 (40.72%)		
Beetal goat	-0.5030 (24.91%)	-0.7070 (17.61%)		
Karagouniko sheep	0.9436 (49.45%)	0.9642 (49.64%)		
Celta pig	1.0184 (50.18%)	0.5275 (44.79%)		
Norfolk rabbit	-0.2130 (32.48%)			
Californian rabbit	-0.0640(35.58%)			
New Zeland rabbit	-0.1960 (32.85%)			
Holstein-Friesian Bull	-0.2230 (32. 26%)			
Nelore cattle	-1.2780 (no inflection point)			
Angus cattle	-1.1070 (no inflection point)			

As summarized in Table 3, all regression analysis of the Richards' model resulted in values of the parameter *m* lower or equal to one. This means that, for the animals studied, the inflection point at each growth curve is lower than 50% of the mature weight. In addition, it was observed that the value of *m* was lower than minus one only for two datasets (Nelore cattle and Angus cattle). This result seems to indicate that the Brody's model is not feasible for most datasets studied.

It was also observed that the values of m were, in general, lower for females than for males (with the exception of Japanese quail – wild line and Karagouniko sheep). Therefore it can be assumed that, for most datasets studied, the males reached the mature weight before the females. In addition,

according to Table 3, it can be seen that Karagouniko sheep and celta pigs reach the mature weight faster than the others.

#### Comparison between models

Tables 4, 5 and 6 summarize the goodness of fit statistics obtained for the five models studied. It was observed that for birds (Table 4), the Richards' and Logistic models provided the best fits. On the other hand, in what concerns mammals, different models provided best fits for different datasets. In this case, it was not possible to establish a model as being superior in relation to the others.

**Table 4.** Goodness of fit statistics obtained from the growth models applied to the experimental data set of birds. Equations with the best goodness of fit are represented in bold.

Growth models (Male) Growth models (Female)				
Animal Growth models (Male) Growth models (Female)  Eq.(1) Eq.(2) Eq.(3) Eq.(4) Eq.(5) Eq.(1) Eq.(2) Eq.(3) Eq.(4) Eq.(5)  Athers-Canadian chicken				
Athens-Canadian chicken				
$R^2$ 0.98600.99830.9964 <b>0.9993</b> 0.99930.98790.99760.9950 <b>0.9982</b> 0.9982				
RMSE 91.11 31.62 45.98 <b>20.76</b> 20.95 63.44 27.99 40.77 <b>24.12</b> 24.61				
BIC 112.7086.96296.066 <b>76.727</b> 77.903103.8983.99593.144 <b>80.389</b> 81.820				
<i>AIC</i> <sub>c</sub> 115.3589.62098.725 <b>79.385</b> 81.853106.5586.65495.802 <b>83.048</b> 85.770				
Guinea fowl				
$R^2$ 0.98410.99820.9967 <b>0.9991</b> 0.99920.98690.99770.9945 <b>0.9980</b> 0.9981				
RMSE 72.48 24.16 32.99 <b>16.85</b> 16.98 66.88 28.07 43.10 <b>25.83</b> 26.32				
BIC 88.25966.31072.536 <b>59.110</b> 60.12486.65469.30977.876 <b>67.650</b> 68.869				
<i>AIC</i> <sub>c</sub> 91.43769.48875.714 <b>62.288</b> 64.89989.83272.48781.054 <b>70.828</b> 73.644				
Japanese quail – White line				
$R^2$ 0.98400.99740.99860.9991 <b>0.9996</b> 0.98860.99790.99800.9990 <b>0.9992</b>				
RMSE 8.701 3.527 2.596 2.046 <b>1.391</b> 8.482 3.64 3.596 2.515 <b>2.364</b>				
BIC 34.20320.87116.34212.828 <b>7.816</b> 33.82721.33721.15415.880 <b>15.646</b>				
<i>AIC</i> <sub>c</sub> 38.35825.02520.49716.983 <b>14.227</b> 37.98125.49225.30920.035 <b>22.058</b>				
Japanese quail – Brown line				
$R^2$ 0.98140.99610.99940.9984 <b>0.9997</b> 0.98700.99790.9975 <b>0.9987</b> 0.9988				
RMSE 8.957 4.120 1.667 2.636 <b>1.233</b> 8.867 3.603 3.870 <b>2.817</b> 2.818				
BIC 34.63123.163 9.804 16.573 <b>6.038</b> 34.48221.18522.241 <b>17.548</b> 18.238				
<i>AIC</i> <sub>c</sub> 38.78527.31813.95920.727 <b>12.449</b> 38.63725.34026.396 <b>21.703</b> 24.650				
Japanese quail – Wild line				
$R^2$ 0.98860.99790.99800.9990 <b>0.9992</b> 0.98810.99650.9966 <b>0.9975</b> 0.9976				
RMSE 8.482 3.640 3.596 2.515 <b>2.364</b> 8.867 4.835 4.770 <b>4.104</b> 4.122				

**Table 5.** Goodness of fit statistics obtained from the growth models applied to the experimental data set of mammals. Equations with the best goodness of fit are represented in bold.

Growth models (Female)

BIC 33.82721.33721.15415.880**15.646**34.48325.52625.329**23.109**23.854 AIC<sub>C</sub> 37.98125.49225.30920.035**22.058**38.63829.68129.484**27.263**30.266

A:	Growth models (Male)	Growth models (Female)				
Amma	al Eq.(1) Eq.(2) Eq.(3) Eq.(4) Eq.(5) E	q.(1) Eq.(2) Eq.(3) Eq.(4) Eq.(5)				
	Beetal goat					
$R^2$	0.9969 <b>0.9978</b> 0.99380.99720.9979 0.	9992 0.99910.9943 0.9983 <b>0.9995</b>				
RMSE	E 0.3948 <b>0.3334</b> 0.56320.37490.3445 0.	1845 0.19440.4953 0.2733 <b>0.1523</b>				
BIC	-8.632 <b>-10.54</b> -4.622-9.216-9.654	7.222 -16.63 -6.074 <sub>12.786</sub> - <b>18.87</b>				
$AIC_C$	-3.308 <b>-5.217</b> 0.703 -3.891-1.110 <sub>1</sub>	- 1.897 -11.30 -0.749 -7.462 <b>-10.32</b>				
	Karagouniko s	heep				
$R^2$	0.96230.9693 <b>0.9728</b> 0.97110.9728 0.	9456 0.9501 <b>0.9520</b> 0.9511 0.9520				
RMSE	E 6.223 5.611 <b>5.289</b> 5.447 5.488 5	i.616 5.380 <b>5.278</b> 5.326 5.477				
BIC	29.25327.725 <b>26.851</b> 27.28828.081 27	7.737 27.105 <b>26.821</b> 26.956 28.051				
$AIC_C$	33.40831.880 <b>31.006</b> 31.44334.492 3	1.892 31.260 <b>30.975</b> 31.111 34.462				
Celta pig						
$R^2$	0.98250.9920 <b>0.9962</b> 0.99420.9962 0.	9841 0.99460.9970 0.9966 <b>0.9975</b>				
RMSE	E 6.479 4.376 <b>3.014</b> 3.746 3.092 5	.607 3.239 2.438 2.601 <b>2.297</b>				
BIC	40.01932.179 <b>24.730</b> 29.07226.093 37	7.131 26.16720.495 21.789 <b>20.153</b>				
$AIC_C$	43.19735.357 <b>27.908</b> 32.25030.868 40	0.309 29.34523.673 24.967 <b>24.929</b>				

**Table 6.** Goodness of fit statistics obtained from the growth models applied to the experimental data set of mammals. Equations with the best goodness of fit are represented in bold.

A 1		Gr	owth model	ls			
Animals	Eq.(1)	Eq.(2)	Eq.(3)	Eq.(4)	Eq.(5)		
Norfolk rabbit							
$R^2$	0.9925	0.9991	0.9950	0.9990	0.9992		
RMSE	106.8	37.30	87.57	39.84	36.83		
BIC	75.373	58.922	72.266	59.953	59.444		
AICε	79.322	62.870	76.214	63.901	65.500		
Californian rabbit							
$R^2$	0.9882	0.9972	0.9943	0.9976	0.9976		
RMSE	110.6	53.98	77.26	49.91	51.45		
BIC	75.917	64.701	70.307	63.477	64.667		
AICε	79.866	68.650	74.255	67.425	70.723		
		New Zeland	d rabbit				
$R^2$	0.9909	0.9985	0.9942	0.9984	0.9986		
RMSE	103.3	42.07	82.27	43.15	41.88		
BIC	74.851	60.803	71.289	61.201	61.450		
$AIC_C$	78.799	64.752	75.238	65.150	67.506		
	Н	lolstein-Frie	sian Bull				
$R^2$	0.9958	0.9988	0.9953	0.9986	0.9988		
RMSE	17.54	9.57	18.61	10.02	9.60		
BIC	67.549	53.886	68.892	54.910	54.872		
$AIC_C$	70.395	55.641	71.738	57.756	59.117		
-		Nelore o	cow				
$R^2$	0.9912	0.9832	0.9641	0.9781	0.9922		
RMSE	14.84	20.55	30.01	23.41	14.81		
BIC	29.856	33.243	37.193	34.603	30.294		
$AIC_C$	35.6187	39.006	42.955	40.365	39.691		
Angus cow							
$R^2$	0.9981	0.9921	0.9766	0.9878	0.9982		
RMSE	8.992	18.26	31.47	22.68	9.955		
BIC	14.188	18.497	21.804	19.813	14.778		
$AIC_C$	25.653	29.961	33.268	31.277	39.397		

Table 7 summarizes comparison between pairs of models used in this study. Each entry of this table accounts for the number of times that the equation of the corresponding row provided better fit than the other equations. It can be seen that Richards' model exhibited a better performance than all the others.

Table 7. Comparison between pairs of models used in this study.

	Eq.(1)	Eq.(2)	Eq.(3)	Eq.(4)	Eq.(5)	Total
Eq.(1)		3	5	3	2	13
Eq.(2)	19		13	7	5	44
Eq.(3)	17	9		5	3	34
Eq.(4)	19	15	17		9	60
Eq.(5)	20	17	19	13		69

As shown in Table 7, Logistic and Brody's model (Equations 3 and 1, respectively) exhibited the worst results in relation to the other models, since they provided a lower amount of better fits than the others. These poor results obtained for the Logistic and the Brody's model can be ascribed to the symmetry of the inflection point and to the hyperbolic shape of the model, respectively. In order to illustrate this behavior, Figure 4 shows residuals obtained after fits of Logistic, Brody and Gompertz equations to Athens-Canadian chickens. As can be seen, the residuals are larger and not normally distributed for the Logistic and Brody models in relation to the Gompertz growth model.

Growth models (Male)

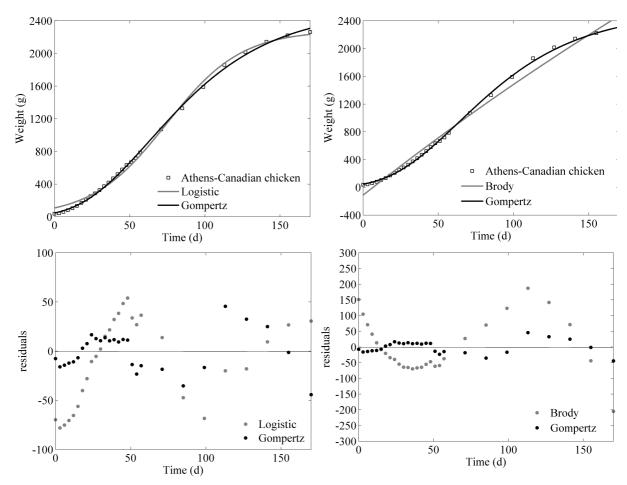


Figure 4. Fits and residuals obtained for the Logistic, Brody and Gompertz models to Athens-Canadian chickens.

In general, it was also observed that all models under investigation in this study exhibited high  $R^2$  values (above 0.94), suggesting overall good fits to the data. According to  $R^2$  values the Richards' model provided better results. Theoretically, the four parameter Richards model, is expected to give a higher  $R^2$  than the three parameter models. However, due to the values of the shape parameter for some animals close to m = 0, m = -1/3, m = -1 or m = 1, the  $R^2$  values are similar among Richards' and the three parameters models (Tables 4, 5 and 6).

The results obtained for Athens-Canadian chicken (m = 0.0541 for male and m = -0.0220 for female) and Guinea fowl (m = 0.0798 for male and m = -0.0760 for female) seem to indicate that the Gompertz model is appropriate to experimental data as previously pointed out by Aggrey (2002) and Nahashon et al. (2006), respectively. For Japanese quail m values showed deviations among lines and sex (Table 3). Only for the wild line, the parameter showed a similar value both for male (m = 0.2321) and female (m = 0.2342). The values of  $W_{\rm inf}/W_{\infty}$  were between 0.39 and 0.46 for all Japanese quail

lines. This justified that the statistical parameters indicated Richards' model as the most appropriated followed by Gompertz model (Table 4). None of the three parameters models generated inflection points between 39 and 46% of the mature weight, and the Gompertz model produced the value closest to this range (37%). These results are in accordance with the study of Sezer and Tarhan (2005), which discussed in details the fit of Richards' model to different lines of Japanese quail.

Among the mammals studied, only Californian rabbit (m = -0.0640) seems to indicate Gompertz model as the best one. Curi et al. (1985) fitted Logistic and Gompertz models to rabbit data for three lines and found that the Gompertz model was better than the Logistic model. However, for Norfolk and New Zealand lines, the von Bertalanffy model was the most appropriated one (Tables 3 and 6).

The results presented in Table 3 for Karagouniko sheep (m = 0.9436 for male and m = 0.9642 for female) and pig (m = 1.0184 for male) indicate Logistic model as the most appropriate. These animals showed the inflection

point at growth curve close to 50% of the mature weight (Table 3). On the other hand, Gbangboche, Glele-kakai, Salifou, Albuquerque, and Leroy (2008) compared the goodness of fit of four non-linear growth models in West African Dwarf sheep and concluded that the Brody model provided the best fit.

The appropriated models for Beetal goat were Brody model for male and Richards model for female (Table 5). Waheed et al. (2011) compared Brody and Gompertz models and concluded that both models efficiently explained the Beetal goat growth. An appropriated model for Beetal goat should exhibit an inflection point fixed close to 0.2 of the mature weight (Table 3).

Holstein-Friesian bull growth curve showed a m value equal to -0.223. Thus, the von Bertalanffy model could be a good choice for fitting the gain of body weight for this animal (Table 6). Vázquez et al. (2012) observed that this model was appropriate to describe the gain of the body weight of cattle. According to results obtained with Richards' model (Table 3), Nelore and Angus cattle exhibit no inflection point (m < -1) at their growth curves. Statistical parameters indicated the use of Brody model for both species (Table 6). Silva et al. (2011) evaluated five non-linear models for the gain of weight for cows of different biological types and found that Richards' and Brody models were the most appropriated for Nelore cow. Beltrán et al. (1992) evaluated growth patterns of two lines of Angus cow using Brody and Richards' models and concluded that both models provided good results.

## Conclusion

In general, all non-linear models demonstrated good capacities of fitting for describing the growth kinetics of several animals. Although the Richards model exhibited the highest  $R^2$  than the three parameters models, the two criteria based on the information theory, AIC and BIC, indicated that Gompertz model was the best model for chickens. In what concerns mammals, the Logistic model was the best model for pigs and sheep, von Bertalanffy for rabbits and bulls and when experimental data showed hyperbolic profiles, like cows and goats, the most appropriated model was the Brody equation. According to AIC and BIC criteria, the Richards' model was the most appropriate only for Japanese quails, female pigs and female goats. However, it provided the best results in average when all animals studied were considered. The Richards' model may be preferable for data based on a sigmoidal behavior, due to the fact that the placement of the inflection

point is flexible. If a fixed inflection point is preferred, any placement is possible by substitution of the parameter *m*, for any given value above -1.

#### Acknowledgements

The authors would like to express their gratitude to Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for financial support (Process 484037/2013-7).

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Received on March 19, 2016. Accepted on August 23, 2016.

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