

1        **Growth Patterns of birds, dinosaurs and reptiles: Are differences real or apparent?**

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18        **Growth Patterns of birds, dinosaurs and reptiles: Are differences real or apparent?**

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20        **Abstract.** Systematics of animals was done on their appearance or genetics. One can also ask  
21        about similarities or differences in the growth pattern. Quantitative studies of the growth of  
22        dinosaurs have made possible comparisons with modern animals, such as the discovery that  
23        dinosaurs grew in relation to their size faster than modern reptiles. However, these studies  
24        relied on only a few growth models. If these models are false, what about the conclusions?  
25        This paper fits growth data to a more comprehensive class of models, defined by the von  
26        Bertalanffy-Pütter differential equation. Applied to data about dinosaurs, reptiles and birds,  
27        the best fitting models confirmed that dinosaurs may have grown faster than alligators.  
28        However, compared to modern broiler chicken, this difference was small.

29

30        **Key words:** Bertalanffy-Pütter differential equation, *Tenontosaurustilletti*, *Alligator*  
31        *mississippiensis*, Athens Canadian Random Bred strain of *Gallus gallusdomesticus*

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## 1. INTRODUCTION

35 Mathematical growth models aim at a simplified description of growth in terms of curves that  
36 fit well to size-at-age data [1]. As the growth of animals depends on multiple factors, the  
37 most-informative data came from controlled studies, where animals were reared under the  
38 same conditions and weighed repeatedly during the entire phase of growth. This was feasible  
39 e.g. for chicken [2]. By contrast, for wildlife and wild-caught fish, in general for each animal  
40 there was only one measurement of mass-at-age. Even with data about thousands of animals  
41 there remained considerable uncertainties about the proper choice of the growth model [3].  
42 For extinct species the situation was even worse, as no weighing of body mass was possible  
43 for fossils. However, recent approaches led to mathematical growth models for dinosaurs [4]  
44 and thereby to a comparison of growth pattern of different species. These quantitative studies  
45 have “revolutionized our understanding of dinosaur biology” [5].

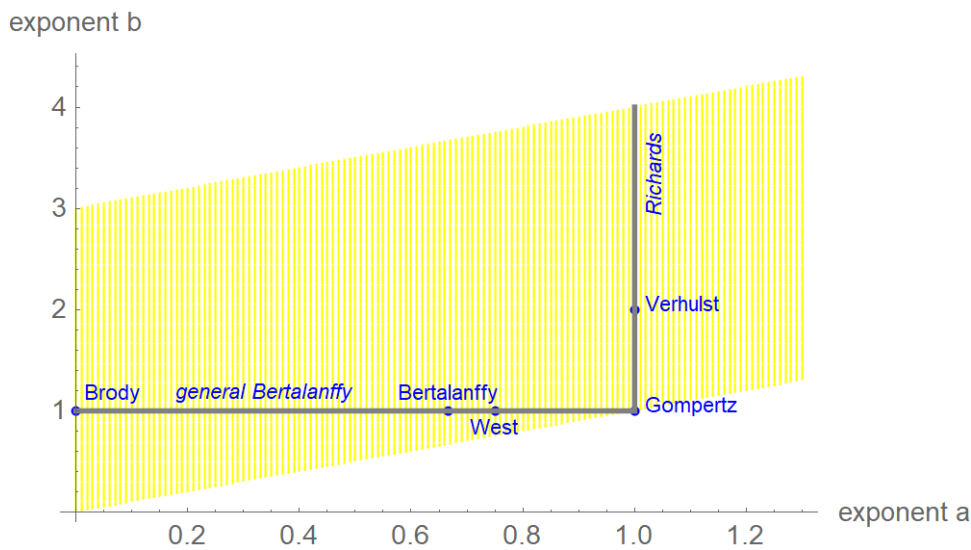
46 Growth studies for vertebrates relied on few models only. Examples are the models of Brody  
47 [6], von Bertalanffy [7], Gompertz [8], Richards [9, 10], West [11], Verhulst [12] logistic  
48 growth, and the generalized Bertalanffy model promoted by Pauly [13]. This paper studies the  
49 comprehensive class of growth models (1).

$$50 \quad m'(t) = p \cdot m(t)^a - q \cdot m(t)^b \quad (1)$$

51 It describes growth about mass  $m(t)$  at time  $t$  and it uses five model parameters, namely the  
52 non-negative exponent-pair  $a < b$ , the constants  $p$  and  $q$ , and the initial mass  $m(0) = m_0 > 0$ :

53 Equation (1) was proposed by Pütter [14] and von Bertalanffy [15]. As shown in Figure 1, the  
54 above-mentioned named models are special cases of it, whereby each model corresponds to a  
55 different exponent-pair or to a line segment of exponent-pairs. The Gompertz model is a limit  
56 case on the diagonal. In view of the exceptional character of the named models, we ask, if

57 there are other models from the Bertalanffy-Pütter class that describe growth pattern of  
58 dinosaurs better and thereby allow for more accurate comparisons between different species.



59  
60 **Figure 1.** Named models (blue) and part of the search-region (yellow) for the exponent-pair of the best  
61 fitting growth model.

62 We illustrate these questions by a case study, where we identify growth models from the  
63 general class (1) with the best fit to mass-at-age data for a species of dinosaurs  
64 (*Tenontosaurus*) and for two modern species of reptiles (alligators) and birds (broiler chicken)  
65 that are often compared with dinosaurs. The data were drawn from literature. In view of the  
66 need to optimize five parameters, the data-fitting problem led to an optimization problem that  
67 hitherto due to numerical instability had been almost intractable, whence practitioners  
68 confined the search for best fitting models basically to the above-mentioned named models  
69 with mathematically elementary growth curves. Recently, the authors succeeded in  
70 developing an advanced optimization method, which allowed to extend the search for the best  
71 fitting model, represented by an exponent-pair, to a much larger class of models (e.g. yellow  
72 region in Figure 1). The optimization for the present paper searched ca. 30,000-70,000  
73 exponent-pairs (i.e. different candidate models) per data-set.

74 Further, in order to study the variability of the exponents, the paper identified the region of  
75 near-optimal exponent-pairs. The exponent-pairs of this region could also be used to model

76 growth without affecting the fit to the data significantly when the other parameters were  
77 optimized.

## 78 2. METHODS

79 **Data:** Mass-at-age of *Tenontosaurus tilletti* (twelve data points with mass 23-1102 kg, and  
80 age 1-26 years) was from Table 2 of [16]. Mass-at-age of *Alligator mississippiensis* (41 data-  
81 points with mass 0.1-40.7 kg and age 1-42 years) was retrieved from Figure 3A of that paper.  
82 The original source was [17], who over a time-span of forty years captured and partly  
83 recaptured ca. 7000 alligators from Louisiana, USA. Mass-at-age of *Gallus gallus domesticus*  
84 (28 data points with mass 0.04-2.23 kg and age 0-170 days) came from Table1 of [2]. This  
85 table records the average mass-at-age of 217 male chicken of the Athens Canadian Random  
86 Bred strain that survived the first 170 days since hatching. They were reared under laboratory  
87 conditions and weighed regularly.

88 **Materials:** Data from graphics were retrieved using DigitizeIt of Bormisoft®. All data were  
89 copied into a spreadsheet (Excel of Microsoft®) and processed in Mathematica 11.3 of  
90 Wolfram Research®. The output of optimization was exported to a spreadsheet.

91 **Methods:** For chicken, the best fitting growth model and the near-optimal models were  
92 identified in [18]. As the paper uses the same approach for the alligator and dinosaur data, the  
93 method is only sketched.

94 Assuming a lognormal distribution of mass-at-age (the standard deviation of mass is  
95 approximately proportional to mass), the maximum-likelihood model-parameters were  
96 estimated. Thereby, the method of least squares was used to fit the logarithmically  
97 transformed growth function  $u(t) = \ln(m(t))$  to the logarithmic transformation of mass data. In  
98 order to identify both the best fitting and the near-optimal exponent-pairs, for each exponent-  
99 pair on a grid the other model-parameters were optimized. Thus, using the abbreviation

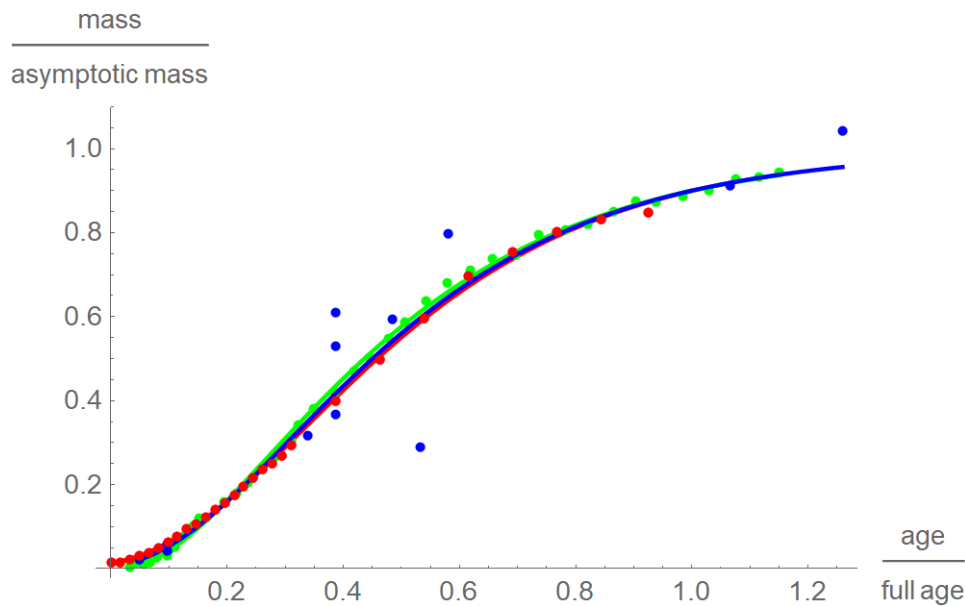
100  $SSLE$ = sum of squared errors between the logarithm of the growth function and the  
101 logarithmically transformed data, the following function (2) on the grid was defined:

$$102 \quad SSLE_{opt}(a,b) = \min_{m_0,p,q} (SSLE), \text{ assuming model (1) with exponents } a, b \quad (2)$$

103 The optimization of  $p$ ,  $q$ ,  $m_0$  used simulated annealing, whereby for a grid point near the  
104 diagonal 50,000 annealing steps were used. For the subsequent grid points in the  $b$ -direction,  
105 these outputs were used as starting values and improved in 1,000 annealing steps. The output  
106 was exported to a table in the format  $(a, b, m_0, p, q, SSLE_{opt}(a, b))$ . It is provided as a  
107 supporting material. An exponent-pair was near-optimal, if its  $SSLE_{opt}(a, b)$  exceeds the least  
108 one by less than 5%.

### 109 **3. RESULTS**

110 The graphical representation of the results uses red for chicken, green for alligators and blue  
111 for dinosaurs. Figure 2 plots the data and the best fitting growth curves in dimensionless  
112 coordinates. Thereby, mass is reported as a fraction of the asymptotic mass  $m_{max}$ . Given the  
113 best fitting growth model, this is the limit of  $m(t)$ , when time approaches infinity. Age is  
114 reported as a fraction of “full age”  $t_{full}$ , at which 90% of the asymptotic mass is reached. This  
115 is used as a proxy for “adulthood”. Thereby  $m_{max}$  and  $t_{full}$  were computed from the best fitting  
116 model. Note the similarity of growth in terms of these dimensionless data.



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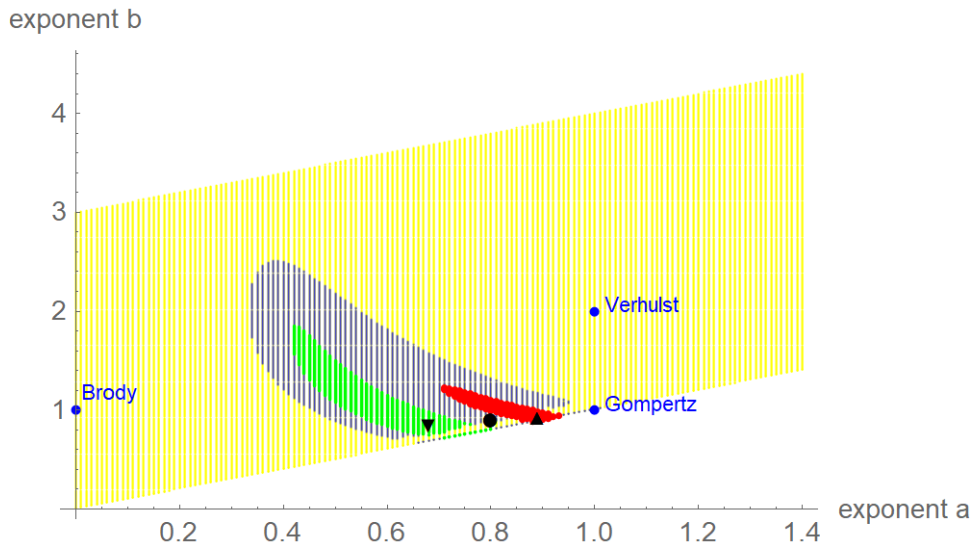
118 **Figure 2.** Growth data and best fitting growth curves in dimensionless coordinates (fraction of the  
119 asymptotic mass  $m_{max}$  at a fraction of the full age  $t_{full}$ ) for broiler chicken (red), alligators (green) and  
120 dinosaurs (blue). For chicken and alligators, but not so for dinosaurs (larger spread of the data), the  
121 data differed only slightly from the growth curves. Further, the curves were barely different.

122 For chicken, results quoted from [18], the optimal model parameters (mass in gram, time in  
123 days) were  $a = 0.89$ ,  $b = 0.93$ ,  $m_0 = 32.92$  g,  $p = 1.0952$ , and  $q = 0.7988$ . This translated into  
124 an asymptotic mass of 2.67 kg, an inflection-point at day 61 with 890 g (33% of the  
125 asymptotic mass) and the maximal weight gain of 19.9 g/day. For better comparison with  
126 dinosaurs, this was a maximal growth rate of 7.3 kg per year. (A dinosaur-year had more  
127 days, but these were shorter, whence overall a year covered about the same time span as  
128 today.) After 184 days (full age) 90% of the asymptotic mass was reached.

129 For alligators (mass in kg, time in years) the best fit was achieved for  $a = 0.68$ ,  $b = 0.85$ ,  $m_0 =$   
130 158.82 g,  $p = 1.6843$ , and  $q = 0.8882$ . The asymptotic mass was 43.12 kg (slightly above the  
131 heaviest data point), the mass at the inflection point was 11.6 kg, i.e. 26% of the asymptotic  
132 mass, and the maximal growth rate was 1.78 kg/year at age 9.85 years. The full age of  
133 alligators was 36 years.

134 For the dinosaur-data (mass in kg, time in years) the best fit parameters were  $a = 0.8$ ,  $b = 0.9$ ,  
135  $m_0 = 22.18$  kg,  $p = 6.3743$ , and  $q = 3.1769$ . The asymptotic mass was 1057.5 kg; this was

136 slightly below the maximum mass-estimate of the data. The mass at the inflection point,  
137 325.7 kg, was 31% of the asymptotic mass. There, at age 6.37 years, the maximal growth rate  
138 was 72.5 kg/year. Further, 90% of the asymptotic mass was reached with 21 years.

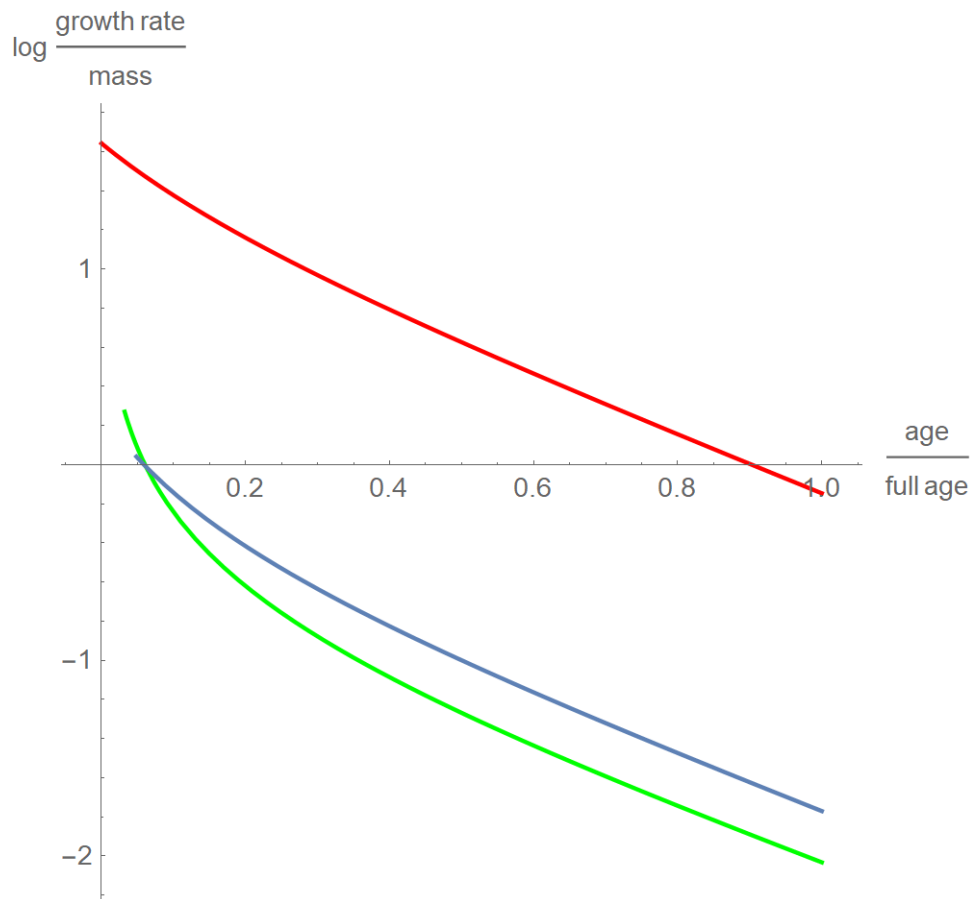


139 **Figure 3.** Optimal and near-optimal exponent-pairs for chicken (triangle and red area), alligators  
140 (upside triangle and green area) and dinosaurs (circle and blue area dots). For comparison with the  
141 named models, three extremal exponent-pairs are plotted (blue).  
142

143 Figure 3 plots the optimal and near-optimal exponent-pairs. Despite the similarity of the data  
144 in dimensionless coordinates, the optimal exponent-pairs were different. However, due to the  
145 larger variance of the dinosaur-data the region of near-optimal exponents for dinosaurs was  
146 larger and it included both regions for alligators and chicken. Thus, judging from perspective  
147 of dinosaurs, their growth data did not display a systematic difference to modern species,  
148 whence there was no fundamental change in the growth pattern.

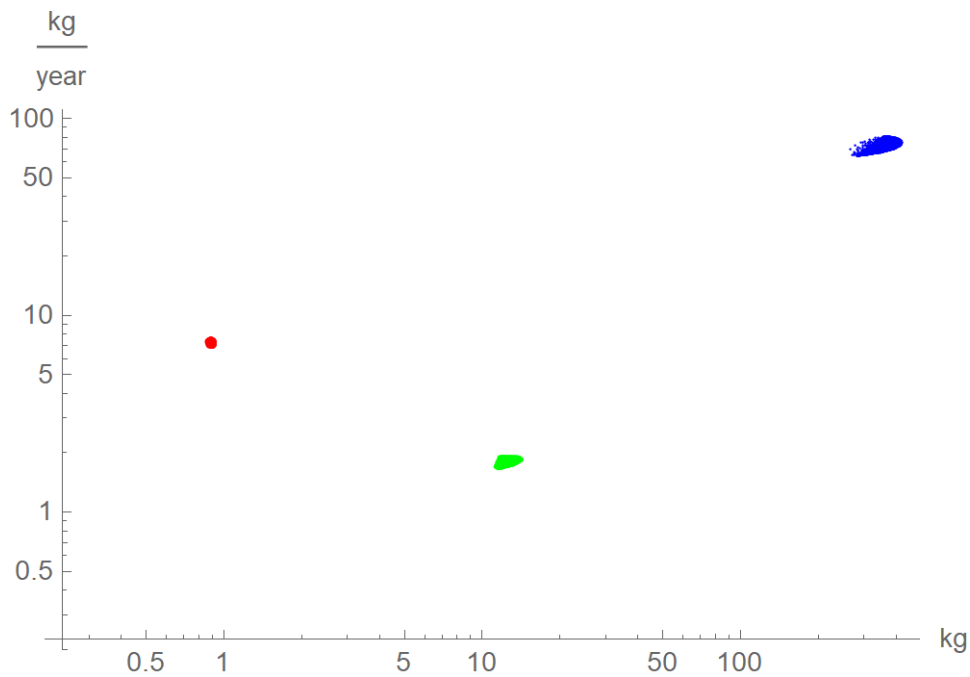
149 While these findings seem to contradict the consensus that dinosaurs grew faster than modern  
150 reptiles [5], Figure 4 compares the growth rates relative to body mass. This displays  
151 differences between the species: Well-fed broiler chicken grew more than ten times faster  
152 than alligators and dinosaurs. Further, except for a short initial period, dinosaurs grew  
153 somewhat faster than alligators. However, these comparisons were done for the best fitting  
154 model curves only.





156 **Figure 4.** Decadic logarithm of the growth rates relative to body mass for chicken (red), alligators  
157 (green) and dinosaurs (blue) with time as a fraction of full age.

158



160 **Figure 5.** Log-log-plot of the maximal growth rate,  $m'$ , and mass at the inflection point for near-  
161 optimal growth curves  $m(t)$  for chicken (red), alligators (green) and dinosaurs (blue).

162 The maximal growth rate (i.e.  $m'$  at the inflection point) is another indicator of interest, as in  
163 comparisons between species it is used as a proxy for the basal metabolic rate [19]. Figure 5  
164 used the near-optimal models to explore, how sensitive this indicator was to the choice of a  
165 model: The clouds were the values of  $m$  and  $m'$  at the inflection point, where  $m(t)$  was a near-  
166 optimal growth curve. Apparently, even well-fitting growth curves resulted in inaccurate  
167 estimates for the basal metabolic rate.

#### 168 **4. DISCUSSION**

169 A large region of near-optimal exponents indicates that data may not carry enough  
170 information to differentiate between growth models. For the data about three species of  
171 dinosaurs from [16] only *Tenontosaurus* provided feasible data, while those for other species  
172 resulted in unreasonably large regions of near-optimal exponent-pairs (i.e. almost every  
173 growth model would be near-optimal). The paper therefore did not use these data. However,  
174 in view of the inherent uncertainties of estimating the mass of dinosaurs [5], it was surprising  
175 that one in three data-sets was suitable.

176 The definition of “full age” to define dimensionless coordinates was somewhat arbitrary. For,  
177 using 90% of the asymptotic mass was a compromise of avoiding excessive extrapolation (for  
178 some data the maximal observed mass was below the asymptotic mass) and the intent to cover  
179 most of the growth phase. Further, for different species the fraction  $t/t_{full}$  may correspond to  
180 different stages of their biological development. However, using this linear transformation  
181 was a convenient tool to combine data and growth curves of several species into one plot  
182 (Figures 2, 4 and 5). With respect to Figure 4, the faster growth of broiler chicken will also be  
183 observed for any nonlinear transformation of time that aims at a proper representation of  
184 biological development.

185 In Figure 3, the regions of near-optimal exponents displayed fuzzy boundaries and points  
186 close to the diagonal were not connected to the regions. This was caused by the optimization  
10

187 strategy, a high number of annealing steps for points next to the diagonal and few steps  
188 thereafter. (This speeded up computations.) However, despite these deficiencies the  
189 visualization of the near-optimal exponents verified the optimal character of the optimal  
190 exponent-pairs. As is evident from this figure, the optimal exponent-pairs were quite remote  
191 from the exponent-pairs for the named models which are more common in growth studies.  
192 However, in fish-biology it has long been accepted that exponent-pairs  $(a, b)$  with  $a < 1$  and  $b$   
193  $= 1$  might be better compatible with biological constraints for growth; e.g. the growth of gill  
194 surface area relative to mass growth [13]. Recently, also exponents  $b < 1$  were considered as  
195 biologically meaningful [20]. Thus, the use of general exponent-pairs was also motivated by  
196 biological considerations.

## 197 **5. CONCLUSION**

198 While it is generally acknowledged that mass-at-age estimates for dinosaurs are highly  
199 uncertain, a data-set for *Tenontosaurus* allowed for the identification of a best fitting growth  
200 model within the comprehensive class of Bertalanffy-Pütter models (1). However, data  
201 uncertainty did not allow to conclude that the dinosaur-data would need a different exponent-  
202 pair (model) than modern alligators or birds. On the contrary, displaying the data in  
203 dimensionless coordinates did not indicate notable differences. Also, the best-fitting growth  
204 curves did barely differ. Yet, there was a difference in the relative growth rate, i.e. growth rate  
205 over mass. Thereby, modern broiler chicken grew much faster than dinosaurs or alligators and  
206 (keeping in mind the uncertainty of mass estimation) dinosaurs may grow faster than  
207 alligators. However, the growth rate is a measure that cannot be observed directly from the  
208 data; it is derived from a growth model and depends on what model is selected. This was  
209 demonstrated for the maximal growth rate, which varied considerably even for growth curves  
210 that fitted well to the data.

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