

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

2 **Authors:**

3 Norbert Brunner, Manfred Kühleitner, Werner-Georg Nowak,

4 Katharina Renner-Martin, and Klaus Scheicher

5

6 **Affiliation of all authors:**

7 University of Natural Resources and Life Sciences,

8 Department of Integrative Biology and Biodiversity Research,

9 A-1180 Vienna, Austria

10

11 **Corresponding author:** Manfred Kühleitner

12 Institute of Mathematics, Department of Integrative Biology and Biodiversity Research,

13 University of Natural Resources and Life Sciences (BOKU)

14 Gregor Mendel Strasse 33, A-1180 Vienna, Austria

15 **E-Mail:** manfred.kuehleitner@boku.ac.at

16

17

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

19

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*

32

33

34

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].

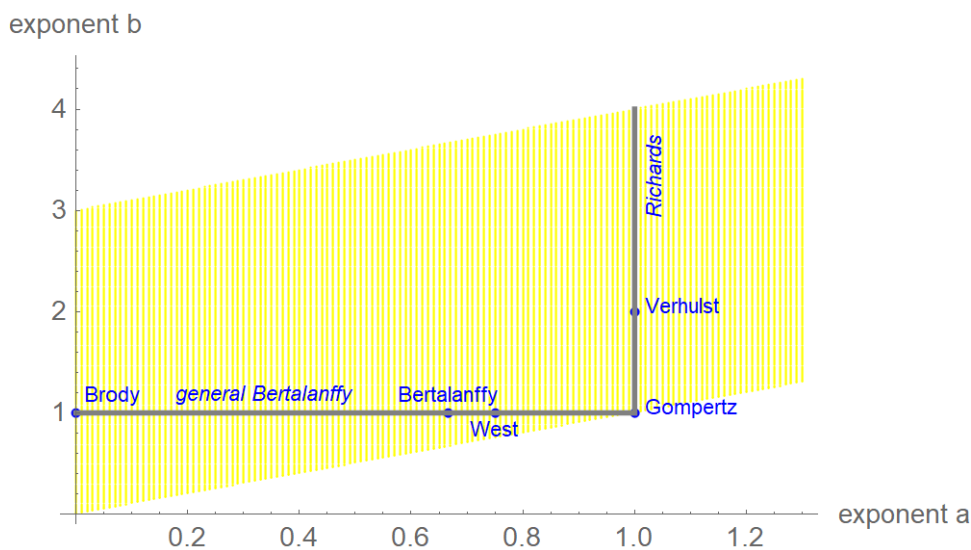
46 Growth studies for vertebrates relied on few models only. Examples are the models of Brody
47 [6], von Bertalanffy [7], Gompertz [8], Richards [9, 10], West [11], Verhulst [12] logistic
48 growth, and the generalized Bertalanffy model promoted by Pauly [13]. This paper studies the
49 comprehensive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

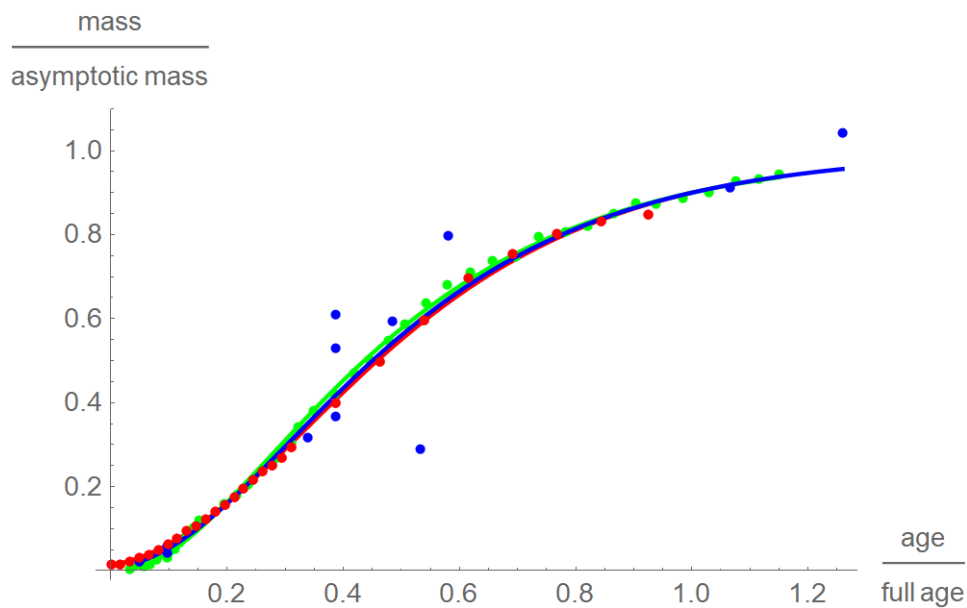
100 $SSLE$ = sum of squared errors between the logarithm of the growth function and the
101 logarithmically transformed data, the following function (2) on the grid was defined:

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

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.



117

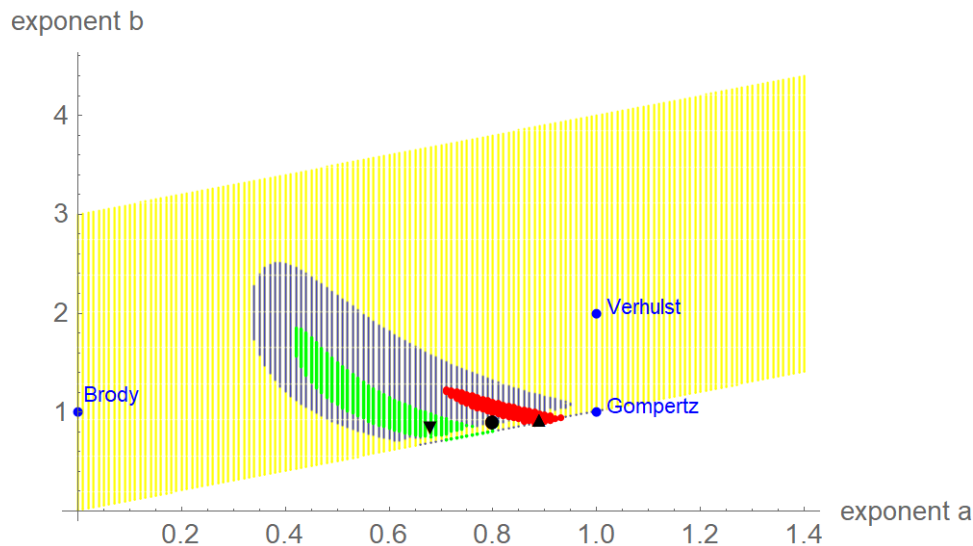
118 **Figure 2.** Growth data and best fitting growth curves in dimensionless coordinates (fraction of the
119 asymptotic mass m_{max} at a fraction of the full age t_{full}) for broiler chicken (red), alligators (green) and
120 dinosaurs (blue). For chicken and alligators, but not so for dinosaurs (larger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

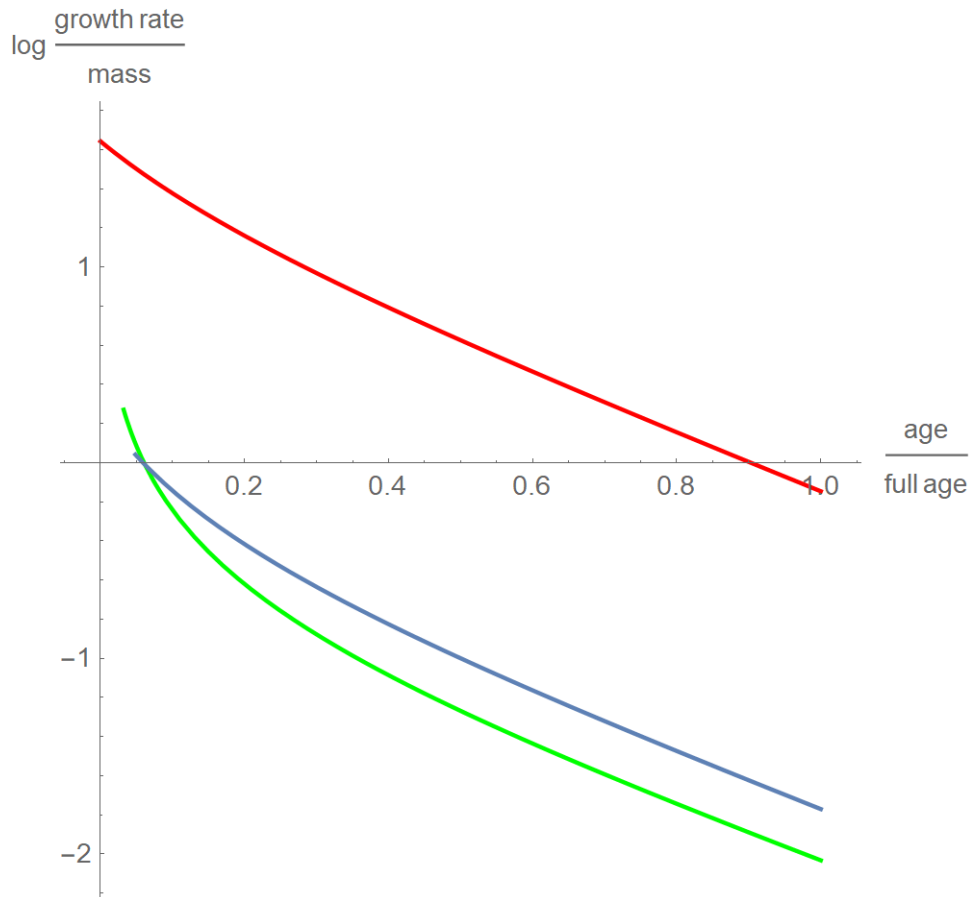
136 slightly below the maximum mass-estimate of the data. The mass at the inflection point,
137 325.7 kg, was 31% of the asymptotic mass. There, at age 6.37 years, the maximal growth rate
138 was 72.5 kg/year. Further, 90% of the asymptotic mass was reached with 21 years.



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

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.

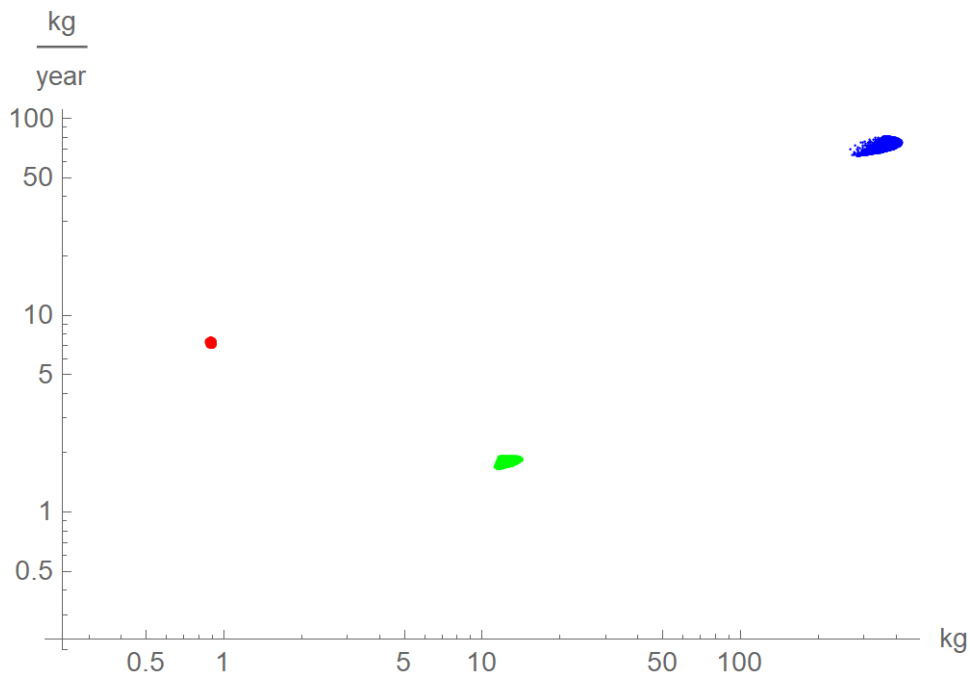
149 While these findings seem to contradict the consensus that dinosaurs grew faster than modern
150 reptiles [5], Figure 4 compares the growth rates relative to body mass. This displays
151 differences between the species: Well-fed broiler chicken grew more than ten times faster
152 than alligators 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.



155

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



159

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.

211 **6. REFERENCES**

- 212 [1] Kahm, M., G. Hasenbrink, H. Lichtenberg-Frate, J. Ludwig, and M. Kschischo. 2010.
213 Fitting Biological Growth Curves with R. *Journal of Statistical Software*, 33: 1-21.
- 214 [2] Aggrey, S.E. 2002. Comparison of Three Nonlinear and Spline Regression Models for
215 Describing Chicken Growth Curves. *Poultry Sciences*, 81:1782-1788.
- 216 [3] Renner-Martin, K., N. Brunner, M. Kühleitner, W.G. Nowak, and K. Scheicher. 2018.
217 Optimal and near-optimal exponent-pairs for the Bertalanffy-Pütter growth model. *PeerJ*
218 6: e5973.
- 219 [4] Lee, A.H., A.K. Huttenlocker, K. Padian, and H.N. Woodward. 2013. Analysis of Growth
220 Rates. In Padian, K. and E.T. Lamm (eds.) *Bone histology of Fossil Tetrapods: Advancing*
221 *Methods, Analysis and Interpretation*. UCLA Press: Berkeley, USA, pp. 217-251.
- 222 [5] Erickson, G.M. (2014). On Dinosaur Growth. *Annual Review of Earth and Planetary*
223 *Sciences*, 42: 675-697.
- 224 [6] Brody, S. (1945) *Bioenergetics and growth*. Hafner Publ. Comp.: New York, NY, USA.
- 225 [7] Bertalanffy, L.v. (1949) Problems of organic growth. *Nature* 163: 156-158.
- 226 [8] Gompertz, B. (1832) On the Nature of the Function Expressive of the Law of Human
227 Mortality, and on a New Mode of Determining the Value of Life Contingencies. *Philos.*
228 *Trans. R. Soc. London* 123: 513-585.
- 229 [9] Richards, F.J. (1959) A Flexible Growth Function for Empirical Use. *Journal of*
230 *Experimental Botany* 10: 290-300.
- 231 [10] Tjørve, M.C., and E. Tjørve. 2017. The use of Gompertz models in growth analyses,
232 and new Gompertz-model approach: An addition to the Unified Richards family. *PLoS*
233 *ONE* 12(6):e0178691.
- 234 [11] West, G.B., Brown, J.H., Enquist, B.J. (2001) A general model for ontogenetic growth.
235 *Nature* 413: 628-631.

- 236 [12] Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroissement,
237 CorrespondenceMathematique et Physique (Ghent) 10: 113-121.
- 238 [13] Pauly D. (1981) The relationship between gill surface area and growth performance in
239 fish: a generalization of von Bertalanffy's theory of growth. Reports on Marine Research
240 (Berichte der deutschen wissenschaftlichen Kommission für Meeresforschung) 28:25–
241 282.
- 242 [14] Pütter, A. (1920) Studien über physiologische Ähnlichkeit. VI.
243 Wachstumsähnlichkeiten. Pflügers Archiv für die Gesamte Physiologie des Menschen und
244 der Tiere 180: 298-340.
- 245 [15] Bertalanffy, L.v. (1957) Quantitative laws in metabolism and growth. Quarterly
246 Reviews of Biology 32: 217-231.
- 247 [16] Lee, A.H. and S. Werning. 2008. Sexual maturity in growing dinosaurs does not fit
248 reptilian growth models. Proceedings of the National Academy of Sciences USA, 105:
249 582-587.
- 250 [17] Rootes, W.L., R.H. Chabreck, V.L. Wright, B.W. Brown, and T.J. Hess. 1991. Growth
251 Rates of American Alligators in Estuarine and Palustrine Wetlands in Louisiana. Estuaries
252 14: 489-494.
- 253 [18] Renner-Martin, K., N. Brunner, M. Kühleitner, W.G. Nowak, and K. Scheicher. 2019.
254 Best-fitting growth curves of the von Bertalanffy-Pütter type. Poultry Science, to appear,
255 DOI: 10.3382/ps/pez122.
- 256 [19] Calder, W.A. III. 1985. Size, Function, and Life History. Harvard Univ. Press:
257 Cambridge, USA.
- 258 [20] Pauly, D., and W.W.L. Cheung. 2017. Sound physiological knowledge and principles in
259 modeling shrinking of fishes under climate change. Global Change Biology. Published
260 online: DOI 10.1111/gcb.13831.