

Choosing the right sigmoid growth function using the unified-models approach

JAKUB VRÁNA,^{1*}  VLADIMÍR REMEŠ,¹ BEATA MATYSIOKOVÁ,¹ KATHLEEN M. C. TJØRVE² & EVEN TJØRVE²

¹Laboratory of Ornithology, Department of Zoology, Palacky University, 17. Listopadu 50, 771 46, Olomouc, Czech Republic

²Inland Norway University of Applied Sciences, Postboks 952, 2604, Lillehammer, Norway

Growth of the young is an important part of the life history in birds. However, modelling methods have paid little attention to the choice of regression model used to describe its pattern. The aim of this study was to evaluate whether a single sigmoid model with an upper asymptote could describe avian growth adequately. We compared unified versions of five growth models of the Richards family (the four-parameter U-Richards and the three-parameter U-logistic, U-Gompertz, U-Bertalanffy and U4-models) for three traits (body mass, tarsus-length and wing-length) for 50 passerine species, including species with varied morphologies and life histories. The U-family models exhibit a unified set of parameters for all models. The four-parameter U-Richards model proved a good choice for fitting growth curves to various traits – its extra *d*-parameter allows for a flexible placement of the inflection point. Which of the three-parameter U-models was the best performing varied greatly between species and between traits, as each three-parameter model had a different fixed relative inflection value (fraction of the upper asymptote), implying a different growth pattern. Fixing the asymptotes to averages for adult trait value generally shifted the model preference towards one with lower relative inflection values. Our results illustrate an overlooked difficulty in the analysis of organismal growth, namely, that a single traditional three-parameter model does not suit all growth data. This is mostly due to differences in inflection placement. Moreover, some biometric traits require more attention when estimating growth rates and other growth-curve characteristics. We recommend fitting either several three-parameter models from the U-family, where the parameters are comparable between models, or only the U-Richards model.

Keywords: bird growth, passerine growth, postnatal growth, regression model, Richards-family models, Unified-Richards model.

Growth rates are crucial for individual survival and reproduction (Roff 1992, Starck & Ricklefs 1998) and many studies suggest that growth rate is evolutionarily flexible (e.g. Ydenberg 1989, Remeš 2006, 2007, Cheng & Martin 2012). Accordingly, a species' growth rate is often discussed with regard to physiological limits (Ricklefs 1968a, 1973), energetic efficiencies (Shalev & Pasternak 1983) and environmental conditions (Case 1978,

Arendt 1997). Moreover, growth patterns are also affected by predation rates (Remeš & Martin 2002, Martin *et al.* 2011), brood size (O'Connor 1978), brood parasitism (Remeš 2006) and sibling competition (Werschkul & Jackson 1979, Bor-tolotti 1986). Exact and reliable methods used to model and describe growth rates and patterns are thus critical for a deep ecological and evolutionary understanding of this important life history trait.

There is a large amount of literature on the modelling of growth in domestic animals, for example cattle (Gbangboche *et al.* 2008, Canaza-

*Corresponding author.
Email: kuba.vrana@email.cz
Twitter: @JakubVrana15

Cayo *et al.* 2014) and poultry (Gille & Salomon 1995, Cho *et al.* 2001, Aggrey 2002, Darmani Kuhi *et al.* 2003, Sengul & Kiraz 2005, Nahashon *et al.* 2006, Atil *et al.* 2007). However, we know much less about modelling growth in wild animals, and birds in particular (but see Ricklefs 1983, Tjørve & Tjørve 2010b, Austin *et al.* 2011). This is reflected by the fact that Ricklefs' (1967, 1968a, 1969, 1973, 1983, 1984) seminal works on sigmoid, asymptotic models still today serve as the main references for modelling bird growth. The most discussed parameters of these growth models are those controlling maximum growth rate (i.e. the slope at inflection) and the time (after hatching) at which maximum growth rate occurs (i.e. inflection time; Ricklefs 1976, 1983, Klaassen *et al.* 1994, Tjørve & Tjørve 2010b). Some other useful models, in addition, exhibit one or more parameters that control the trait value at which maximum growth rate occurs (i.e. body mass or length at inflection; Ricklefs 1983, Tjørve & Tjørve 2010a, 2017a,b). These growth models thus provide information about the postnatal characteristics of avian offspring, which are tightly linked to overall strategies of growth and important environmental factors (Remeš & Martin 2002, Martin *et al.* 2011).

Despite the large number of sigmoid, asymptotic models available today, usually only one of the traditional models is fitted: the logistic model (e.g. Starck & Ricklefs 1998, Smith *et al.* 2007, Tjørve *et al.* 2009, Albano *et al.* 2011, Cheng & Martin 2012, Martin 2015, Ton & Martin 2016), the Gompertz model (e.g. Kentie *et al.* 2013, Mullers & Amar 2015, Navarro *et al.* 2015) or the von Bertalanffy model (e.g. Penteriani *et al.* 2005). The main caveat of relying on a single three-parameter model is that the model may not be flexible enough to return accurate parameter values (Viñuela & Ferrer 1997, Huin & Prince 2000, Tjørve & Tjørve 2010b). Although the choice of model depends on the research question (Brown *et al.* 2007), choosing a poor-fitting model can result in unrealistic and hence biologically meaningless growth rates, inflection points, upper asymptotes and other parameter values (Ricklefs 1968a, Austin *et al.* 2011, Tjørve & Tjørve 2017a). The remedy may be to fit several three-parameter models and compare them. This approach has been adopted in some recent studies (Tjørve & Tjørve 2010b, Jones *et al.* 2014, Lok *et al.* 2014, Holt *et al.* 2016). Other studies have even considered additional models, such as the

extreme-value model (Tjørve & Tjørve 2010b), the Weibull model (McKinnon *et al.* 2012) and the Janoschek model (Gille & Salomon 1995). Huin and Prince (2000) created their own model and Faridi *et al.* (2015) discussed a number of models listed in Tjørve (2003) and in Thornley *et al.* (2007). Another solution might be to fit a single model with more parameters, as for example the four-parameter Richards model (Richards 1959), which has also been applied to bird growth data (Ricklefs 1983, Brisbin *et al.* 1987, Tjørve & Tjørve 2010a).

Thus far, no studies have tested the quality-of-fit between the U-versions of the three-parameter models or compared them with the four-parameter U-Richards model across a range of datasets expected to cover different bird-growth patterns and life histories. A complicating factor in comparing the outcomes of different traditional models is that the fitted parameter values of growth-rate constants (and for some model versions also the parameter(s) controlling the inflection value) are not directly comparable between models (Tjørve & Tjørve 2010a, 2017a). However, within the U-family all parameters, including the growth-rate parameter, are directly comparable across all models (Tjørve & Tjørve 2010a, 2017a, see Materials and Methods). Thus, this new family of models allows us for the first time to compare directly (between fitted models) not only asymptotes and inflection time but also relative growth rate.

The purpose of this study is to investigate which growth model or models are useful in current research on bird growth. Thereby, we aim to determine whether a single growth model is sufficient to describe several biometrics in different passerine species or whether several models are needed. We selected datasets for 50 passerine species (a well-studied order where the logistic model is frequently used), a manageable number but sufficient to include species with a wide range of morphologies and life histories. We then fit passerine growth data to the unified versions (U-versions) of four-three-parameter models: the U-Gompertz model as proposed by Tjørve and Tjørve (2017c) and the U-logistic, U-Bertalanffy and U4-models as proposed by Tjørve and Tjørve (2017a). In addition, we fit the four-parameter U-Richards model as proposed by Sugden *et al.* (1981) and Tjørve and Tjørve (2010a) to the same datasets. We evaluated the models according to their fit (R^2 and corrected Akaike information

criterion (AIC_c) and the variability of the fitted parameter values, as well as some derived measurements and their mutual correlations. In addition, we fitted the same models by setting the parameter that controls the upper asymptote to average adult size (Tjørve & Underhill 2009, Austin *et al.* 2011) in order to discuss if and when this might be useful.

MATERIALS AND METHODS

Data

We collected growth data from the primary literature focusing on songbirds (order Passeriformes). To cover much of the variability found in the order, we chose 50 species (Table S1) with different average clutch sizes (1–8.3 eggs), adult biometrics (body mass 8.5–228.2 g, tarsus-length 12.7–54.6 mm, wing-length 52–233.2 mm), nest-predation rates (daily predation rate 0.002–0.032), zoogeographical distributions (all zoogeographical regions), foraging modes (ground, vegetation and aerial), and types (cavity or open) and heights of nests (0–11.55 m above the ground).

From the original articles, we extracted data on postnatal growth of three biometrics (body mass, tarsus-length and wing-length) that are frequently measured in avian research (Earlé 1986, Badyaev & Martin 2000, Frei *et al.* 2010). Subsequently, the candidate models were fitted to the data in GraphPad PRISM 6.07 for Windows (GraphPad Software Inc. 2014) using non-linear regressions with ordinary least-squares.

Regression models

Growth of the chosen biometrics follows a sigmoid shape and many mathematical curves will

potentially fit this type of growth (Ricklefs 1983, Brown & Rothery 1993, Remeš & Martin 2002). Commonly used growth curves belong to the Richards-model family (Brown & Rothery 1993, Tjørve & Tjørve 2010a, 2017a). We used the ‘unified’ versions of these models (‘U-models’) because they have a unified set of parameters which are comparable across all these models (Tjørve & Tjørve 2010a, 2017a,b,c). This set of parameters consists of the upper asymptote (A), the time of inflection (T_i), value at starting point (initial trait value or intersection with y -axis; W_0), maximum relative growth rate (k_U) and the ‘exponent’ (d) which controls the relative value at inflection (w_i , see Table 1 for details). Not all the U-family models have all these parameters but, when present, the respective parameters are in the same units and control the same curve traits. All these models fit parameters A and k_U . There are two forms of each of these curves (Tjørve & Tjørve 2010a), the T_i -version (where time of inflection is modelled) and the W_0 -version (where size at hatching or birth is modelled instead). For this study, we used the T_i -versions (Table 2), because they are more frequently used when traditional models (not U-models) are fitted (see also Tjørve & Tjørve 2010b).

The four-parameter Richards model (Richards 1959) is more flexible than a three-parameter model (Brisbin *et al.* 1987, Viñuela & Ferrer 1997) due to the extra d -parameter, which determines the exponent and controls the trait value at which the inflection occurs (i.e. body mass or length at maximum growth rate; Tjørve & Tjørve 2017b). However, some versions of the Richards model have been criticized for correlations between its parameter estimates (Zach 1988, Viñuela & Ferrer 1997). In the Unified-Richards re-parameterizations

Table 1. Fitted parameters, derived measurements and their units, and interpretation for the tested sigmoid growth models.

	Calculation	Units	Interpretation
Fitted parameter			
A	Fitted	g or mm	Upper asymptote; trait value at which the curve converges
k_U	Fitted	days ⁻¹	Slope at inflection; maximum relative growth rate (at inflection)
T_i	Fitted	days	Time at inflection; age at maximum growth (at inflection)
d	Fitted	–	Affects trait value at maximum growth (at inflection)
Derived measurement			
K_U	$k_U \cdot A$	g/day or mm/day	Maximum absolute growth rate (at inflection)
w_i	$d^{1/(1-d)}$	–	Relative trait value (proportion of A) at maximum growth (at inflection)
W_i	$w_i \cdot A$	g or mm	Absolute trait value at maximum growth (at inflection)

Table 2. Sigmoid models used to fit growth trajectories of body mass, tarsus-length and wing-length of 50 species of passerines.

Model	Equation	Inflection point
Four parameters U-Richards	$W = A \left(1 + (d - 1) \cdot \exp\left(\frac{-k_U(t-T_i)}{d^{d/(1-d)}}\right) \right)^{1/(1-d)}$	Fitted at $d^{1/(1-d)}$ times 100% of the upper asymptote
Three parameters U-Bertalanffy	$W = A \left(1 - \left(\frac{1}{3}\right) \cdot \exp\left(\frac{-9k_U(t-T_i)}{4}\right) \right)^3$	Fixed at 29.63% ($d = 2/3$) of asymptote
U-Gompertz	$W = A \cdot \exp(-\exp(-e \cdot k_U(t-T_i)))$	Fixed at 36.79% ($d \rightarrow 1$ but $d \neq 1$) of asymptote
U-logistic	$W = \frac{A}{1 + \exp(-4k_U(t-T_i))}$	Fixed at 50.0% ($d = 2$) of asymptote
U4-model	$W = \frac{A}{1 + 3 \cdot \exp(-4^{4/3}k_U(t-T_i))^{1/3}}$	Fixed at 63.0% ($d = 4$) of asymptote

Their unified, T_i versions are given together with the location of inflection point as a proportion of the upper asymptote (for original model formulations see Ricklefs 1983, for details on U-versions see Tjørve & Tjørve 2010a, 2017a,c). The U-Richards becomes the special case of either of the three-parameter models, when the ‘exponent’ (d -parameter value) is fixed to the relevant value (for the specific model). W is trait value (mass or length), and t is time (age); see Table 1 for interpretation of other parameters.

(Table 2) each parameter controls one curve characteristic (Tjørve & Tjørve 2017b). It is a great advantage over other versions of the Richards model.

The traditional three-parameter models (logistic, Gompertz and Bertalanffy) are special cases of the Richards model (Brown & Rothery 1993, Tjørve & Tjørve 2010a); restricting the d -parameter value to a set value reduces the U-Richards to a three-parameter model where the inflection position is locked to a fixed fraction of the upper asymptote (Tjørve & Tjørve 2010a). The Unified-Richards model reduces to:

- the U-logistic model if the d -parameter value is set to two ($d = 2$), causing the inflection value to fall to 50% of the upper asymptote;
- the U-Gompertz model if the d -parameter value approaches one but is different from one ($d \rightarrow 1$ but $d \neq 1$), causing the inflection value to fall to 36.79% of the upper asymptote;
- the U-Bertalanffy model if the d -parameter value is fixed to two-thirds ($d = 2/3$), causing the inflection value to fall to 29.63% of the upper asymptote;
- the U4-model if the d -parameter value is set to four ($d = 4$), causing the inflection value to fall to 63.0% of the upper asymptote (see also Table 1, Fig. S1).

We fitted the above models to our data with both unrestrained (free) and restrained (fixed) upper asymptotes. The fixed asymptotes were set to averaged adult biometric values. A free asymptote is sometimes problematic as data above a certain trait value may be missing, either because nestlings become difficult to catch (causing truncation of the data) or because of body mass recession before

fledging (Ricklefs 1968b, Huin & Prince 2000, Mauck & Ricklefs 2005). Therefore, the fitted asymptote could either under- or overestimate adult size (Remeš & Martin 2002, Tjørve & Tjørve 2010b, Austin *et al.* 2011). We used free and fixed asymptotes to identify the more biologically meaningful model (which does not assume unrealistic growth parameters). However, it is important to note that fixing one or more parameters renders the model less flexible, causing a poorer fit to the data (Austin *et al.* 2011, Tjørve & Tjørve 2017a,b).

We used the R^2 -value and the AIC_c to compare the quality-of-fit between candidate models. The R^2 -value is a good measure of closeness of fit but a poorer criterion for selecting number of variables, whereas AIC_c (Akaike 1974, De Luna & Skouras 2003) penalizes models with extra parameters and can therefore suggest a worse-fitting model. From AIC_c we identified the best and second-best performing models. It has become customary to consider differences in AIC_c (i.e. ΔAIC_c) of more than two to indicate ‘substantial evidence’ for one model performing better than another (Burnham & Anderson 2002). To evaluate how the models performed according to the AIC_c , for each model we summed the proportion of species where it was the best performing model and where it was the second-best performing models (in per cent, meaning that for all models the total height of the bar may reach up to more than 100% in Fig. 1). In addition, the highest R^2 -values and differences in R^2 -values between models were also recorded. This type of regression typically returns high R^2 -values. Therefore, we divided the differences in R^2 -values into three categories (< 0.001, 0.001–0.01, > 0.01) better to determine similarity of the quality-of-fit across models.

We also utilized AIC_c to investigate whether the preferred three-parameter model is correlated with adult size. The biometric data on adults were obtained from the original articles or, when unavailable, from handbooks (Table S1). We analysed this relationship with one-way ANOVA in R software 3.1.1 (R Core Team 2015). The adult values for all traits were transformed by decadic logarithms to meet the assumption of normal distribution.

Parameter values and their statistical analyses

For all biometrics, we compared the mean fitted parameter and the derived measurement values of the U-Richards model with both a free and a fixed asymptote (Table 1) using a paired t -test in GraphPad PRISM 6.07 (GraphPad Software Inc 2014). First, we looked at the A -parameter to see whether the free asymptote returns averages that

are the same as the species' average (used to fix the asymptote, A).

Secondly, we looked at whether fixing the asymptote changed the average inflection values, represented by the time of inflection (T_i), relative inflection value (w_i) and the absolute inflection value (W_i). The w_i -value represents the placement of the inflection point as a proportion of the asymptote (Tjørve & Tjørve 2017a). For the U-Richards model it is given as $w_i = d^{1/(1-d)}$, whereas W_i , the absolute inflection value at the time of inflection (T_i), is calculated as $W_i = A \cdot w_i$. We note that the asymptote (A) for body mass and wing-length in addition to the absolute value at inflection (W_i) of body mass were log-transformed to meet the assumption of a normal distribution. The W_i of wing-length was square root-transformed for the same reason.

Thirdly, we looked for growth rate (k_U), which controls the maximum slope of the curve. This

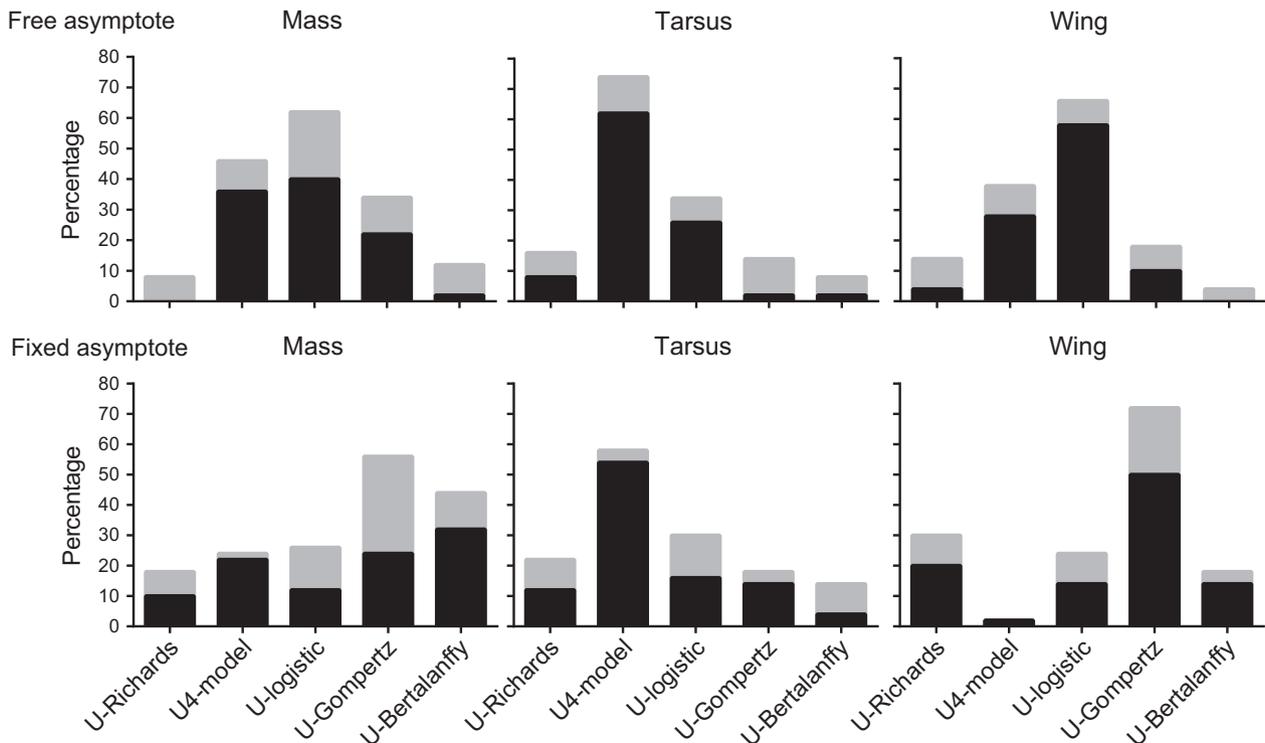


Figure 1. Percentage of the 50 passerine species for which a given model performed best, according to AIC_c . The three-parameter models were placed in order from the highest (U4-model) to the lowest (U-Bertalanffy) inflection placement (left to right; note that the U-Richards is a four-parameter model with variable inflection placement). Panels show the results separately for body mass, tarsus-length and wing-length, where the top row represents results for free asymptotes and the bottom row represents results for fixed upper asymptotes. Black areas represent the percentage of the species where the model is most likely to be the correct one (has the lowest AIC_c). The grey areas represent the percentage of species where the model is the second best and where $\Delta AIC_c \leq 2$ between this and the best model. The total maximum percentage summed for all models may exceed 100%. The higher the bar, the better suited a given model is for a given trait.

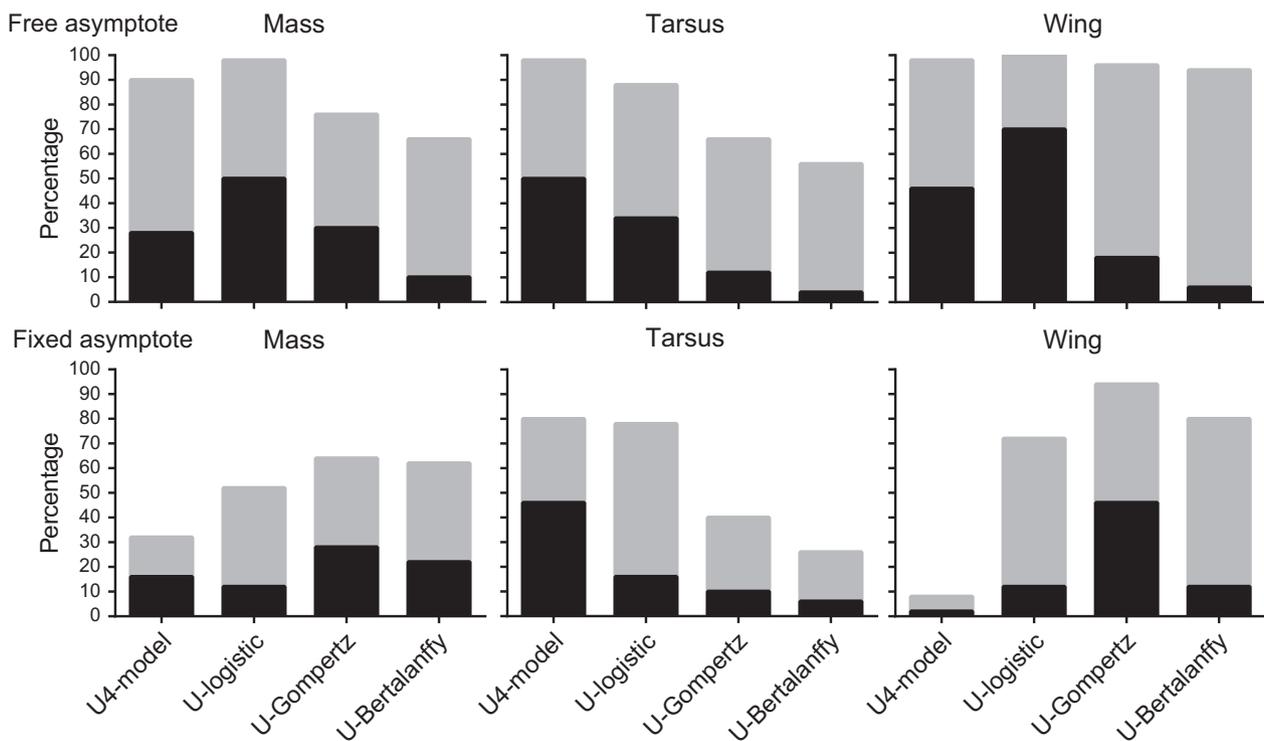


Figure 2. Summary of the differences in R^2 -values between the four-parameter U-Richards (as a reference) and each of the four three-parameter models, given separately for body mass, tarsus-length and wing-length of all 50 passerine species. The top row represents results for free asymptotes and the bottom row represents results for fixed upper asymptotes. The black areas represent the proportion of species where the difference in R^2 -value is less than 0.001 and the grey areas represent the proportion where the difference is between 0.001 and 0.01. The higher the bar, the closer the fit of the particular three-parameter model is to that of the more flexible four-parameter U-Richards model.

parameter in the U-family models is not merely a coefficient but represents the actual maximum relative growth rate at the time of inflection, T_i . Knowing the asymptote (A), we can derive the absolute growth rate (K_U) from the relative growth rate as $K_U = k_U \cdot A$ (Table 1). The k_U -parameter also receives the most attention in growth studies (e.g. Starck & Ricklefs 1998, Remeš & Martin 2002, Remeš 2006, Tjørve *et al.* 2009, Tjørve & Tjørve 2010b). Therefore, we also assessed how k_U -parameter values of pairs of models were correlated with each other in order to evaluate whether this parameter measured the same phenomenon in all models. The R software 3.1.1 (R Core Team 2015) was used for this analysis.

RESULTS

Model performance

All growth models appeared to fit the data reasonably well, judging by the R^2 -values. The four-

parameter U-Richards was understandably the best under this criterion (Table S2) but differences between the U-Richards and the other models were usually comparatively small (Fig. 2, see Table S2 for complete results and their overview). According to AIC_c , which penalizes the U-Richards for its extra parameter, different three-parameter models emerged as the best choice for the different biometric traits (Fig. 1; see Table S3 for complete results and their overview). These were usually the models closest to the U-Richards under the R^2 -criterion (97.45% of times). No single model produced a better fit across all three traits and under both criteria (Figs 1 and 2). When we fixed the upper asymptote of all models (including U-Richards), the differences in the R^2 -value on average increased, suggesting that the U-Richards is comparatively the better choice (Fig. 2). However, under AIC_c , other models were preferred and reached different values for body mass and wing-length compared with results with free asymptotes (Fig. 1).

Table 3. Differences in fitted parameter values and derived measurements of the U-Richards model with free vs. fixed upper asymptotes for body mass (g), tarsus-length (mm) and wing-length (mm).

Parameters	Free asymptote, mean (sd)	Fixed asymptote, mean (sd)	<i>t</i>	<i>P</i>
Body mass				
<i>d</i>	2.64 (1.74)	1.88 (2.10)	2.36	0.022
<i>A</i>	38.10 (37.95)	43.76 (45.05)	-4.07	< 0.001
<i>W_i</i>	17.40 (15.31)	13.43 (12.63)	3.75	< 0.001
<i>w_i</i>	0.52 (0.11)	0.39 (0.20)	4.61	< 0.001
<i>K_U</i>	3.60 (2.57)	3.41 (2.42)	3.12	0.002
<i>k_U</i>	0.12 (0.04)	0.10 (0.04)	3.53	< 0.001
<i>T_i</i>	5.56 (1.71)	4.41 (2.39)	1.15	< 0.001
Tarsus-length				
<i>d</i>	4.46 (2.92)	3.42 (1.73)	2.82	0.007
<i>A</i>	26.20 (9.70)	26.41 (9.39)	-0.86	0.397
<i>W_i</i>	15.70 (5.99)	15.08 (6.39)	1.99	0.052
<i>w_i</i>	0.61 (0.12)	0.57 (0.12)	2.38	0.021
<i>K_U</i>	2.20 (0.66)	2.17 (0.66)	1.30	0.200
<i>k_U</i>	0.09 (0.03)	0.09 (0.03)	1.85	0.071
<i>T_i</i>	5.23 (2.07)	4.92 (2.22)	0.31	0.040
Wing-length				
<i>d</i>	2.62 (1.14)	1.29 (0.63)	7.65	< 0.001
<i>A</i>	72.98 (36.68)	95.71 (36.30)	-9.36	< 0.001
<i>W_i</i>	37.44 (14.43)	37.27 (15.45)	0.68	0.498
<i>w_i</i>	0.54 (0.07)	0.40 (0.09)	4.91	< 0.001
<i>K_U</i>	5.28 (1.43)	4.89 (1.60)	2.31	0.025
<i>k_U</i>	0.08 (0.03)	0.05 (0.01)	8.39	< 0.001
<i>T_i</i>	9.26 (3.03)	8.99 (3.66)	0.28	0.261

The *d*-parameter value, upper asymptote (*A*, g or mm), time of inflection (*T_i*, days) and the relative maximum growth rate (*k_U*, per day) are fitted parameters, whereas the absolute inflection value (*W_i*, g or mm), relative inflection value (*w_i*, fraction of *A*) and absolute maximum growth rate (*K_U*, g/day or mm/day) are derived measurements. In paired *t*-tests we used ln-transformation for *A* of body mass and wing-length and for *W_i* of body mass. *W_i* of wing-length was square root-transformed.

Inflection placement

When we record the number of datasets (species) for which each three-parameter model performed best (according to the R^2 or AIC_c), we ordered them according to inflection placement, from the one having the highest (fixed) relative inflection value (63% of the asymptote in the U4-model) to the one having the lowest (30% in the U-Bertalanffy). Such an ordering resulted in most cases in a unimodal distribution (note that the bars for the U-Richards model have to be disregarded when discussing a possible unimodal distribution resulting from comparing the three-parameter models because the position of the inflection placement in this model is not fixed; Fig. 1). The exception was tarsus-length growth (both for free and for free asymptote), where the maximum fell in the model with the highest inflection placement (the U4-model), indicating that the maximum may lie at an even higher

percentage of the upper asymptote. At the same time, there was a tendency for the best performing model to be shifted slightly towards a lower inflection value when the upper asymptote was fixed (Fig. 1). A shift in the same direction in relative inflection values was apparent in the *d*-parameter values (and the corresponding *w_i*-values) returned by the U-Richards model (Table 3). According to the best-performing models indicated by AIC_c (Fig. 1) and the fitted values from the U-Richards (Table 3), the inflection point fell by 39–55% of the asymptote in body mass, by 55–65% in tarsus-length and by 40–55% in wing-length.

Correlations of *k_U*-parameter values between models

We compared the estimates of maximum relative growth rate (*k_U*) returned by different pairs of growth models to evaluate their consistency.

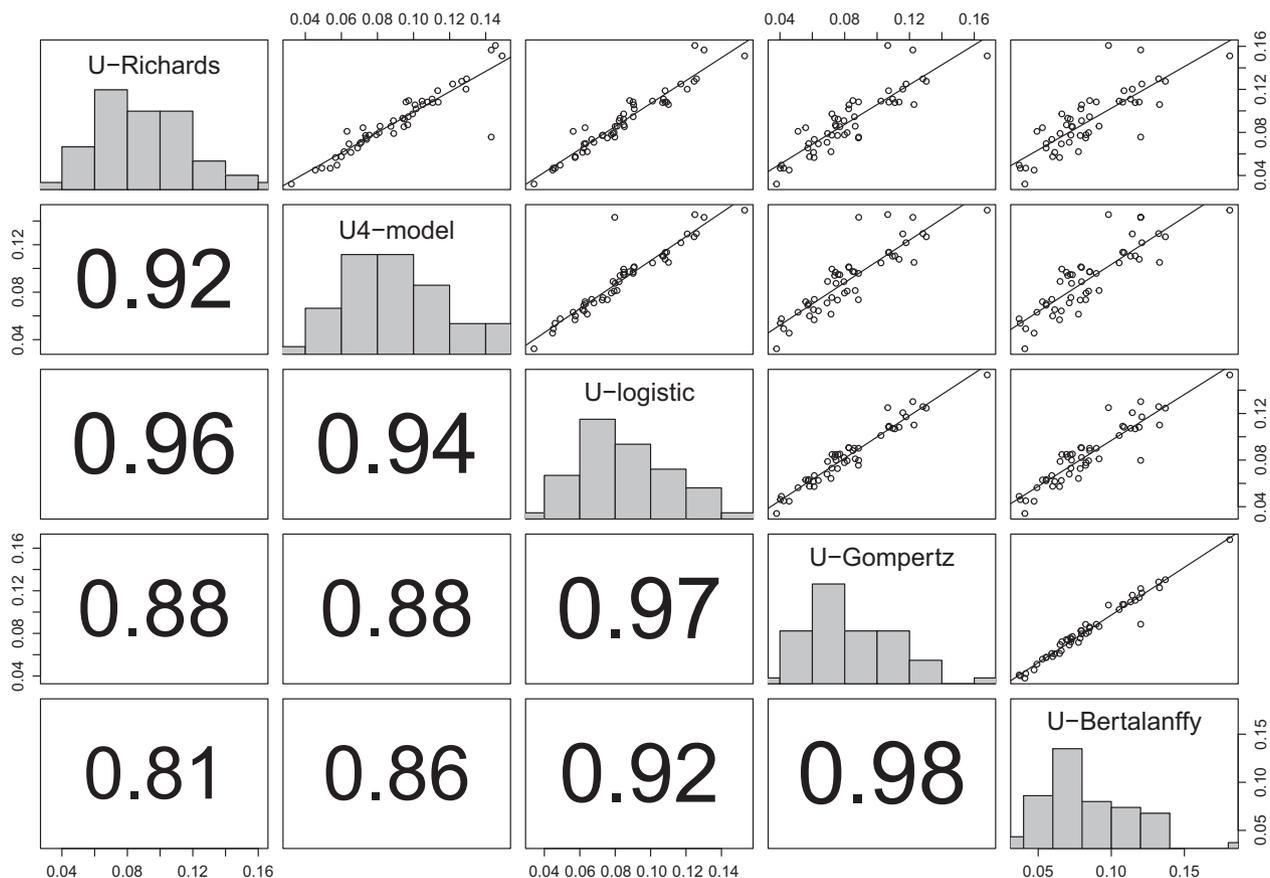


Figure 3. Correlations of returned k_U -parameter values (maximum relative growth) between pairs of growth models fitted to tarsus-length with a free asymptote for all 50 species. All combinations of growth-model pairs are shown as scatter plots (above diagonal) and associated correlation coefficients (below diagonal), and distributions of k_U -parameter values are depicted along the diagonal. The three-parameter models are placed in order from the highest (63% of asymptote in U4-model) to the lowest inflection placement (30% of asymptote in U-Bertalanffy). Remaining plots (for free and fixed asymptotes) are given in Fig. S2.

Three results emerged. First, pairs of three-parameter regression models correlated better when models with more similar inflection values (d -parameter values) were compared (Figs 3 and S2). Secondly, the k_U -parameter values of the U-Richards model correlated better with those of the three-parameter models with more similar inflection placements (represented by the fitted d -parameter value in U-Richards; Tables 1 and 3). Thirdly, the data on wing-length growth returned, in general, the lowest correlation coefficient, whereas body mass returned the highest, with tarsus-length in between. Restricting the upper asymptote to a fixed value caused higher correlations in k_U -parameter values (between pairs of models) in wing-length but little difference in body mass and tarsus-length was found (Figs 3 and S2).

Differences in parameter values between free and fixed asymptotes

In terms of body mass and wing-length, the asymptote was generally lower when fitted with a free rather than a fixed upper asymptote (Table 3). On the other hand, relative inflection placement, time of inflection and growth rates were generally higher when the asymptote was free than when it was fixed (Table 3). Differences between parameter estimates (for free and fixed asymptotes) in tarsus-length were mostly not statistically significant (Table 3).

Body size and preferred model

The choice of the best model according to the AIC_c depended on adult body mass for both free

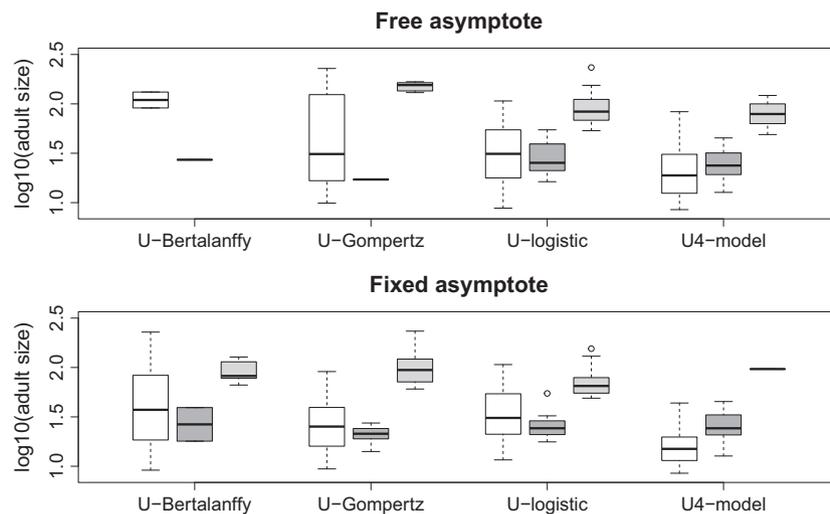


Figure 4. Variation in adult size of three biometric traits and the best fitting model. Median adult value (together with interquartile range) is shown for species for which a given model fitted the data best. Results are shown for body mass (white box), tarsus-length (dark grey box) and wing-length (light grey box).

($F_{3,46} = 3.47$, $P = 0.024$) and fixed ($F_{3,46} = 4.23$, $P = 0.01$) asymptotes. In both cases, the U4-model was preferred over the U-Bertalanffy model in species with low body mass (Fig. 4). For wing-length fitted with a free asymptote, the U-Gompertz model was preferred over models with higher inflection placements in species with long wings ($F_{2,47} = 8.51$, $P < 0.001$, Fig. 4). However, this pattern was not observed for wing-length with a fixed asymptote ($F_{3,46} = 2.52$, $P = 0.069$). For tarsus-length there were no significant differences (in adult size) in the distribution of the species between the models, for either free ($F_{3,46} = 1.26$, $P = 0.298$) or fixed asymptote ($F_{3,46} = 0.75$, $P = 0.527$). For complete results of all analyses, see Appendix S1.

DISCUSSION

Model performance

No model was the best for all species and traits. When judged by R^2 -values, the U-Richards was always the preferred model but its advantage relative to the best performing three-parameter model was generally negligible (Fig. 2, Table S2). Accordingly, when judged by AIC_c , which penalizes the U-Richards for its extra parameter, it failed to be supported, and different three-parameter models were favoured instead (Fig. 1). However, this change had its logic: the favoured three-parameter

models were usually those closest to the U-Richards using the R^2 -criterion (compare Figs 1 and 2). Of the three-parameter models, the U-logistic (body mass and wing-length) and the U4-model (tarsus-length) were the most frequently supported (Fig. 1). These results together demonstrate that growth trajectories of different traits and different species typically have different shapes and therefore require different three-parameter regression models (see also Tjørve & Tjørve 2010b). However, some researchers may still prefer to select only one three-parameter growth model for a broad-scale interspecific comparison of a given trait. One should then still test a number of models to be able to choose the model that performs well with as many of the datasets as possible (for example based on the R^2 -criterion or the AIC_c as shown in Figs 1 and 2). The reason for this is that model choice without testing in this way may lead to suboptimal fit with misleading growth parameter estimates. We suggest that similar analyses should be run for other taxa and traits to identify the most appropriate growth models and the models that might also be useful for modelling phenotypic plasticity in growth within species or other related phenomena.

Inflection placement

The three-parameter models we used have different relative inflection values (w_i) fixed at between

29.6 and 63.0% of the upper asymptote (Tjørve & Tjørve 2017a). For body mass fitted with a free asymptote, the U-logistic with an inflection at 50% of the upper asymptote was the most frequently preferred model. This finding seems to support Ricklefs' (1968a) recommendation of fitting the logistic model to the body mass of songbirds and smaller altricial birds with fast growth rates. This is also consistent with passerines typically having a fast growth of body mass and a late onset of maximum growth rate.

The logistic model is the traditional three-parameter model with the highest inflection value, which usually means maximum growth rate falling late in the postnatal period. However, the U4-model and the U-Gompertz model combined were preferred for more species than the U-logistic (Fig. 1), a pattern that became even stronger when fixing the upper asymptote. This indicated that in many species the inflection falls at different parts of the curve, suggesting quite diverse growth strategies within passerine birds. It also illustrates that the biology of passerines is not similar enough for body mass growth of all species to be realistically described by a single three-parameter model.

Compared with body mass, the maximum wing-length growth rate is usually expected to come later in the ontogeny (Badyaev & Martin 2000). However, its d -parameter value returned from the U-Richards was on average quite similar to that of body mass (Table 3); similarly, the U-logistic and the U-Gompertz were more often supported as the best model (Fig. 1). Similar results were described for the growth of the Black-bellied Sandgrouse *Pterocles orientalis* (Aourir *et al.* 2016) and could indicate that the two traits follow each other throughout the growth period (Wright *et al.* 2006, Jones *et al.* 2017).

Tarsus-length was, on the other hand, usually best modelled by the U4-model (inflection at 63% of upper asymptote), which also agrees well with the high d -parameter values returned from the U-Richards (Table 3). The high relative inflection placement is consistent with the fact that the tarsus is already well developed at hatching, typically grows fast (Tjørve & Underhill 2009, Pacheco *et al.* 2010) and is close to adult size at fledging (Holcomb 1968, Ricklefs 1968a, Earlé 1986, Frei *et al.* 2010). In addition, the high inflection placement in tarsus reflects the biological advantage of being able to 'stand on one's own feet' as early as possible, which is attained by quickly increasing

the growth rate of tarsus-length and finishing most of its growth. These findings are supported by Tjørve and Tjørve (2017b), who fitted the U-Richards to the tarsus-length growth of the African Oystercatcher *Haematopus moquini*: and the model returned a d -parameter value representing an inflection point at 73% of the upper asymptote.

This demonstrates how we can link differences in d -parameter values (or in preferred three-parameter models) to evolutionary adaptations, not only among traits (biometrics) but also among species. The variation in performance of the three-parameter models is directly attributable to the differences in inflection placement and how this affects curve shape. This is likely because the respective relative inflection placements of the preferred model reflect the underlying avian biology.

The correlations of k_U -parameter values between models

Growth rate is the most studied trait in life-history studies and thus the reliability of its estimation is of great interest (Ricklefs 1968a, 1969, 1976, Remeš & Martin 2002, Remeš 2006, 2007, Martin 2015). Overall, we found the k_U -parameter values to be highly correlated in all pairs of models, which is not surprising as they are all members of the Richards family (see Brown & Rothery 1993, Tjørve & Tjørve 2010a). However, the correlation was higher when relative inflection values of the two three-parameter models were closer (see Table 2 for inflection placements) and the k_U -parameter values from the U-Richards model correlated better with those of the three-parameter models with more similar inflection placements. These findings suggest that estimates are closer for more similar models. Moreover, in models with relative inflection values closer to (or including) the best performing model (according to R^2 or AIC_c) the k_U -parameter values correlated better with those of this best performing model (than the k_U -parameter values from models with inflection further away from the best performing model). This indicates that poorly fitting models often return unrealistic k_U -parameter values, potentially compromising ecological and evolutionary inferences based on these estimates. Lastly, traits differ in their susceptibility to these biases: estimates for wing-length correlated worst (Fig. S2), suggesting that certain traits require special attention when quantifying their growth rates and patterns.

Fixed asymptotes

When fixing the upper asymptote to the adult value, we saw a general shift in preferred models towards those with lower inflection values (U-Bertalanffy and U-Gompertz) in body mass and wing-length but not in tarsus-length (Figs 1 and 2). This was supported by lower d -parameter values (translating to lower inflection placement) returned from the U-Richards when the asymptote was fixed (Table 3). Tjørve and Tjørve (2010b) report a similar shift towards lower relative inflection placement when fixing the asymptote in body mass and wing-length in waders and explain this as a result of truncation (because the free A -parameter causes a lower asymptote). The parameter estimates for A were higher and for w_i and k_U lower when fixing the asymptote for body mass and wing-length, whereas tarsus-length was not affected (Table 3). Moreover, estimates of growth rate (k_U) for wing-length were more consistent across models when fixing the asymptote (Fig. S2), whereas this effect was negligible for body mass and tarsus-length (Figs 3 and S2).

Fixing the asymptote to the adult value thus certainly has pros and cons. Tjørve and Tjørve (2010b) and Austin *et al.* (2011) recommend fixing because free asymptotes often return unrealistic values for the asymptote compared with the adult value of the trait in question (also see above). Moreover, sometimes fixing the asymptote will return more consistent estimates of growth rate across models, as was the case with wing-length in our study. If so, these estimates are probably more robust and less biased. On the other hand, fitted values for the remaining parameters might become less trustworthy because of the reduced model flexibility (Austin *et al.* 2011, see our Table 3). Then, the solution might be to use the four-parameter U-Richards, as it is more flexible even when fixing the asymptote and therefore is more likely to return a reliable growth curve (Zach 1988). This appears to agree with our results, as the R^2 -difference between the U-Richards and the other models increased when we fixed the asymptote (Fig. 2). However, because of its extra parameter, the U-Richards requires more data points to avoid overfitting (Tjørve & Tjørve 2017b). Thus, whether to fix the upper asymptote or not is a complex issue and depends on one's research questions and the data to hand.

Body size and preferred model

There has been speculation regarding which of the sigmoid growth models are best suited for different taxa of birds (Ricklefs 1968a, 1973, Tjørve & Tjørve 2010b). We tested whether the preferred three-parameter model depends on adult body size. We found that models with high inflection placement (percentage of the upper asymptote) were preferable in small species and species with short wings, making them especially suitable for taxa with small-sized representatives, e.g. passerines.

This may be explained by small birds having a much higher hatching mass or length (initial trait value) compared with adult size (Blueweiss *et al.* 1978). Such higher relative hatching values should contribute to higher inflection values in smaller birds. Moreover, factors such as a shorter time available to attain adult values and possible food restrictions may cause smaller birds to reach maximum growth rate relatively later in the growth period and therefore also contribute to higher relative inflection placement. By implication, models with low inflection placement should be suitable for taxa with large species, e.g. waders, ducks or birds of prey. These suggestions agree with the literature (Ricklefs 1968a, 1973). Moreover, Tjørve and Tjørve (2017b), who fitted the U-Richards to three shorebird species, also report that fitting the U-Richards to the smaller species returned a higher relative inflection placement, indicating that the above discussion may also hold for precocial (and semi-precocial) birds. However, pairwise comparisons (Appendix S1) revealed significant differences only between the most extreme models in terms of inflection placement. Thus, the growth model for a given taxon cannot be chosen automatically, for example by selecting the model that on average fits the species in the taxon best, but should be carefully considered.

We conclude that fitting several models, or the U-Richards with its flexible relative inflection value, might be an informative approach when analysing growth strategies in birds. This is because growth trajectories of different traits and different species may require either different three-parameter regression models or the application of the U-Richards with four parameters, the latter being the most convenient way to avoid bias. However, if fitting only one growth model for a broad-scale

interspecific comparison of a certain trait in passerines, all models should still first be tested (on all or a selected number of datasets). Then the model that performs best for the highest number of species (according to the R^2 -value or AIC_c , as we show in Figs 1 and 2) should be chosen. It is therefore timely to run similar analyses for other taxa and traits to identify the most convenient growth models. Such approaches could also be applied to model phenotypic plasticity in growth within species and related phenomena.

This study was supported by EEA and Norway grants (CZ07/MSNG/INSNG03) and Palacky University (IGA PrF_2016_004, IGA_PrF_2017_006). We thank the anonymous reviewers for comments that improved the quality of our manuscript.

REFERENCES

- Aggrey, S.E.** 2002. Comparison of three nonlinear and spline regression models for describing chicken growth curves. *Poultry Sci.* **81**: 1782–1788.
- Akaike, H.** 1974. A new look at the statistical model identification. *IEEE Trans. Autom. Control* **19**: 716–723.
- Albano, N., Masero, J.A., Villegas, A., Maria Abad-Gomez, J. & Sanchez-Guzman, J.M.** 2011. Plasma metabolite levels predict bird growth rates: a field test of model predictive ability. *Comp. Biochem. Physiol. A* **160**: 9–15.
- Aourir, M., Znari, M., El Abbassi, A. & Radi, M.** 2016. Growth patterns and developmental strategy in the Black-bellied Sandgrouse *Pterocles orientalis*. *Ardeola* **63**: 311–327.
- Arendt, J.D.** 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**: 149–177.
- Atil, H., Grossman, M. & Takma, C.** 2007. Comparison of growth curve models on average and individual body weights in chickens. *Arch. Geflügelkunde* **71**: 1–5.
- Austin, S.H., Robinson, T.R., Robinson, W.D. & Ricklefs, R.E.** 2011. Potential biases in estimating the rate parameter of sigmoid growth functions. *Methods Ecol. Evol.* **2**: 43–51.
- Badyaev, A.V. & Martin, T.E.** 2000. Individual variation in growth trajectories: phenotypic and genetic correlations in ontogeny of the House Finch (*Carpodacus mexicanus*). *J. Evol. Biol.* **13**: 290–301.
- Bluweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. & Sams, S.** 1978. Relationships between body size and some life history parameters. *Oecologia* **37**: 257–272.
- Bortolotti, G.R.** 1986. Evolution of growth rates in eagles: sibling competition vs. energy considerations. *Ecology* **67**: 182–194.
- Brisbin, I.L., Collins, C.T., White, G.C. & McCallum, D.A.** 1987. A new paradigm for the analysis and interpretation of growth data – the shape of things to come. *Auk* **104**: 552–554.
- Brown, D. & Rothery, P.** 1993. *Models in Biology: Mathematics, Statistics and Computing*. Chichester: John Wiley & Sons.
- Brown, W.P., Eggermont, P., Lariccia, V. & Roth, R.R.** 2007. Are parametric models suitable for estimating avian growth rates? *J. Avian Biol.* **38**: 495–506.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd edn. New York, NY: Springer.
- Canaza-Cayo, A.W., Huanca, T., Gutiérrez, J.P. & Beltrán, P.A.** 2014. Modelling of growth curves and estimation of genetic parameters for growth curve parameters in Peruvian young Llamas (*Lama glama*). *Small Ruminant Res.* **130**: 81–89.
- Case, T.J.** 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q. Rev. Biol.* **53**: 243–282.
- Cheng, Y.R. & Martin, T.E.** 2012. Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *Am. Nat.* **180**: 285–295.
- Cho, Y.M., Sang, B.D., Lee, H.K., Yoon, H.B. & Park, Y.I.** 2001. A comparison of nonlinear models for describing weight-age relationship in Korean native chicken. *Poultry Sci.* **43**: 811–816.
- Darmani Kuhl, H., Kebreab, E., Lopez, S. & France, J.** 2003. An evaluation of different growth functions for describing the profile of live weight with time (age) in meat and egg strains of chicken. *Poultry Sci.* **82**: 1536–1543.
- De Luna, X. & Skouras, K.** 2003. Choosing a model selection strategy. *Scand. J. Stat.* **30**: 113–128.
- Earlé, R.A.** 1986. The breeding biology of the South African Cliff Swallow. *Ostrich* **57**: 138–156.
- Faridi, A., Lopez, S., Ammar, H., Salwa, K.S., Golian, A., Thornley, J.H.M. & France, J.** 2015. Some novel growth functions and their application with reference to growth in Ostrich. *J. Anim. Sci.* **93**: 2641–2652.
- Frei, B., Bird, D.M. & Titman, R.D.** 2010. Bobolink egg mass variability and nestling growth patterns. *Wilson J. Ornithol.* **122**: 432–438.
- Gbangboche, A.B., Glele-Kakai, R., Salifou, S., Albuquerque, L.G. & Leroy, P.L.** 2008. Comparison of non-linear growth models to describe the growth curve in West African Dwarf Sheep. *Animal* **2**: 1003–1012.
- Gille, U. & Salomon, F.** 1995. Bone growth in ducks through mathematical models with special reference to the Janoschek growth curve. *Growth Dev. Aging* **59**: 207–214.
- GraphPad Software Inc.** 2014. *GraphPad Curve Fitting Guide*. La Jolla, CA: GraphPad.
- Holcomb, L.C.** 1968. Growth of nestling Goldfinches compared to adult size and differential development rate of structures in relation to their function. *Nebraska Bird Rev.* **32**: 22–32.
- Holt, D.W., Gray, K., Maples, M.T. & Korte, M.A.** 2016. Mass growth rates, plumage development, and related behaviors of Snowy Owl (*Bubo scandiacus*). *J. Raptor Res.* **50**: 131–143.
- Huin, N. & Prince, P.A.** 2000. Chick growth in albatrosses: curve fitting with a twist. *J. Avian Biol.* **31**: 418–425.
- Jones, M.G.W., Dilley, B.J., Hagens, Q.A., Louw, H., Mertz, E.M., Visser, P. & Ryan, P.G.** 2014. The effect of parental age, experience and historical reproductive success on Wandering Albatross (*Diomedea exulans*) chick growth and survival. *Polar Biol.* **37**: 1633–1644.
- Jones, T.M., Ward, M.P., Benson, T.J. & Brawn, J.D.** 2017. Variation in nestling body condition and wing development

- predict cause-specific mortality in fledgling Dickcissels. *J. Avian Biol.* **48**: 439–447.
- Kentie, R., Hooijmeijer, J.C.E.W., Trimbos, K.B., Groen, N.M. & Piersma, T.** 2013. Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *J. Appl. Ecol.* **50**: 243–251.
- Klaassen, M., Habekotte, B., Schikelskoek, P., Stienen, E. & Van Tienen, P.** 1994. Influence of growth rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks. *Ibis* **136**: 197–204.
- Lok, T., Overdijk, O. & Piersma, T.** 2014. Interpreting variation in growth of Eurasian Spoonbill chicks: disentangling the effects of age, sex and environment. *Ardea* **102**: 181–194.
- Martin, T.E.** 2015. Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science* **349**: 966–970.
- Martin, T.E., Lloyd, P., Bosque, C., Barton, D.C., Biancucci, A.L., Cheng, Y.R. & Ton, R.** 2011. Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. *Evolution* **65**: 1607–1622.
- Mauck, R.A. & Ricklefs, R.E.** 2005. Control of fledging age in Leach's Storm-Petrel, *Oceanodroma leucorhoa*: chick development and pre-fledging mass loss. *Funct. Ecol.* **19**: 73–80.
- McKinnon, L., Picotin, M., Bolduc, E., Juillet, C. & Bety, J.** 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the high Arctic. *Can. J. Zool.* **90**: 961–971.
- Mullers, R.H.E. & Amar, A.** 2015. Parental nesting behavior, chick growth and breeding success of Shoebills (*Balaeniceps rex*) in the Bangweulu wetlands, Zambia. *Waterbirds* **38**: 1–9.
- Nahashon, S.N., Aggrey, S.E., Adefope, N.A., Amenyenu, A. & Wright, D.** 2006. Growth characteristics of Pearl Gray Guinea Fowl as predicted by the Richards, Gompertz, and logistic models. *Poultry Sci.* **85**: 359–363.
- Navarro, R.A., Mullers, R.H.E., Meijer, H.A.J. & Underhill, L.G.** 2015. Energy expenditure of free-ranging chicks of the Cape Gannet *Morus capensis*. *Physiol. Biochem. Zool.* **88**: 406–415.
- O'Connor, R.J.** 1978. Growth strategies in nestling passerines. *Living Birds* **16**: 209–238.
- Pacheco, M.A., Beissinger, S.R. & Bosque, C.** 2010. Why grow slowly in a dangerous place? Postnatal growth, thermoregulation, and energetics of nestling Green-rumped Parrotlets (*Forpus passerinus*). *Auk* **127**: 558–570.
- Penteriani, V., Delgado, M.M., Maggio, C., Aradis, A. & Sergio, F.** 2005. Development of chicks and dispersal behaviour of young in the Eagle Owl *Bubo bubo*. *Ibis* **147**: 155–168.
- R Core team** 2015. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.R-project.org> (accessed 20 March 2016).
- Remes, V.** 2006. Growth strategies of passerine birds are related to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). *Evolution* **60**: 1692–1700.
- Remes, V.** 2007. Avian growth and development rates and age-specific mortality: the roles of nest predation and adult mortality. *J. Evol. Biol.* **20**: 320–325.
- Remes, V. & Martin, T.E.** 2002. Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* **56**: 2505–2518.
- Richards, F.J.** 1959. A flexible growth function for empirical use. *J. Exp. Bot.* **10**: 290–301.
- Ricklefs, R.E.** 1967. A graphical method of fitting equation to growth curves. *Ecology* **48**: 978–983.
- Ricklefs, R.E.** 1968a. Patterns of growth in birds. *Ibis* **110**: 419–451.
- Ricklefs, R.E.** 1968b. Weight recession in nestling birds. *Auk* **85**: 30–85.
- Ricklefs, R.E.** 1969. Preliminary models for growth rates in altricial birds. *Ecology* **50**: 1031–1039.
- Ricklefs, R.E.** 1973. Patterns of growth in birds II. Growth rate and mode of development. *Ibis* **115**: 177–201.
- Ricklefs, R.E.** 1976. Growth rates of birds in the humid New World tropics. *Ibis* **118**: 179–207.
- Ricklefs, R.E.** 1983. Avian postnatal development. In Farner, D.S., King, J.R. & Parkes, K.C. (eds) *Avian Biology*. New York, NY: Academic Press.
- Ricklefs, R.E.** 1984. Components of variance in measurements of nestling European Starlings (*Sturnus vulgaris*) in southern Pennsylvania. *Auk* **101**: 319–333.
- Roff, D.A.** 1992. *The Evolution of Life Histories: Theory and Analysis*. New York, NY: Chapman & Hall.
- Sengul, T. & Kiraz, S.** 2005. Non-linear models for growth curves in Large White Turkeys. *Turk. J. Vet. Anim. Sci.* **29**: 331–337.
- Shalev, B.A. & Pasternak, H.** 1983. Genetic-economic evaluation of traits in a broiler enterprise: the relative genetic-economic values. *Br. Poultry Sci.* **24**: 521–529.
- Smith, D.M., Kelly, J.F. & Finch, D.M.** 2007. Avian nest box selection and nest success in burned and unburned southwestern riparian forest. *J. Wildl. Manage.* **71**: 411–421.
- Starck, J.M. & Ricklefs, R.E. (eds)** 1998. *Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum*. New York, NY: Oxford University Press.
- Sugden, L.G., Driver, E.A. & Kingsley, M.C.S.** 1981. Growth and energy-consumption by captive Mallards. *Can. J. Zool.* **59**: 1567–1570.
- Thornley, J.H.M., Shepherd, J.J. & France, J.** 2007. An open-ended logistic-based growth function: analytical solutions and the power-law logistic model. *Ecol. Model.* **204**: 531–534.
- Tjørve, E.** 2003. Shapes and functions of species-area curves: a review of possible models. *J. Biogeogr.* **30**: 827–835.
- Tjørve, E. & Tjørve, K.M.C.** 2010a. A unified approach to the Richards-model family for use in growth analyses: why we need only two model forms. *J. Theor. Biol.* **267**: 417–425.
- Tjørve, K.M.C. & Tjørve, E.** 2010b. Shapes and functions of bird-growth models: how to characterise chick postnatal growth. *Zoology* **113**: 326–333.
- Tjørve, K.M.C. & Tjørve, E.** 2017a. A proposed family of Unified models for sigmoidal growth. *Ecol. Model.* **359**: 117–127.
- Tjørve, K.M.C. & Tjørve, E.** 2017b. Modelling avian growth with the Unified-Richards: as exemplified by wader-chick growth. *J. Avian Biol.* **48**: 770–784.

- Tjørve, K.M.C. & Tjørve, E.** 2017c. The use of Gompertz models in growth analyses, and new Gompertz-model approach: an addition to the Unified-Richards family. *PLoS ONE* **12**: e0178691.
- Tjørve, K.M.C. & Underhill, L.G.** 2009. Growth and its relationship to fledging success of African Black Oystercatcher *Haematopus moquini* chicks. *Zoology* **112**: 27–37.
- Tjørve, K.M.C., Garcia-Pena, G.E. & Szekely, T.** 2009. Chick growth rates in Charadriiformes: comparative analyses of breeding climate, development mode and parental care. *J. Avian Biol.* **40**: 553–558.
- Ton, R. & Martin, T.E.** 2016. Metabolism correlates with variation in post-natal growth rate among songbirds at three latitudes. *Funct. Ecol.* **30**: 743–748.
- Viñuela, J. & Ferrer, M.** 1997. Regulation of growth in Red Kites and Imperial Eagles. *Wilson Bull.* **109**: 92–101.
- Werschkul, D.F. & Jackson, J.A.** 1979. Sibling competition and avian growth-rates. *Ibis* **121**: 97–102.
- Wright, J., Markman, S. & Denney, S.M.** 2006. Facultative adjustment of pre-fledging mass loss by nestling Swifts preparing for flight. *Proc. R. Soc. B* **273**: 1895–1900.
- Ydenberg, R.C.** 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the Alcidae. *Ecology* **70**: 1494–1506.
- Zach, R.** 1988. Growth-curve analysis: a critical reevaluation. *Auk* **105**: 208–210.

Received 29 May 2017;
 revision accepted 18 February 2018.
 Associate Editor: José Alves.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Comparison of the cumulative increase and the relative growth rate of the three-parameter sigmoid growth curves (special cases of the U-Richards) having identical trait values at hatching = 0.1 (at age = 0), upper asymptotes $A = 1$ and maximum relative growth rates at inflection $k_U = 0.1$. The comparison shows how the time of inflection (maximum relative growth, T_i) differs between the models.

Figure S2. Correlations between k_U -parameter values (maximum relative growth) estimated by pairs of growth models fitted to all remaining biometrics for all 50 datasets (i.e. species).

Table S1. List of literature sources.

Table S2. R^2 -values for all biometrics with free and fixed upper asymptote.

Table S3. Differences in AIC_c (ΔAIC_c) for all biometrics between the model with the highest probability of being the correct model and other models.

Appendix S1. Results of ANOVA and Tukey post-hoc tests for adult size of all biometrics and choice of the best models according to the AIC_c .