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## Article

### Richards's equation and nonlinear mixed models applied to avian growth: why use them?

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Postnatal growth is an important life-history trait that varies widely across avian species, and several equations with a sigmoidal shape have been used to model it. Classical three-parameter models have an inflection point fixed at a percentage of the upper asymptote which could be an unrealistic assumption generating biased fits. The Richards model emerged as an interesting alternative because it includes an extra parameter that determines the location of the inflection point which can move freely along the growth curve. Recently, nonlinear mixed models (NLMM) have been used in modeling avian growth because these models can deal with a lack of independence among data as typically occurs with multiple measurements on the same individual or on groups of related individuals. Here, we evaluated the usefulness of von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards's equations modeling chick growth in the imperial shag *Phalacrocorax atriceps*. We modelled growth in commonly used morphological traits, including body mass, bill length, head length and tarsus length, and compared the performance of models by using NLMM. Estimated adult size, age at maximum growth and maximum growth rates markedly differed across models. Overall, the most consistent performance in estimated adult size was obtained by the Richards model that showed deviations from mean adult size within 5%. Based on AICc values, the Richards equation was the best model for all traits analyzed. For tarsus length, both Richards and  $U_4$  models provided indistinguishable fits because the relative inflection value estimated from the Richards model was very close to that assumed by the  $U_4$  model. Our results highlight the bias incurred by three-parameter models when the assumed inflection placement deviates from that derived from data. Thus, the application of the Richards equation using the NLMM framework represents a flexible and powerful tool for the analysis of avian growth.

Keywords: growth models, nonlinear mixed models, asymptotic size, grouped data, maximum growth rate, random effects



## Introduction

Postnatal growth is an important life-history trait that varies widely across avian orders and life-history strategies (Ricklefs 1968a, Stearns 1992, Starck and Ricklefs 1998a, b). Patterns of growth also vary broadly among morphological traits such as bill length, tarsus length or wing length (Velando et al. 2000, Svagelj and Quintana 2017). In virtue of that variation, several equations with a sigmoidal shape have been used to model avian growth (Ricklefs 1967, 1968a). In general, these nonlinear models comprise a small number of parameters with biological meaning (usually three) that are useful for inter- and intraspecific comparisons. For example, parameters that are often used include the estimated adult size ( $A$ ), a growth rate constant ( $k$ ) and the inflection point ( $T_i$ ) that indicates the age when growth is greatest (Starck and Ricklefs 1998b).

Ornithologists have mainly used logistic, Gompertz, and von Bertalanffy models (Ricklefs 1967, 1968a, Starck and Ricklefs 1998b) to describe the postnatal growth. Despite their utility and simplicity, these three-parameter models have fixed forms with an inflection placement fixed at a percentage of the upper asymptote (30, 37 and 50% for von Bertalanffy, Gompertz and logistic models, respectively) which is often an unrealistic assumption (Tjørve and Tjørve 2017a). An interesting alternative to these equations is the Richards model (Richards 1959, Nelder 1962, Sugden et al. 1981, Tjørve and Tjørve 2010). This four-parameter model includes an extra parameter  $d$  that determines the location of the inflection point which can move freely along the growth curve (Tjørve and Tjørve 2010). Moreover, logistic, Gompertz, and von Bertalanffy models represent particular cases of the Richards equation

when the  $d$ -parameter is fixed at specific values (Tjørve and Tjørve 2010, 2017a, b). Even though the Richards equation might be preferred over simpler models because of its greater flexibility and accuracy, model performance can vary based on data characteristics as well as the methods used to fit the model. Unfortunately, studies comparing the performance of the Richards model in relation to typical three-parameter models are scarce and comparisons that are made often incorrectly assume independence across the data used to construct growth curves (Sugden et al. 1981, Aggrey 2002, Tjørve and Tjørve 2017b, Vrána et al. in press).

Recently, nonlinear mixed-effect models (Pinheiro and Bates 2000) have become a powerful tool to analyze postnatal growth (Oswald et al. 2012, Sofaer et al. 2013, Aldredge 2016). Nonlinear mixed-effect models (hereafter, NLMM) can deal with a lack of statistical independence among data, as occurs with multiple measurements on the same individual or measurements on groups of related individuals (e.g. broods). These models allow the simultaneous inclusion of growth parameters as fixed effects, describing the average growth curve, as well as random effects allowing for random variation around the average values (Sofaer et al. 2013, Aldredge 2016). Moreover, NLMM allow a regressive approach where the effect of predictor variables can be evaluated for each growth parameter (Kalmbach et al. 2009, Giudici et al. 2017, Svagelj and Quintana 2017, Tuero et al. 2018). Therefore, the application of the Richards equation using the NLMM approach appears as a flexible analytical tool to be considered for the analysis of avian growth.

In this paper, we assess the utility of three- and four-parameter equations modeling chick growth in the imperial shag *Phalacrocorax atriceps*, a medium sized seabird. We

Table 1. Parameterizations for von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards growth models.  $W_{(t)}$  is size at age  $t$ , and  $A$ ,  $k$ ,  $T_i$  and  $d$  are the upper asymptote, maximum relative growth rate, age at the inflection point and shape parameter, respectively.  $W_i$  is the absolute value at maximum growth (size at the inflection point). Relative values at maximum growth are presented as percentage of upper asymptote at inflection.

Growth model	Parameterization	Value at inflection	
		$W_i$	in % of $A$
von Bertalanffy	$W_{(t)} = A \cdot \left(1 - \frac{1}{3} \cdot e^{-\frac{9}{4}k(t-T_i)}\right)^3$	$\frac{8}{27} \cdot A$	29.6
Gompertz	$W_{(t)} = A \cdot e^{-e^{-k(t-T_i)}}$	$\frac{1}{e} \cdot A$	36.8
Logistic	$W_{(t)} = \frac{A}{1 + e^{-4k(t-T_i)}}$	$\frac{1}{2} \cdot A$	50.0
$U_4$	$W_{(t)} = A \cdot \left(1 + 3 \cdot e^{-\frac{4}{3}k(t-T_i)}\right)^{-\frac{1}{3}}$	$4^{-\frac{1}{3}} \cdot A$	63.0
Richards	$W_{(t)} = A \cdot \left(1 + (d-1) \cdot e^{-\frac{k(t-T_i)}{d^{1-d}}}\right)^{\frac{1}{1-d}}$	$d^{\frac{1}{1-d}} \cdot A$	0 to 100

Table 2. Instantaneous growth rate equations for von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards models. Equations were obtained as first derivatives of growth models.  $Y_{(t)}$  is daily growth rate at age  $t$ , and  $A$ ,  $k$ ,  $T_i$  and  $d$  are the upper asymptote, maximum relative growth rate, age at the inflection point and shape parameter, respectively.

Growth model	Instantaneous rate of growth
von Bertalanffy	$Y_{(t)} = \frac{9}{4} \cdot A \cdot k \cdot e^{-\frac{9}{4}k \cdot (t-T_i)} \cdot \left( 1 - \left( \frac{1}{3} \cdot e^{-\frac{9}{4}k \cdot (t-T_i)} \right) \right)^2$
Gompertz	$Y_{(t)} = e \cdot A \cdot k \cdot e^{-e \cdot k \cdot (t-T_i)} \cdot e^{-e^{-k \cdot (t-T_i)}}$
Logistic	$Y_{(t)} = 4 \cdot A \cdot k \cdot \frac{e^{-4 \cdot k \cdot (t-T_i)}}{(1 + e^{-4 \cdot k \cdot (t-T_i)})^2}$
$U_4$	$Y_{(t)} = 4^{\frac{4}{3}} \cdot A \cdot k \cdot e^{-\frac{4}{3}k \cdot (t-T_i)} \cdot \left( 1 + \left( 3 \cdot e^{-\frac{4}{3}k \cdot (t-T_i)} \right) \right)^{\frac{4}{3}}$
Richards	$Y_{(t)} = \frac{1-d}{(1-d) \cdot d^{\frac{1}{1-d}}} \cdot A \cdot k \cdot e^{-\frac{k \cdot (t-T_i)}{d^{1-d}}} \cdot \left( 1 + \left( (d-1) \cdot e^{-\frac{k \cdot (t-T_i)}{d^{1-d}}} \right) \right)^{\frac{d}{1-d}}$

model growth patterns in four traits and compare the performance of different growth models fitted by NLMM.

## Material and methods

Data were collected from November to December 2015 at Punta León (43°05'S, 64°30'W), Chubut, Argentina. During egg hatching, we checked nests every ~3 d to establish hatching date. Nestlings were marked on the tarsus with tape bands labeled with their associated hatching order. During chick rearing, we checked nests every 3–5 d to obtain morphological measurements of chicks until it was impossible to capture

them, at an age of 35–40 d. At an age of ~20 d, chicks were ringed with numbered aluminum rings. Four measurements were considered in this study: body mass, bill length (exposed culmen), head length (from the tip of the bill to the posterior ridge) and tarsus length (from the middle of the midtarsal joint to the distal end of the tars-metatarsus) following Svagelj and Quintana (2007). For bill, head and tarsus measurements, we used a digital caliper (nearest 0.01 mm). We recorded body mass using 100, 300, 600, 1000 and 2500 g spring scales.

Imperial shags are sexually dimorphic in size with males being larger and heavier than females (Svagelj and Quintana 2007). To simplify statistical analyses, we only considered female chicks and one chick per nest. For each nest, the female chick with the highest number of morphometric measurements was selected. To determine the sex of chicks, we used measurements of tarsus and head lengths when chicks were 25 d old or older and applied discriminant functions (Svagelj and Quintana 2017). In total, the growth data analyzed corresponds to 209 measurements from 33 females (mean = 6.3, SD = 0.6 measurements per chick).

We analyzed growth using NLMM fitted by maximum likelihood (Pinheiro and Bates 2000). Growth data were fitted to the von Bertalanffy, Gompertz, logistic and Richards models using parameterizations in the  $T_i$ -form (from Tjørve and Tjørve 2017a) shown in Table 1. In these parameterizations,  $W_{(t)}$  is size at age  $t$ , and  $A$ ,  $k$ ,  $T_i$  and  $d$  are the upper asymptote (i.e. predicted adult size), maximum relative growth rate, age at the inflection point and shape parameter, respectively (Tjørve and Tjørve 2017a). In addition, we also evaluated the  $U_4$  model (Tjørve and Tjørve 2017a) which is a three-parameter model generated from a Richards equation where  $d=4$ , thus fixing the inflection point at 63% of the upper asymptote (Table 1). We used unified parameterizations proposed by Tjørve and Tjørve (2017a), so  $k$  parameter is in the same scale across all models. Lack of independence among repeated measurements

Table 3. Summary of model-selection results for von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards models explaining variation in growth of female chicks of the imperial shag for body mass, bill, head and tarsus lengths.  $k_p$  is the number of estimated parameters. Best models are shown in bold. AICc values for best models; body mass: 2404.57<sup>A</sup>, bill length: 675.35<sup>B</sup>, head length: 1018.33<sup>C</sup>, and tarsus length: 729.81<sup>D</sup>. See Methods for details.

	Body mass			Bill length		
	$k_p$	$\Delta AICc$	Weight <sub>AICc</sub>	$k_p$	$\Delta AICc$	Weight <sub>AICc</sub>
von Bertalanffy	6	93.15	0.000	6	115.29	0.000
Gompertz	6	36.39	0.000	6	76.98	0.000
Logistic	7	17.48	0.000	7	2.12	0.257
$U_4$	6	106.88	0.000	7	61.90	0.000
Richards	<b>8</b>	<b>0.00<sup>A</sup></b>	<b>1.000</b>	<b>8</b>	<b>0.00<sup>B</sup></b>	<b>0.743</b>
	Head length			Tarsus length		
	$k_p$	$\Delta AICc$	Weight <sub>AICc</sub>	$k_p$	$\Delta AICc$	Weight <sub>AICc</sub>
von Bertalanffy	6	105.20	0.000	4	365.41	0.000
Gompertz	6	76.83	0.000	5	324.01	0.000
Logistic	6	10.73	0.005	6	199.85	0.000
$U_4$	6	27.55	0.000	7	0.01	0.499
Richards	<b>7</b>	<b>0.00<sup>C</sup></b>	<b>0.995</b>	<b>8</b>	<b>0.00<sup>D</sup></b>	<b>0.501</b>

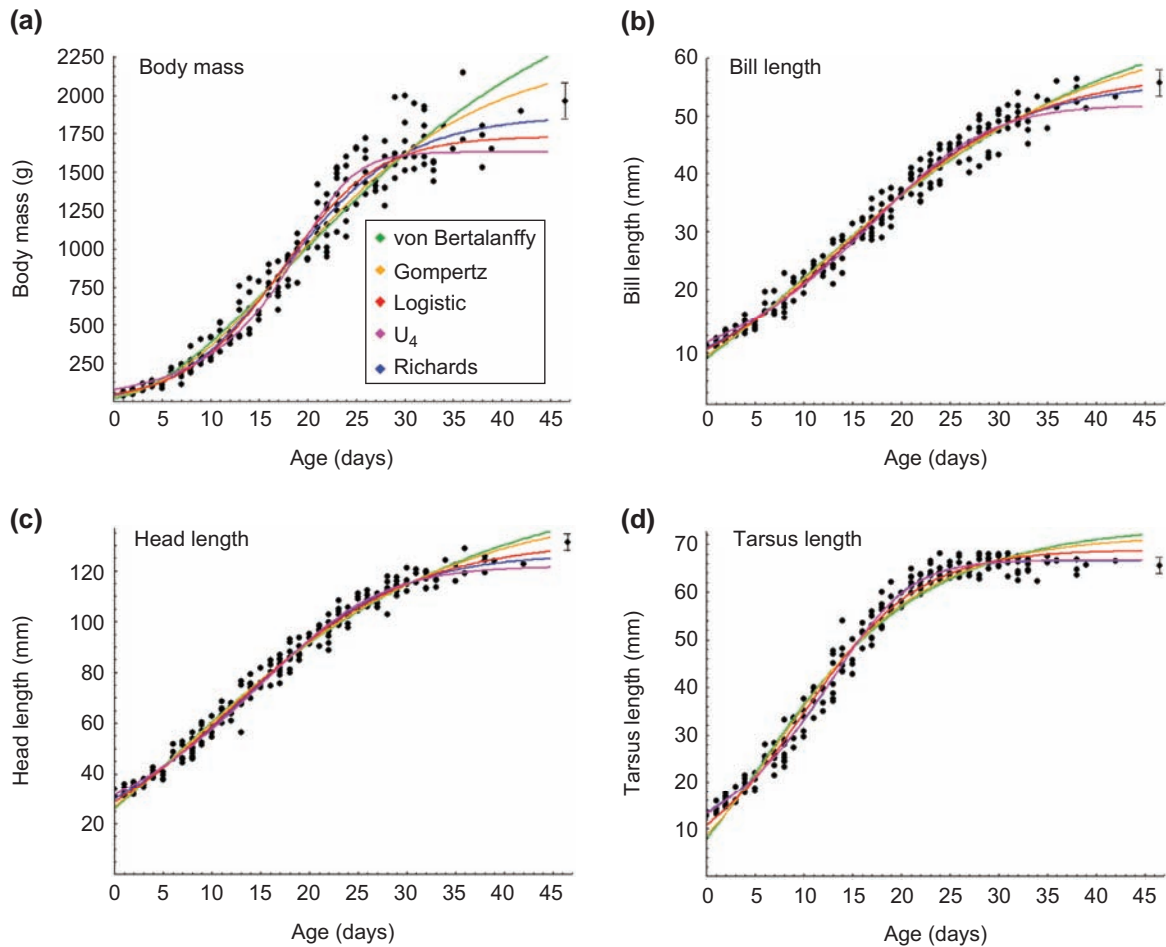


Figure 1. Growth curves of female chicks of the imperial shag ( $n=33$ ) for (a) body mass, (b) bill length, (c) head length and (d) tarsus length. Curves were obtained from nonlinear mixed models applied to von Bertalanffy (green), Gompertz (orange), logistic (red),  $U_4$  (pink) and Richards (blue) models. Measured values are shown as circles. Mean  $\pm$  SD of adult values are shown.

Table 4. Estimated upper asymptotes ( $A$ , as mean (SE)) for body mass, bill, head and tarsus lengths of female chicks of the imperial shag for von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards equations. We obtained estimated values from nonlinear mixed models fitted by maximum likelihood. Adult values are reported as mean  $\pm$  SD. All parameters are significant ( $t \geq 18.1$ ,  $p < 0.001$ ). Deviation represents the percentage of deviation between estimated asymptotes and adult values. See methods for details.

	Body mass (g)		Bill length (mm)	
	$A$ (SE)	Deviation (%)	$A$ (SE)	Deviation (%)
	Adults: 1965 $\pm$ 119		Adults: 55.7 $\pm$ 2.3	
von Bertalanffy	2993 (166)	52	72.3 (1.7)	30
Gompertz	2299 (78)	17	66.0 (1.2)	18
Logistic	1731 (34)	-12	57.4 (0.6)	3
$U_4$	1630 (31)	-17	51.9 (0.5)	-7
Richards	1866 (60)	-5	55.8 (0.9)	0
	Head length (mm)		Tarsus length (mm)	
	$A$ (SE)	Deviation (%)	$A$ (SE)	Deviation (%)
	Adults: 131.2 $\pm$ 3.3		Adults: 65.5 $\pm$ 1.7	
von Bertalanffy	156.7 (2.9)	19	73.9 (1.0)	13
Gompertz	146.5 (1.9)	12	71.8 (0.7)	10
Logistic	131.5 (1.1)	0	68.8 (0.4)	5
$U_4$	121.8 (0.8)	-7	66.7 (0.3)	2
Richards	126.6 (1.5)	-3	66.6 (0.3)	2

Table 5. Coefficients of variation ( $CV = (SD/\bar{x}) \times 100$ ) of estimated upper asymptotes ( $A$ ), maximum relative growth rates ( $k$ ), age at the inflection points ( $T_i$ ) and maximum absolute growth rates ( $g_{max} = A k$ ) for body mass, bill length, head length and tarsus length of female chicks of the imperial shag. Coefficients represent the variation in estimates between von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards's models.

	Coefficient of variation (%)			
	$A$	$k$	$T_i$	$g_{max}$
Body mass	26.6	40.0	5.2	19.5
Bill length	13.7	17.5	23.2	4.5
Head length	10.7	11.9	35.1	2.0
Tarsus length	4.6	5.5	38.6	1.8

on the same individuals was accounted by the inclusion of growth parameters from chick identity as random effects on the intercept, allowing for random individual variation around average values. Prior to model comparisons, we evaluated the significance of random effects using likelihood ratio tests, with non-significant random effects (i.e. parameters with negligible levels of variability among individuals,  $p > 0.05$ ) being discarded to avoid over-fitting (Pinheiro and Bates 2000). Structures of random effects retained in the models are in the appendix (Supplementary material Appendix 1 Table A1). Models in body mass exhibited heteroscedasticity which was modeled considering a power variance function where variance increase with fitted values (Pinheiro and Bates 2000). Adequacy of models was evaluated using Akaike information criterion corrected for sample size (AICc) (Burnham and Anderson 2002). Model comparisons were made with  $\Delta AICc$ , which is the difference between the lowest AICc value (i.e. best of suitable models) and AICc from each model. The AICc weight of a model ( $Weight_{AICc}$ ) indicates the relative likelihood that the specific model is the best of the suite of candidate models (Burnham and Anderson 2002). As an

additional indicator of model fit, we also evaluated deviations between estimated upper asymptotes and mean adult values (from Svagelj and Quintana 2007). For all traits and growth parameters, coefficients of variation ( $CV = (SD/\bar{x}) \times 100$ ) were calculated to indicate the degree of variability in growth parameter estimates among models. Finally, we generated equations of the instantaneous growth rate  $Y_{(t)}$  for each growth model (Table 2). These functions – obtained as first derivatives – represent the absolute daily increment in size at a given age and are particularly useful to visualize the maximum absolute growth rate ( $g_{max} = A k$ ; Tjørve and Tjørve 2017a) and daily variations in growth trajectories (Ricklefs 1968a, Velando et al. 2000, Kalmbach et al. 2009, Martin 2015).

Statistical analyses were carried out using the nlme (Pinheiro et al. 2018) package from R software, ver. 3.4.4 (R Development Core Team). Results are presented as mean  $\pm$  SE except where noted.

## Data deposition

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.s448n5d>> (Svagelj et al. 2018).

## Results

Based on AICc values, the Richards model performed the best for all traits analyzed (Table 3). For body mass (Fig. 1a) and head length (Fig. 1c), there was no model uncertainty or competing models ( $Weight_{AICc}$ : 1.000 and 0.995 for Richards models in body mass and head length, respectively; Table 3). Bill length (Fig. 1b) was best modelled by the Richards equation ( $Weight_{AICc} = 0.743$ ), followed by the logistic model that received some support ( $Weight_{AICc} = 0.257$ ; Table 3). Both Richards and the  $U_4$  models provided good fits for tarsus

Table 6. Maximum relative growth rates ( $k$ , in  $d^{-1}$ ), age at the inflection points ( $T_i$ , in days) and shape parameters ( $d$ ) for body mass, bill, head and tarsus lengths of female chicks of the imperial shag for von Bertalanffy, Gompertz, logistic,  $U_4$  and Richards equations. We obtained estimated values from nonlinear mixed models fitted by maximum likelihood. All parameters are significant ( $t \geq 12.9$ ,  $p < 0.001$ ). Standard errors are shown within parentheses. See methods for details.

	Body mass			Bill length		
	$k$ (SE)	$T_i$ (SE)	$d$ (SE)	$k$ (SE)	$T_i$ (SE)	$d$ (SE)
von Bertalanffy	0.0218 (0.0011)	18.1 (0.8)	–	0.0206 (0.0007)	9.6 (0.4)	–
Gompertz	0.0307 (0.0008)	17.4 (0.5)	–	0.0227 (0.0005)	11.7 (0.3)	–
Logistic	0.0510 (0.0008)	17.3 (0.3)	–	0.0271 (0.0004)	14.9 (0.2)	–
$U_4$	0.0650 (0.0014)	19.4 (0.2)	–	0.0321 (0.0004)	17.7 (0.2)	–
Richards	0.0433 (0.0020)	17.2 (0.3)	1.56 (0.09)	0.0282 (0.0006)	15.6 (0.3)	2.34 (0.15)
	Head length			Tarsus length		
	$k$ (SE)	$T_i$ (SE)	$d$ (SE)	$k$ (SE)	$T_i$ (SE)	$d$ (SE)
von Bertalanffy	0.0224 (0.0008)	6.0 (0.3)	–	0.0407 (0.0015)	5.0 (0.2)	–
Gompertz	0.0237 (0.0007)	8.2 (0.3)	–	0.0411 (0.0012)	6.7 (0.2)	–
Logistic	0.0267 (0.0004)	11.9 (0.2)	–	0.0424 (0.0007)	9.9 (0.2)	–
$U_4$	0.0300 (0.0004)	15.4 (0.2)	–	0.0455 (0.0004)	13.0 (0.2)	–
Richards	0.0281 (0.0005)	13.5 (0.4)	2.71 (0.21)	0.0458 (0.0005)	13.2 (0.3)	4.21 (0.15)

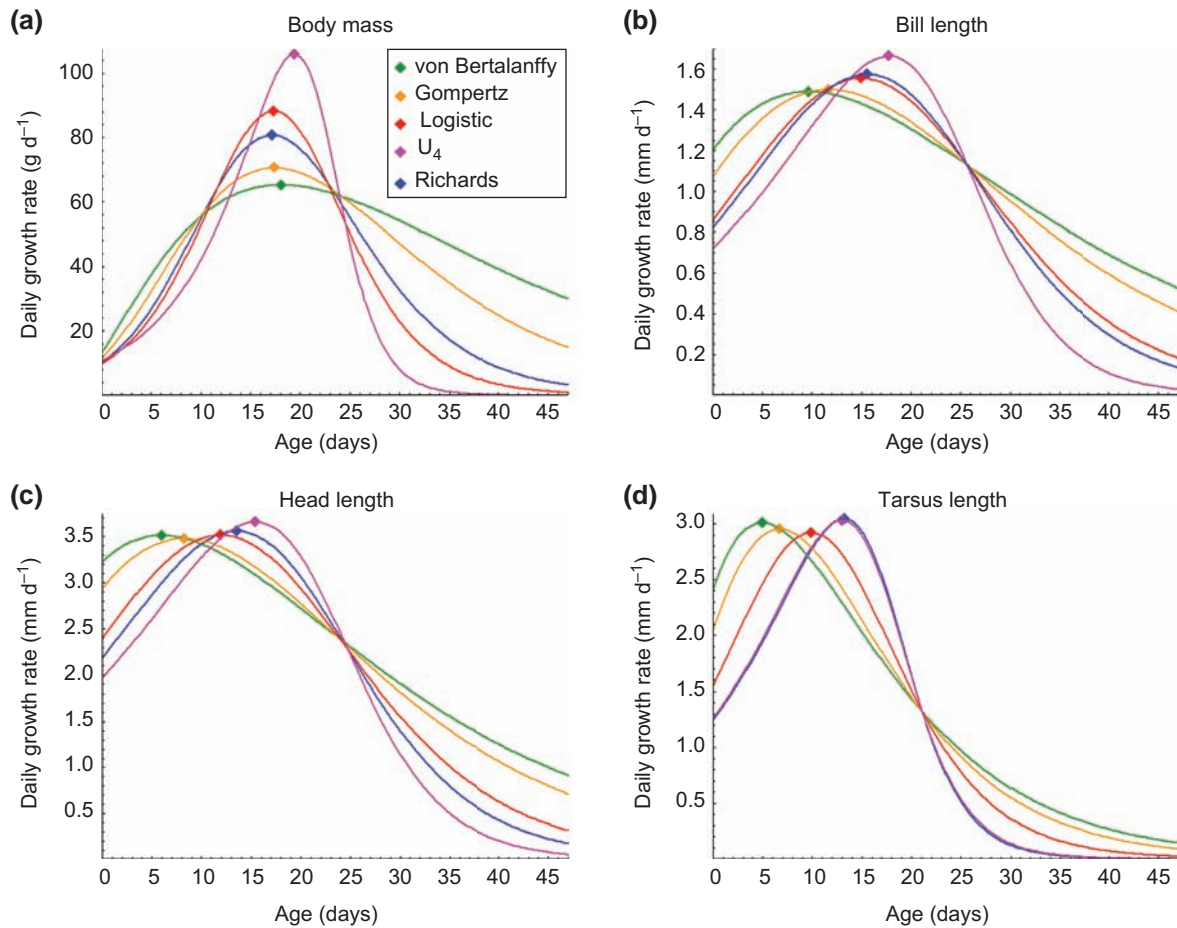


Figure 2. Instantaneous growth rate of female chicks of the imperial shag for (a) body mass, (b) bill length, (c) head length and (d) tarsus length. Equations were obtained from first derivatives of growth models, and parameters were obtained from nonlinear mixed models applied to von Bertalanffy (green), Gompertz (orange), logistic (red),  $U_4$  (pink) and Richards (blue) models. Maximum absolute growth rates ( $g_{max} = A k$ ) at the inflection point are shown as rhombs. See Methods for details.

length (Weight<sub>AICc</sub>: 0.501 and 0.499 for Richards and  $U_4$  models, respectively; Table 3). These models were essentially identical with indistinguishable fits (Fig. 1d).

Overall, the most consistent performance in the upper asymptote estimates ( $A$ ) across traits was obtained by the Richards model with deviations of within 5% of mean adult values (Table 4). The logistic model exhibit positive and negative deviations of within 12%. The  $U_4$  model tended to underestimate the adult values, while von Bertalanffy and Gompertz models always overestimated the adult values by as much as 52% (Table 4).

Estimates of the upper asymptote, maximum relative growth rate ( $k$ ) and the age at the inflection point ( $T_i$ ) had considerable levels of variation between models (Table 5). Both upper asymptotes (Table 4) and maximum relative growth rates (Table 6) were highly variable across models in body mass (Table 5). On the other hand, the age at the inflection point widely differed across models for bill, head and tarsus length (Table 5 and 6). Curves on daily growth showed more clearly the differences in the age at the inflection point and maximum absolute growth rates ( $g_{max}$ ) between models (Fig. 2).

Differences in maximum absolute growth rate between models were particularly notorious for body mass, while bill, head and tarsus length showed less variation (Fig. 2, Table 5). For tarsus length – where both Richards and  $U_4$  models were similarly supported by the data –, curves on daily growth showed indistinguishable fits between competing models (Fig. 2d).

## Discussion

In the present study, we compared the performance of several growth equations using nonlinear mixed-effect models fitted by maximum likelihood. Based on AICc values, we found that the Richards equation was the best model for all traits analyzed. Also, the most consistent performance in the upper asymptote estimates was obtained by the Richards model. These results are a consequence of the flexibility provided by the fourth parameter  $d$  which allows an inflection placement derived from data, thus permitting an unbiased fit.

Von Bertalanffy, Gompertz, logistic and  $U_4$  are three-parameter models with inflection points fixed at 30, 37, 50

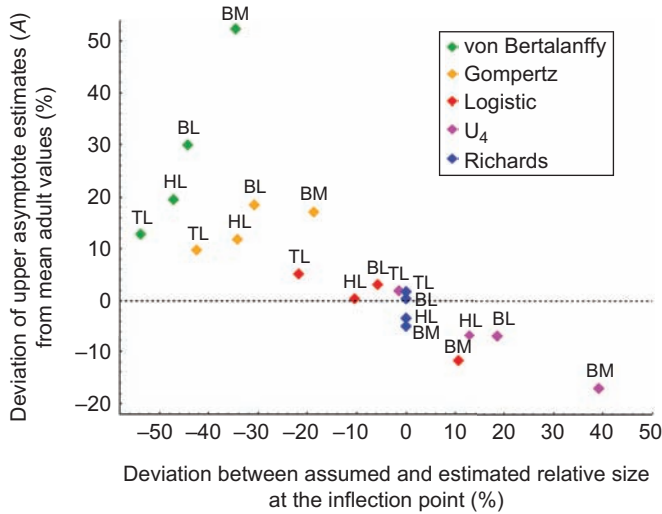


Figure 3. Deviation of upper asymptote estimates ( $A$ ) from mean adult values (as %) versus the deviation of assumed relative size at inflection in relation to the relative size at inflection estimated using the Richards model (as %). Relative size is calculated as  $d^{1/(1-d)}$  (Tjørve and Tjørve 2010). Upper asymptote estimates of body mass (BM), bill length (BL), head length (HL) and tarsus length (TL) were obtained from von Bertalanffy (green), Gompertz (orange), logistic (red),  $U_4$  (pink) and Richards (blue) models. See Methods for details.

and 63% of the upper asymptote (Tjørve and Tjørve 2010, 2017a). These models are particular cases of the Richards model for  $d$ -values of  $2/3$ ,  $\rightarrow 1$  (but  $\neq 1$ ), 2 and 4, respectively (Tjørve and Tjørve 2010, 2017a). In our study, inflection points for body mass, bill length, head length and tarsus length were located at 45% ( $d=1.56$ ), 53% ( $d=2.34$ ), 56% ( $d=2.71$ ) and 64% ( $d=4.21$ ) of the upper asymptote, respectively. Thus, von Bertalanffy and Gompertz models always underrated the  $d$  parameter while the logistic model underrated  $d$  for bill, head and tarsus lengths and overrated it for body mass. Contrary to von Bertalanffy and Gompertz models, the  $U_4$  model overrated  $d$  for body mass, bill length and head length. In the case of tarsus length, both Richards and  $U_4$  models similarly supported the data because the relative inflection value estimated from the Richards model was very close to that assumed by the  $U_4$  model. Only in the particular case in which the estimated  $d$ -parameter coincides with that assumed by any three-parameter model, fits would be similar between models and the estimation of  $d$ -parameter, redundant.

Estimates of growth parameters showed substantial variation between models. Upper asymptote estimates were particularly variable for body mass, exhibiting a lower variation for bill, head and tarsus lengths. Interestingly, upper asymptotes were systematically over- and underestimated when assumed inflection points were lower and higher (as percentage of asymptotic size) than those estimated by the Richards model (Table 4 and 6, Fig. 3). Also, the magnitude of the bias increased with the deviation from the estimated inflection point. Estimates of the age at maximum growth (for bill, head and tarsus lengths) and maximum relative growth rate (for body mass) were also highly variable across models.

In addition, daily growth curves exposed the notorious differences in maximum absolute growth rates across models in body mass. All these potential biases could be avoided by using the Richards model because the relative inflection value is calculated from the  $d$ -parameter which is estimated from data (Tjørve and Tjørve 2010). All in all, our results showed that the best alternative to model chick growth in the Imperial Shag would be the Richards model. This finding agrees with previous studies comparing the performance of Richards versus three-parameter models, where Richards was the preferred model or provided similar fits and parameters than best simpler models (Sugden et al. 1981, Tjørve and Tjørve 2010, 2017b, Vrána et al. in press).

Our main goal was to compare basic fits of different growth models by using nonlinear mixed models. However, it is important to mention that several alternatives, extensions and refinements also can be implemented. First, we used parameterizations in the  $T_i$ -form because we were interested in the estimation of the age at maximum growth. All models analyzed here also can be considered in their  $W_0$ -form where  $T_i$  is replaced by a  $W_0$  parameter representing size at hatching (Tjørve and Tjørve 2017a). Second, truncation of data at the beginning or at the end of growth trajectory can produce unrealistic fits. Truncation at the beginning could be a consequence of lack of data close to hatching date, while truncation at the end is mainly associated with birds fledging before achieving adult size or the difficulty of capturing birds as fledging nears. When data are truncated at the beginning or at the end, size at hatching ( $W_0$ ) and/or asymptotic size ( $A$ ) can be fixed to population values to produce realistic growth curves and growth-rate parameters (Austin et al. 2011, Svagelj and Quintana 2017, Tjørve and Tjørve 2017a, b). Third, typical growth models are monotonic in the sense that show a unique (steady) trajectory throughout the growth curve. However, there are situations of non-monotonic (or multiphasic) growth, usually associated with an overshooting (chick body mass exceeding adult mass) and subsequent recession (decrease) of body mass in some seabird species (Ricklefs 1968b, Huin and Prince 2000, Oswald et al. 2012, Arnold et al. 2016). If growth is not monotonic, two coupled growth models can be used (e.g. Richards–Richards; Oswald et al. 2012). In our study, the use of coupled models was unnecessary because imperial shags does not overshoot body mass prior to fledging (Svagelj and Quintana 2017). Fourth, we only considered one chick per brood but our analyses could be extended to multiple chicks per brood. NLMM can handle a lack of independence from different levels by including growth parameters from each level as random effects (Pinheiro and Bates 2000). Thus, growth models could deal with multiple observations per chick and multiple chicks per brood, allowing for individual (among chicks) and grouped (among broods) variation around average values (Sofaer et al. 2013, Aldredge 2016). Fifth, here, we have used NLMM to fit average growth curves. However, one of the most interesting features of NLMM is that they allow a regressive approach that considers predictor variables

modelling growth parameters (Pinheiro and Bates 2000). Thus, the effect of predictor variables (e.g. sex, hatching order, brood size or hatching date) can be evaluated for each growth parameter (Kalmbach et al. 2009, Giudici et al. 2017, Svagelj and Quintana 2017). In summary, the combination of NLMM with the Richards equation represents a flexible and powerful analytical tool that deserves future consideration by ornithologists.

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Supplementary material (Appendix JAV-01864 at <[www.avianbiology.org/appendix/jav-01864](http://www.avianbiology.org/appendix/jav-01864)>). Appendix 1–2.