

Potential Biases in Estimating the Rate Parameter of Sigmoid Growth Functions

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ABSTRACT: 1. We compare biases in estimates of the rate constant of the logistic and Gompertz functions applied to avian growth using three methods of parameter estimation. The methods differ in how the asymptote is determined, and consist of either floating asymptotes estimated from the full data (floating A) or data truncated at 70% of the adult mass (70%A), or fixing the asymptote at the adult mass (fixed A). 2. First, using data for two passerine species exhibiting different growth patterns, we truncated mass measurements at different ages to explore how each method of growth rate estimation responded to simulated differences in nestling period. We bootstrapped growth rates and error measures from these data to produce unbiased error terms, which we used to compare the different models. 3. We tested the effects of age truncation on both real and simulated data, and found that the fixed A method produced less bias and better fits than using estimates of floating asymptotes from the full growth curve (floating A) or truncated at 70% of the adult mass (70%A). Logistic and Gompertz models with a floating asymptote generally provided poorer fits than those with a fixed asymptote, although fits were improved by including a variable accounting for the ratio of asymptotic to adult mass. 4. To evaluate the performance of the methods across an array of species, we applied the three methods to growth data for 45 species of New World songbirds spanning diverse rates of growth, developmental periods and geographic origins. To determine whether choice of method influenced interpretation of regional and life-history differences in avian growth, we used model selection to estimate the influence of three independent variables (adult mass, nestling period and tropical vs. temperate region) with known effects on nestling growth rate calculated by each method. The coefficients of determination in these analyses suggest that the most appropriate method to estimate growth rates, regardless of the growth function (i.e. logistic, Gompertz), is the fixed A method, taking care to use accurate and appropriate estimates of adult mass.

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Introduction

The rate of postnatal growth varies widely among species of birds and is associated with variation in other life-history traits (Starck & Ricklefs 1998). For example, growth rates are negatively related to adult mass and are generally more rapid in altricial compared to precocial species (Starck & Ricklefs 1998). Growth influences the energy and nutrient requirements of nestlings and their exposure to time-dependent mortality. Hence, it is an important life-history trait that directly affects individual fecundity and survival (Ricklefs 1969, 1984; Case 1978; Stearns 1992; Konarzewski, Kooijman & Ricklefs 1998; Blount et al. 2006). Nestling growth rates vary broadly (Starck & Ricklefs 1998), reflecting differences in the mode of development (Ricklefs 1973a, 1979b), nest predation pressure (Remeš & Martin 2002; Remeš 2007; but see Ricklefs 1984; Ricklefs, Starck & Konarzewski 1998), parental investment (Martin 1987), sibling competition (Werschkul & Jackson 1979; Ricklefs 1982), adult size (Ricklefs 1973b), geographic region (Ricklefs 1976), and environmental factors that affect energy and nutrient availability (Lack 1968). However, evaluating potential influences on nestling growth rate and understanding the evolution of growth and development as part of a life-history strategy depends on accurately quantifying growth rate for comparisons within and among species (Ricklefs 1968a, 1979a).

Because the form of the avian growth curve varies considerably, several mathematical functions have been used to describe growth. As growth curves are typically sigmoidal, the most frequently applied functions are the logistic and Gompertz equations (Ricklefs 1967a, 1983; Remeš & Martin 2002). Due to the difference in shape, growth rates from logistic and Gompertz equations are not directly comparable, although the relationship of $1/0.68$ (logistic : Gompertz;) has been used as a rough conversion (Ricklefs 1968a). The logistic growth equation often provides a good fit to the increase in mass of rapidly growing species, such as passerine birds, and has been widely used in comparative studies. It takes the form $M_t = A / (1 + \exp(-K(t-i)))$, where t is age [day; hatch = 1]; M_t is mass [g] at age t ; A [g] is the asymptote (or upper plateau) of the growth curve where mass reaches its highest point; i [day] is the age at the inflection point of the growth curve where $M_t = A/2$; and K [day^{-1}] is the growth rate constant (Ricklefs 1967a); which describes the exponential rate of approach of mass to the asymptote. The Gompertz equation has the form $M_t = A \exp(-\exp(-K(t-i)))$; the inflection point of the growth curve occurs at $M_t = A/e$. The Gompertz function differs from the logistic function in having an earlier phase of rapid growth followed by a slower approach to the asymptote following the inflection point (Ricklefs 1983). Inappropriate application of these models can provide ill-fitting growth curves and inaccurate estimates of the growth rate constant, K .

Quantifying nestling growth from field observations can be challenging because access to nests can be

difficult, relatively frequent measurements of known-age birds are needed, growth is often incomplete when birds fledge, and measurements during the post-fledging period are rare; therefore, growth data are often incomplete. Fitting growth functions to incomplete data can bias estimates of growth rate (Ricklefs 1983). Additional bias can result from weight recession – a decrease in mass prior to fledging – in some species, which can inflate growth rate estimates (for a more complete review see Ricklefs 1983 or, Remeš & Martin 2002). Further, some species attain a transient plateau in growth below adult mass associated with leaving the nest, which can lead to inflated estimates of K by setting an asymptote (A) lower than adult mass, i.e. the final mass plateau.

Substantial variability in estimates of K can arise depending on how data are fitted by growth functions. Such variability could influence conclusions drawn from comparative studies of avian growth rates. In particular, fitting asymptotes substantially below adult mass in species that leave the nest at an early age can bias growth rate upward and create the impression that earlier fledging species grow more rapidly. In this study, we compared three methods of fitting growth functions to measurements of nestling mass based on different approaches to estimating the asymptote, and we evaluated their potential for producing bias when estimating growth rates. We used three approaches: (i) detailed analysis of two species with complete growth curves where we evaluated the influence of progressive truncation of data on growth parameters, (ii) fitting Gompertz and logistic growth equations to simulated growth curves where we could assess the effects of age-truncated data and inappropriate growth models, and finally (iii) testing the influence of curve-fitting method on life-history correlations of growth data in a sample of 45 species representing a wide range of nesting periods and fledging masses.

Materials and methods

The parameters of growth functions (A , i and K) were estimated by applying nonlinear regression to nestling mass, using (i) data recorded to the point of fledging [hereafter referred to as 'floating A '; (Ricklefs 1967a, 1983)], (ii) data truncated at the age when the mean nestling mass was $> 70\%$ of the mean adult mass [$70\% A$; (Remeš & Martin 2002)], and (iii) data recorded to the point of fledging, but with the asymptotic mass fixed at the mean adult mass (fixed A).

To assess how each method affects estimates of growth rate, we applied each of the three curve-fitting methods to two real and one simulated dataset.

1. We explored differences using curve-fitting methods by analysing measurements of nestling mass taken at 1- to 2-day intervals from two passerine species with different growth patterns (short vs. long nesting periods). For the species with the longer

nestling period, we truncated data at different ages to explore the effect of different fledging ages on growth rate parameter estimates.

2. Next, we simulated growth curves using each of the three curve-fitting methods and logistic and Gompertz functions with the same parameter estimates (A , i and Gompertz $K = 0.68 \times \text{logistic } K$). This allowed us to: (i) investigate how biases from deviations in the shape of the growth curve can influence estimates depending on the model and method employed to fit the curve, and (ii) to assess bias associated with incomplete sampling (or truncation) of the growth curve.

3. Finally, to establish criteria for deciding which approach produces the least bias from a biological standpoint, we examined the goodness of fit of the estimated growth rate constants for 45 species of New World temperate and tropical passerines. In addition, we analysed the relationship of growth rate to adult mass, region (tropical vs. temperate), and nestling period (days) to determine which curve-fitting method resulted in the highest explanatory power. In this analysis we also included the ratio of asymptotic to adult mass (R) for models with a free asymptote. If R were to vary consistently with nestling period, for example, this could bias the relationship between the apparent growth rate and nestling period.

FIELD METHODS

We collected data on nesting passerines from 2003 to 2006 at three sites (two temperate: Kellogg Biological Station/Lux Arbor Reserve, Michigan, and rural Benton County, Oregon; and one tropical: Soberania National Park, Republic of Panama). For a more detailed description of our study sites, see (Robinson, Brawn & Robinson 2000, Etterson, Nagy & Robinson 2007; Cohen et al. 2008).

We conducted generalized nest searching for passerine species. We also installed artificial nest boxes in Michigan and Oregon to study several secondary-cavity nesting species. Within each nest, we colour-marked each nestling's metatarsus with a non-toxic felt marker to facilitate individual identification. We measured mass (± 0.1 g) of individually marked nestlings every 1–3 days throughout the breeding season, using an electronic balance (Acculab PocketPro 60 g Electronic Balance; Salter Brecknell Electronic Pocket Balance, Fairmont, MN, USA).

In addition to our original field observations, we included growth data from several literature sources (Putnam 1949; Barber 1950; Haverschmidt 1952; Southern 1958; Kluyver 1961; Holcomb 1968; Murphy 1981, 1988) or from unpublished sources [R.E.R., unpublished data; Jongsomjit et al. 2007 and unpublished data from Marin County, California, on wrentits (*Chamaea fasciata*)] to increase representation of species with a wider range of growth rates.

Adult mass for many tropical species was measured on individuals captured in the study area (Robinson & Robinson, unpublished); however, for most temperate species and some tropical species, values for adult mass were obtained from Dunning (1993).

Analyses

FITTING GROWTH FUNCTIONS

Floating A

We estimated nestling growth curves following the methodology of curve-fitting outlined by Ricklefs (1967a, 1983). As the logistic and Gompertz growth functions are sigmoidal, or S-shaped, fitting growth curves required nonlinear regression (proc nlin; SAS Institute, Cary, NC, USA, v9.1; see Ricklefs 1983). We fitted the model parameters [asymptotic nestling mass (A), inflection point (i) and growth rate (K)] to nestling mass or to simulated data (Oniki & Ricklefs 1981; Ricklefs 1983). This produced individual species' growth rate estimates based on pooled measurements for all nestlings. Nestlings that showed signs of malnourishment were excluded. All methods of estimating growth rate were generated based on this approach apart from a few key differences that are outlined below.

70% adult mass

We estimated nestling growth rates using the method described by Remeš & Martin (2002). The rationale for this method is that by limiting the growth curve to measures of chick mass $\leq 70\%$ of the adult mass (approximately the fledging mass for many temperate passerines), the growth curve is standardized and issues related to weight recession are circumvented. Accordingly, we excluded all nestling body mass measurements obtained beyond the age that average nestling mass exceeded 70% of the average adult mass for that species. Growth functions were fit to the remaining growth curve as with the Floating A method.

Fixed asymptote

We fit the complete growth curve of each species using nonlinear regression, as with the Floating A method, except that the asymptote was fixed at each species' average adult mass. For the floating and 70% methods, this parameter (A) is estimated by the model based on the trajectory of the growth curve near fledging, or at the age that nestlings reached $> 70\%$ adult mass. The rationale for using an asymptote fixed at the adult mass was that mass of mature adults represents the end point of the growth process and is a natural standard for estimating the rate of increase towards this point.

Weight recession

If a species exhibited weight recession, growth curves were truncated after birds had achieved average peak nestling mass: We truncated the data to avoid artificially inflating K (see Ricklefs 1983). Weight recession occurs when nestlings exceed adult mass prior to fledging and then plateau or decrease in mass prior to fledging. This is caused largely by loss of water from body tissues, especially the integument, associated with the development of mature function (Ricklefs 1968b; Konarzewski 1988). Using lipid-free dry mass would circumvent this issue (Konarzewski 1988); however, this would not prevent the problem presented when fledging truncates data collection before growth is complete.

For fixed A , we truncated the data, as with the floating A method, and then fixed the asymptotic value at the average peak nestling mass. We fixed the asymptotic mass at peak nestling mass to remain consistent among the various methods – the floating A estimate could be substituted for fixed A among species that experience weight recession although the error terms would need to be bootstrapped to remove bias associated with having different parameters in the model. As the 70% A method truncates the data at a lower part of the growth curve, weight recession was not present and further truncating of the mass data was unnecessary.

MODEL COMPARISON

Greater ambiguity in a model is associated with increased error in estimated parameters: two-parameter models have narrower parameter confidence intervals than three-parameter models simply because there are fewer variables. However, because the asymptote is fixed at the mean adult mass in the Fixed A method, these models will always have a poorer fit to the growth curves (measured as the mean squared error, MSE) because the form of the growth curve is constrained. Hence, the floating A and 70% A methods will always provide the best fits because they only use the observed data and do not constrain the asymptote. For otherwise identical input data, two parameter (fixed A) models should produce narrower confidence intervals for the parameter estimates than three-parameter models due to the inverse relationship between A and K . In the three-parameter models, the generally high goodness of fit applies to a ridge of inversely related values of A and K . When A is fixed, however, K is estimated with relatively little ambiguity. As estimates of growth rate and the asymptote are inversely related to each other, a bias in the asymptote, A , produces a converse bias in the growth rate, K . Logically, the fixed A approach also better reflects the biological reality that all individuals grow to adult mass, which must therefore represent the eventual asymptote of the growth process.

Bootstrapping growth rate parameters eliminates bias associated with comparing two- (Fixed A) and three-parameter (Floating A and 70% A) models. Thus, we conducted bootstrapping to directly compare model goodness of fit using a subset of *Tachycineta thalassina* (violet-green swallow) and *Chamaea fasciata* (wren-tit) data. We chose these data because sample sizes of known-age birds were relatively large, and measurement intervals were typically 1–2 days. These species represent two distinct growth patterns, with *C. fasciata* fledging before attaining adult mass and *T. thalassina* overshooting adult mass prior to fledging. To bootstrap the growth parameters, we re-sampled nestling masses 1000 times (with replacement) for each species (sampling rate = 1000, replicates = 1000; sas v9.1; Cassell 2007). We then estimated growth rates for each replicate (proc nlin), pooling the parameter estimates by species to calculate unbiased means and standard errors of A , i and K (proc univariate).

To further investigate the influence of the range of ages on growth rate estimates produced by the three methods, we excluded individuals from the *T. thalassina* and *C. fasciata* data sets whose peak mass exceeded adult mass. This data treatment eliminated issues associated with weight recession while providing a complete growth curve. *Chamaea fasciata* did not experience weight recession though some individuals were within the upper 95% interval of the reported adult average. We estimated bootstrapped growth rates for each method as above. To determine how the inversely related A - and K -values are influenced by the age range from which measurements were included, we estimated growth rates using masses truncated at different ages (8–15 days, *T. thalassina*) and 6–11 days (*C. fasciata*). We limited data to truncation at ± 8 days (*T. thalassina*) or ± 6 days (*C. fasciata*) because model convergence criteria (1000 iterations; proc nlin) were not met for truncation at younger ages due to the linearity of early growth.

REGION AND LIFE-HISTORY VARIABLES

To further assess bias of each curve-fitting method, we conducted comparative analyses of the growth rate data. We wished to understand whether or not selection of method influenced conclusions about associations of growth rates measurements with other species' characteristics. Here, we distinguished species from tropical and temperate latitudes, which have different average growth rates in several studies (e.g. Ricklefs 1976; Oniki & Ricklefs 1981).

Growth rate and adult mass are negatively related (Starck & Ricklefs 1998). It has also been suggested that growth rate increases with the daily nest mortality rate (Remeš & Martin 2002), and hence inversely with the length of the nestling period (Ricklefs, Starck & Konarzewski 1998). Generally, species with short nestling periods tend to have higher daily nest mortality rates (Starck & Ricklefs 1998; Remeš & Martin (2002). Accordingly, we also

related growth rate estimates to adult mass and to the length of the nestling period. We expected that if growth rate responded to the intensity of nest predation (Remeš & Martin 2002; Remeš 2007), all three estimates of growth rate would be inversely related to the length of the nestling period. If, however, only estimates of growth rates that allow A to float were inversely related to nestling period, then the relationship could be an artefact resulting from bias in the estimation of the asymptote of the growth curve. We assessed this possibility by including the ratio of the asymptote to adult mass (R) in another comparative analysis. If bias in the asymptote relative to nestling period were responsible for a relationship between growth rate and length of the nestling period, then including R would remove nestling period as a significant variable.

For the comparative analyses, we conducted model selection by AIC using the reg procedure in sas software. Models included adult mass, R, nestling period, and region, the last was converted to a dummy (0,1) variable for these analyses. We then used GLM to analyse the relationship between K estimated by each method and the consequential independent variables in an analysis of variance approach, with region as a random effect. Because of nonlinearities in the data, adult mass, R, K and nestling period were log₁₀-transformed to adjust the distributions.

Results

The three methods for estimating the three key parameters in growth curves (A, i and K) produced disparate estimates in two species with exceptionally complete data on nestling growth (Table 1). Results from *T. thalassina* showed that floating A and fixed A methods produced similar estimates of K, but estimates for 70% A method fell outside the confidence intervals of estimates from the other methods. Data from *C. fasciata* indicated that estimates of K from the floating A and 70% A methods were similar while both were higher than the K from the fixed A method.

When data on mass growth of *T. thalassina* were truncated at different ages to determine how shorter sampling periods (i.e. 'nestling periods') influenced A and K, we found that K increased as A decreased with earlier age truncation using the floating A method (Fig. 1). This relationship could differ for other species because model estimates of A depend on the shape of the growth curve immediately prior to data truncation.

Table 1. Estimates of mass growth rate parameters and unbiased standard deviations for two species of songbird with different growth patterns

	A	i	K
<i>Tachycineta thalassina</i> (n = 7–24)			
Floating A	17•701 ± 0•176	6•781 ± 0•079	0•401 ± 0•007
Fixed A	18•725	7•189 ± 0•034	0•366 ± 0•004
70% A	17•776 ± 0•371	7•384 ± 0•157	0•462 ± 0•058
<i>Chamaea fasciata</i> (n = 6–15)			
Floating A	12•319 ± 0•124	5•470 ± 0•070	0•388 ± 0•007
Fixed A	14•715	7•297 ± 0•038	0•308 ± 0•003
70% A	12•122 ± 0•207	5•382 ± 0•109	0•393 ± 0•009

This is seen in *C. fasciata*, where the growth rate decreased from 0•443 for day 7 truncation to 0•386 for day 6 truncation. With further truncation of the *T. thalassina* data, the same trend occurs, and convergence of the model declines in the bootstrapped growth curves below a certain threshold for both species. As the amount of information decreases and the trajectory of the growth curve changes, growth rate generally increases until there are too few data (convergence criteria not met) and the parameter estimates become more variable. Additionally, for the three-parameter model, A tended to increase while K decreased, which differs from both the two parameter (fixed A) model, and both two- and three-parameter models, where K increased (and in three-parameter models, A decreased) as the nestling period decreased. However, for species such as *T. thalassina* and *C. fasciata*, which grow in a nearly linear fashion in the middle of the nestling period, truncation of data prior to ages at which growth decelerates will upwardly bias estimates of A and K. In species where the period of nearly linear growth is short, a slight curvature in the growth data prior to truncation will allow the model to fit an asymptote more easily than when the data are linear, and may be closer to those that were generated from complete sets of growth data.

Uncertainty of model estimates of A and K increased as sampling period was shortened, as indicated by increasingly large standard deviations (Tables 2 and 3). K estimated by the floating A method varied more than K estimated by the fixed A method, but the latter estimates of K still increased as sample period decreased regardless of growth pattern. This indicates that even though error estimates were smaller for the fixed A method, data truncation still influenced estimates of K. The 70% A method, which is a type of floating A method, produced estimates of K that were 0•150 (*T. thalassina*) or 0•085 (*C. fasciata*) units higher than those estimated by the fixed A method. Overall, the fixed A method produced the least variation in parameter estimates and the smallest error terms.

TRUNCATION OF SIMULATED DATA

Another issue that may bias parameter estimates is use of an inappropriate growth function to model the growth curves. The shapes of logistic and Gompertz functions differ enough that use of one when the other provides a better fit to the data could bias estimates regardless of which method is employed. To understand the direction and magnitude of these biases, we used data simulations of equivalent growth rates described by the logistic or Gompertz functions. The simulated data were successively truncated at earlier ages and each data set was fit by both growth functions. Because the shapes of the two growth functions differ, it seemed plausible that an inappropriate growth function might create a bias in the estimates. In particular, because early growth following a Gompertz function is relatively rapid, using a logistic function to fit the data might produce lower estimated asymptotes and higher estimated growth rates as the data were truncated at earlier ages. We expected the opposite from Gompertz functions fitted to logistic growth data.

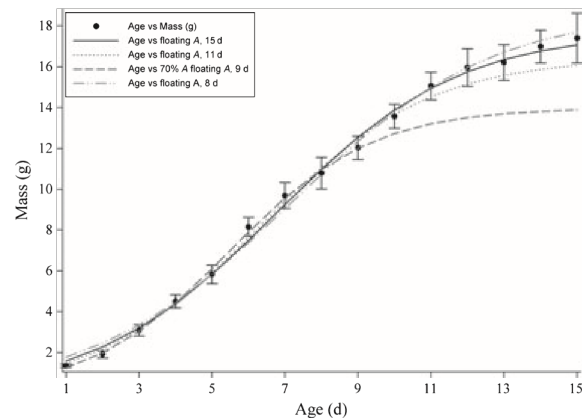


Fig. 1. The mass growth curve of the violet-green swallow *Tachycineta thalassina* ($X \pm SD$; filled circles with error bars) for chicks aged 1–15 days ($n = 7–26$). The fitted lines indicate growth curves generated for three-parameter models (floating and 70% A) truncated at 15, 11 and 9 days and the two-parameter, fixed A method at 15 days.

Table 2. Estimates of growth rate parameters and bootstrapped standard deviations for *Tachycineta thalassina* with mass truncated at different ages to simulate various nestling periods (8–15 days). Estimates were generated for two- and three-parameter models to illustrate how different models behave with increasing uncertainty. Bold indicates our primary methods of interest

Number of parameters in model	Truncated age (hatch day = 1)	A	i	K
3	15 (floating A)	17•701 ± 0•348	6•776 ± 0•154	0•402 ± 0•013
	14	17•564 ± 0•386	6•725 ± 0•166	0•406 ± 0•014
	13	17•359 ± 0•476	6•649 ± 0•197	0•412 ± 0•016
	12	17•282 ± 0•619	6•620 ± 0•246	0•415 ± 0•019
	11	16•424 ± 0•625	6•322 ± 0•247	0•439 ± 0•022
	10	15•082 ± 0•566	5•864 ± 0•22	0•480 ± 0•024
	9 (70% A)	14•039 ± 0•606	5•515 ± 0•22	0•516 ± 0•025
	8	13•917 ± 1•108	5•467 ± 0•346	0•522 ± 0•031
	2	15 (fixed A)	18•725	7•185 ± 0•064
14		18•725	7•182 ± 0•064	0•366 ± 0•007
13		18•725	7•178 ± 0•064	0•368 ± 0•008
12		18•725	7•155 ± 0•064	0•373 ± 0•007
11		18•725	7•150 ± 0•066	0•374 ± 0•007
10		18•725	7•142 ± 0•072	0•375 ± 0•008
9		18•725	7•095 ± 0•083	0•383 ± 0•010
8		18•725	6•931 ± 0•096	0•409 ± 0•013

Table 3. Estimates of growth rate parameters and bootstrapped standard deviations for *Chamaea fasciata* with mass truncated at different ages to simulate various nestling periods (6–11 days). Estimates were generated for two- and three-parameter models to illustrate how different models behave with increasing uncertainty. Bold indicates our primary methods of interest

Number of parameters in model	Truncated age (hatch day = 1)	A	i	K
3	11 (floating A)	12•319 ± 0•124	5•470 ± 0•070	0•388 ± 0•007
	10	12•752 ± 0•208	5•679 ± 0•109	0•374 ± 0•008
	9 (70% A)	12•122 ± 0•207	5•382 ± 0•109	0•393 ± 0•009
	8	10•876 ± 0•225	4•797 ± 0•115	0•435 ± 0•011
	7	10•663 ± 0•414	4•695 ± 0•198	0•443 ± 0•016
	6	13•643 ± 1•706	5•868 ± 0•601	0•386 ± 0•023
2	11 (fixed A)	14•715	7•297 ± 0•038	0•308 ± 0•003
	10	14•715	7•165 ± 0•034	0•319 ± 0•003
	9	14•715	7•098 ± 0•037	0•322 ± 0•003
	8	14•715	6•936 ± 0•043	0•332 ± 0•004
	7	14•715	6•733 ± 0•041	0•341 ± 0•005
	6	14•715	6•626 ± 0•047	0•367 ± 0•005

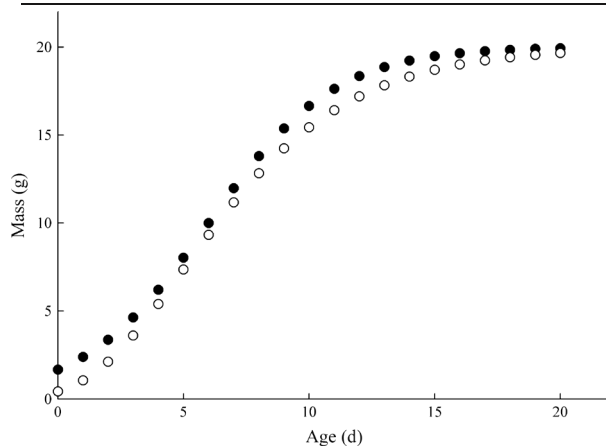


Fig. 2. Artificial growth data generated by a logistic function (closed circles: A = 20, K = 0•400, i = 6) and a closely matched Gompertz function (open circles: A = 20, K = 0•270, i = 5).

Table 4. Logistic growth functions fitted to growth data produced by a Gompertz equation with A = 20, i = 5 and K = 0•270. Fits were produced using the floating asymptote and fixed asymptote approaches. The growth curve reached 70% of the asymptote at 9 days

Age limit	Fixed A = 20		
	Floating asymptote	A	K
20	19•3	0•418	0•382
18	19•1	0•428	0•382
16	18•8	0•442	0•384
14	18•3	0•461	0•389
12	17•7	0•489	0•398
10	16•6	0•530	0•415
8	14•8	0•592	0•448

Table 5. Gompertz growth functions fitted to growth data produced by a logistic equation with $A = 20$, $i = 6$ and $K = 0.400$. Fits were produced using the floating asymptote and fixed asymptote approaches. The growth curve reached 70% of the asymptote at 8 days

Age limit	Floating asymptote		Fixed A = 20
	A	K	K
20	20.7	0.258	0.284
18	21.0	0.251	0.283
16	21.5	0.240	0.282
14	22.3	0.226	0.279
12	24.1	0.206	0.273
10	28.0	0.178	0.263
8	38.5	0.144	0.245

We generated 21 daily masses [ages 0 (hatching)–20] based on a logistic function with $A = 20$, $i = 6$ and $K = 0.400$, which are fairly typical values fitted to data for small temperate passerine birds (Ricklefs 1968a). Daily masses for the Gompertz function were generated using $A = 20$, $i = 5$ and $K = 0.270$, which produces a closely parallel growth curve to that of the logistic function (Fig. 2). The most important difference is that the growth rate for the Gompertz function is relatively rapid prior to the inflection point while that of the logistic function is relatively rapid following the inflection point.

When the growth data produced by the Gompertz function were fitted by logistic functions, with the data truncated at different ages between 8 and 20 days, earlier truncation led to lower estimated asymptotes and higher estimated growth rates. The magnitude of the bias was substantial, amounting to extremes of -23% for A and +42% for K (Table 4). When the asymptote was fixed at $A = 20$, the estimates of the growth rate showed a much reduced bias, with an extreme of +17%.

When the growth data produced by the logistic function were fitted by Gompertz functions, with the data truncated at different ages between 8 and 20 days, earlier truncation led to a higher estimated asymptote and lower estimated growth rate. The magnitude of the bias was also substantial, amounting to extremes of +86% for A and -44% for K (Table 5). When the asymptote was fixed at $A = 20$, the estimates of the growth rate showed a much reduced bias, with an extreme of -14%.

Clearly, an inappropriate growth model combined with truncation of the data resulting from differences in the time of fledging relative to the growth curve can produce large biases in the estimation of both asymptotes and growth rates. Because actual growth curves do not necessarily follow any particular growth function, the potential for truncation biases would appear to be substantial. Unfortunately, these biases are associated with variation in a biologically important parameter, the length of the nestling period (Ricklefs, Starck & Konarzewski 1998; Remeš &

Martin 2002). In addition, the biases might be positive or negative depending on the relationship of the shape of the growth curve to the model used to fit the curve. The bias in the floating A estimate of K increases with the truncation of the data. In the examples in Tables 4 and 5, the 70% A estimate is close to the most extreme bias. The use of a fixed asymptote reduces the bias in both A and K substantially.

GENERAL METHOD AND REGIONAL COMPARISONS

Are the differences in estimates of A and K generated by the different methods and models large enough to influence interpretations of the relationships between growth rate and other life-history traits? We estimated K for 46 species of New World temperate and tropical passerines according to the floating A, 70% A, and fixed A methods, and then compared the estimates of K with other life-history traits. Estimated growth rate constants (K) tended to be lowest for fixed A and highest for 70% A (Appendix S1, Supporting Information). Comparing means of all estimates of K for the 46 species, those estimates generated by fixed A and floating A methods were the most similar (0.377 and 0.414, respectively). The mean estimate generated by the 70% A method was 0.452. Estimated standard errors of K were uniformly higher for floating A and 70% A than for fixed A estimates, indicating greater uncertainty in estimates of K generated by the former two methods (Appendix S1).

In comparisons of K with life-history traits, the values obtained with the fixed A and floating A methods were similarly well explained by the independent variables (adjusted $R^2 \leq 0.355$ and 0.357 , respectively). In comparison, 70% A estimates of K were poorly explained by the independent variables ($R^2 \leq 0.117$), most likely because of the discrepancy between adult mass and the values of A estimated by the logistic model from incomplete data on growth. To evaluate this possibility, we included a ratio of A to adult mass (R) in statistical comparisons. We found that including R improved the fit of floating A estimates and, especially, 70% A estimates, in the latter case more than doubling the explained variance.

Choice of method affected outcome of comparisons of K with other traits. Values of K estimated by all three methods differed between tropical and temperate regions, while the length of the nestling period appeared consistently in the best AIC models only for the floating A estimates (Table S1, Supporting Information). Thus, different methods of estimating growth rates are correlated to different life-history or distributional traits and result in different interpretations of the biological relationships between growth rate and other attributes of species.

Choice of model (logistic vs. Gompertz) could also influence interpretation of results. We conducted a parallel analysis of the relationship of growth rate to adult mass, region, nestling period and R using estimates of K obtained from fitting Gompertz growth

functions to the data (Table S2, Supporting Information) The results were even more dramatic in some ways than for the fitted growth rates from the logistic equation. Estimates based on fixed asymptotes had about the same amount of explained variance as with estimates for logistic functions, and both region and adult mass were significant effects. Adding R to the regression improved the fit in models addressing floating and 70% A but not for the fixed A method.

Neither the floating A method nor the 70% A method resulted in good fits to the data (adjusted $R^2 < 0.10$ and 0.03 , respectively), although region was nonetheless identified as a significant effect. However, when R was added to the regressions, the adjusted R^2 values increased to 0.62 and 0.72 , respectively. This suggests that Gompertz fits to the data were strongly biased by the discrepancy between the estimated asymptote and the adult mass, and that these biases were not strongly related to differences between regions or the length of the nestling period.

Discussion

Our evaluations of the three methods (floating A, 70% A and fixed A) for estimating the growth rate constant (K), and the two models, logistic and Gompertz, revealed variation in estimates substantial enough to influence interpretation of biological associations between growth rate and other traits of species. In particular, generation of estimates from incomplete data of nestling growth can bias estimates of K when the asymptotic value of growth curves (A) is allowed to float, as it does in the floating A and 70% A methods. Using an inappropriate model, e.g. logistic models when Gompertz models provide better fits (and vice versa), can still introduce bias; however, fixing A at average adult mass reduces this bias.

Ideally, models of growth should be based on frequent measurements of individual nestlings until they reach mature size, but this is difficult to achieve in multi-species comparative studies. Previous studies of this kind have used curve-fitting approaches that estimate the asymptotic value within the model. This approach can be problematic when chicks depart from the nest prior to attaining adult mass. In these cases, a transient asymptote, caused by a levelling-off in mass related to the concurrent processes of tissue proliferation and water loss from maturing tissues, may occur (Ricklefs 1967b, 1968b, 1975; Austin & Ricklefs 1977; Konarzewski 1988; Konarzewski, Kooijman & Ricklefs 1998). Such variations in growth curves can bias estimates of growth rate if data from the entire growth curve are not included, causing estimates to be higher than if the entire growth curve was analysed. Systematic inflation of K could confound understanding of relationships between length of the nestling period and time-dependent mortality (Ricklefs, Starck & Konarzewski 1998; Remeš & Martin 2002; Remeš 2007).

Truncation of data, whether intentional as in the 70% A method or because of absence of data from older nestlings (a common situation in field studies), increases error in estimates of A, inflection points of growth curves (i) and biases K. We demonstrated the problems associated with relying on incomplete growth curves using sample data from *T. thalassina*, and *C. fasciata*, and simulated growth curves. By truncating the maximum age, we found that as fledging age was reduced, K increased while A decreased. These examples demonstrate how growth rate can be affected by limited data, with reduction in fledging age typically inflating K-values. This bias can be reduced by fixing the asymptote at the natural end point of growth curves for species with determinate growth, i.e. adult mass. Additionally, an inappropriate growth model can bias estimates of growth rate, and of the asymptote in floating A methods (Ricklefs 1983).

We suggest that fixing the asymptote at adult mass (or maximum nestling mass in species that exceed adult mass prior to fledging) produces the most consistently accurate and biologically interpretable estimates of nestling growth rates. Fixing A stabilizes the growth model and makes it less sensitive to truncation of the growth data by early fledging. In our data set, this method resulted in the lowest estimates of growth rate with the least bias from variation in nestling period. It also accounted for the most variance in models relating growth rate to adult mass, geographic region, taxon and nestling period. While the fixed A method does not completely eliminate bias from incomplete growth curves, it does avoid problems inherent in models using a free asymptote. Because the value of A becomes critical in the fixed A method, careful attention to its measurement is required. Body mass varies geographically in many bird species, so local measurements of adult mass taken during the breeding season should be used in the calculations. In species with strong sexual dimorphism, for example, sex of chicks should be established so that the appropriate value of A can be used in growth rate models. Given the apparent bias of the commonly used floating A method, published growth rates should be evaluated carefully. Thus, when published estimates of growth rate have primarily used floating A, and to a lesser extent, 70% A methods (e.g. Starck & Ricklefs 1998; Remeš & Martin 2002), the estimates are likely to be biased high, and when possible, should be re-calculated using the fixed A method.

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References

- Austin, G.T. & Ricklefs, R.E. (1977) Growth and development of the Rufous winged Sparrow (*Aimophila carpalis*). *Condor*, 79, 37–50.
- Barber, R.W. (1950) Growth and feather development of towhee nestlings. *American Midland Naturalist*, 44, 742–749.
- Blount, J.D., Metcalfe, N.B., Arnold, K.E., Surai, P.F. & Monaghan, P. (2006) Effects of neonatal nutrition on adult reproduction in a passerine bird. *Ibis*, 148, 509–514.
- Case, T.J. (1978) On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology*, 53, 243–282.
- Cassell, D.L. (2007) Don't be Loopy: Re-sampling and Simulation the SAS Way. Proceedings of the SAS Global Forum 2007 Conference. SAS Institute, Inc., Cary, NC.
- Cohen, A.A., McGraw, K.J., Wiersma, P., Williams, J.B., Robinson, W.D., Robinson, T.R., Brawn, J.D. & Ricklefs, R.E. (2008) Interspecific associations between circulating antioxidant levels and life-history variation in birds. *The American Naturalist*, 172, 178–193.
- Dunning, J.B. (1993) *CRC Handbook of Avian Masses*. CRC Press, Boca Raton, FL.
- Etterson, M.A., Nagy, L.R. & Robinson, T.R. (2007) Partitioning risk among different causes of nest failure. *Auk*, 124, 432–443.
- Haverschmidt, F. (1952) Nesting behavior of the Southern House Wren in Surinam. *Condor*, 54, 292–295.
- 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 Review*, 32, 22–32.
- Jongsomjit, D., Jones, S.L., Gardali, T., Geupel, G.R. & Gouse, P.J. (2007) A guide to nestling development and aging in altricial passerines. US Department of Interior, Fish, and Wildlife Service. Biological Technical Publication, FWS/BTP-R6008-2007, Washington, DC.
- Kluyver, H.N. (1961) Food consumption in relation to habitat in breeding chickadees. *Auk*, 78, 532–550.
- Konarzewski, M. (1988) A model of growth in altricial birds based on changes in water content of the tissues. *Ornis Scandinavica*, 19, 290–296.
- Konarzewski, M., Kooijman, S. & Ricklefs, R.E. (1998) Models for avian growth and development. *Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum* (eds J.M. Starck & R.E. Ricklefs), pp. 340–365. Oxford University Press, New York.
- Lack, D.L. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Martin, T.E. (1987) Food as a limit on breeding birds: a life history perspective. *Annual Review of Ecology and Systematics*, 18, 453–487.
- Murphy, M.T. (1981) Growth and aging of nestling Eastern Kingbirds and Eastern Phoebes. *Journal of Field Ornithology*, 52, 309–316.
- Murphy, M.T. (1988) Comparative reproductive biology of kingbirds (*Tyrannus* spp.) in eastern Kansas. *Wilson Bulletin*, 100, 357–376.
- Oniki, Y. & Ricklefs, R.E. (1981) More growth rates of birds in the humid New World tropics. *Ibis*, 123, 349–354.
- Putnam, L. S. (1949) The life history of the Cedar Waxwing. *Wilson Bulletin*, 61, 141–182.
- Remeš, V. (2007) Avian growth and developmental rates and age-specific mortality: the roles of nest predation and adult mortality. *Journal of Evolutionary Biology*, 20, 320–325.
- Remeš, V. & Martin, T.E. (2002) Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution*, 56, 2502–2518.
- Ricklefs, R.E. (1967a) A graphical method of fitting equations to growth curves. *Ecology*, 48, 978–983.
- Ricklefs, R.E. (1967b) Relative growth, body constituents and energy content of nestling barn swallows and red-winged blackbirds. *Auk*, 84, 560–570.
- Ricklefs, R.E. (1968a) Patterns of growth in birds. *Ibis*, 110, 419–451.
- Ricklefs, R.E. (1968b) Weight recession in nestling birds. *Auk*, 85, 30–35.
- Ricklefs, R.E. (1969) Preliminary models for growth rates of altricial birds. *Ecology*, 50, 1031–1039.
- Ricklefs, R.E. (1973a) Fecundity, mortality, and avian demography. *Breeding Biology of Birds* (ed. D.S. Farner), pp. 366–435. National Academy of Sciences, Washington, DC.
- Ricklefs, R.E. (1973b) Patterns of growth in birds. II. Growth rate and mode of development. *Ibis*, 115, 177–201.
- Ricklefs, R.E. (1975) Patterns of growth in birds. III. Growth and development of the cactus wren. *Condor*, 77, 34–45.
- Ricklefs, R.E. (1976) Growth rate of birds in the humid New World tropics. *Ibis*, 118, 176–207.
- Ricklefs, R.E. (1979a) Adaptation, constraint, and compromise in avian postnatal development. *Biological Reviews*, 54, 269–290.
- Ricklefs, R.E. (1979b) Patterns of growth in birds. V. A comparative study of the growth and development in the starling, common tern, and Japanese quail. *Auk*, 96, 10–30.
- Ricklefs, R.E. (1982) Some considerations on sibling competition and avian growth rates. *Auk*, 99, 141–147.
- Ricklefs, R.E. (1983) Avian postnatal development. *Avian Biology* (eds D.S. Farner, J.R. King & K.C. Parkes), pp. 1–82. Academic Press, New York.
- Ricklefs, R.E. (1984) The optimization of growth rate in altricial birds. *Ecology*, 65, 1602–1616.
- Ricklefs, R.E., Starck, J.M. & Konarzewski, M. (1998) Internal constraints on growth in birds. *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum* (eds J.M. Starck & R.E. Ricklefs), pp. 266–287. Oxford University Press, New York.
- Robinson, W.D., Brawn, J.D. & Robinson, S.K. (2000) Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecological Monographs*, 70, 209–235.
- Southern, W.E. (1958) Nesting of the red-eyed vireo in the Douglas Lake region, Michigan. *Jack-Pine Warbler*, 36, 105–207.
- Starck, J.M. & Ricklefs, R.E. (eds) (1998) Variation, constraint, and phylogeny. *Comparative analysis of variation in growth. Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*, pp. 247–265. Oxford University Press, New York.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, New York.
- Werschkul, D.G. & Jackson, J.A. (1979) Sibling competition and avian growth rates. *Ibis*, 121, 97–102.

Supporting Information

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

Table S1. Goodness-of-fit statistics for the best combinations of independent variables for three methods of estimating growth rate based on the logistic growth function. All other models produced significantly worse fits to the data.

Table S2. Goodness-of-fit statistics for the best combinations of independent variables for three methods of estimating growth rate based on the Gompertz growth function. All other models produced significantly worse fits to the data.

Appendix S1. Growth rates parameter estimates of species by suborder.