Shapes and functions of bird-growth models: how to characterise chick postnatal growth

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ABSTRACT

We compare four candidate models (logistic, Gompertz, von Bertalanffy, and extreme value function) for modelling the growth of birds. We fitted the models to two empirical data sets of chick growth (six biometric measurements) of African black oystercatchers *Haematopus moquini* from South Africa and little stints *Calidris minuta* from Russia, and identified the best-fitting growth curves by Akaike's information criterion. We also determine fitted and derived parameters, including the relative value (size) at hatching, the placement of inflection, the (normalised) growth rate constant, and the adult value (upper asymptote). The preferred model together with these factors describes how fast (or abruptly) the curves asymptote, and illustrates why growth is poorly characterised by the growth rate constant alone. Though the extreme value function model has not (as far as we know) been applied to chick growth data before, it appears to return the best fit for some parameters in our data sets. For example, we found that in African black oystercatchers two very different models best characterise two of the measurements: the extreme value function model and the Bertalanffy model for tarsus growth and body mass growth, respectively. In addition, we discuss the usefulness of fixing the upper asymptote to the adult value (e.g., adult body mass) and recommend a fixed upper asymptote in most cases.

1. Introduction

Growth analysis is an important and one of the most studied patterns in avian physiology (Zach et al., 1984; Zach, 1988; Starck and Ricklefs, 1998; Pearce-Higgens and Yalden, 2002; Karkach, 2006; Tjørve et al., 2009). Whether body mass or another biometric measure is plotted against age, descriptions of growth typically involve fitting sigmoid regression models to empirical data to obtain parameter estimates (e.g., Ricklefs, 1976; Klaassen et al., 1994; Hazlitt et al., 2002) or separate estimations of the value of each parameter in the model (Ricklefs, 1967; Tjørve and Underhill, 2009).

The study of growth in birds began with studies of domestic forms (e.g., Laird, 1965; Ricklefs, 1973). In 1965, Taylor concluded that birds grow more rapidly than mammals but noted the requirement for further growth data of wild birds. Ricklefs (1968) compared the growth of almost 100 species of wild altricial bird species. Since then, many studies on the growth of birds have appeared. Analyses of growth in birds have been carried out using different methods and models (Ricklefs, 1967; Schekkerman et al., 2003; Narushin and Takma, 2003; Tjørve and Underhill, 2009). The candidate regression models most commonly applied to the growth

of body mass and other biometric measurements in young birds (i.e., prefledging) are the logistic, the Gompertz, and the von Bertalanffy (hereafter referred to as the "Bertalanffy") growth models, as described by Ricklefs (1968, 1973) and Starck and Ricklefs (1998). Remarkably enough, very little has changed since Ricklefs' (1968, 1973) landmark papers in *Ibis* more than 35 years ago. Researchers are still fitting the same models to their growth data, and with very little discussion for justifying this practice. Yet any sigmoid model with a positive value for the upper asymptote when $x = 0$ and an inflection point may suffice (see, e.g., Tjørve, 2003, 2009 for a review of sigmoidal candidate models).

Upon closer examination, the method of calculating and comparing growth rate constants is not well founded. The often scant explanations of the methods make the replication of calculations difficult and the comparison of studies impossible. In addition, the choice of model is rarely linked to the reasons for fitting a given curve (e.g., defined descriptive, explicative or predictive purposes). Also, the choice rarely refers to statistical arguments, such as goodness of fit and considerations of normal distribution(s) and homoscedasticity (i.e., assumptions of the regression method) or non-statistical arguments (e.g., expected curve shape and the purpose of comparing data sets). Subsequent discussions of the fitted growth curve typically found in the literature are usually limited to one parameter of the model, k, which has been called the "growth rate parameter", "growth parameter", "growth rate constant", and even "growth rate". The last term is the most misleading, because

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this parameter is not the slope or rate at which the curve increases with age in arithmetic space, but the rate at which the slope changes with age. Further, the comparison of growth is made difficult due to the use of different models that produce different growth parameters. Ricklefs (1973) has determined approximate factors to convert the growth rate constants between three regression models, the logistic model, the Gompertz model, and the Bertalanffy model, in order to compare studies that used different models.

Several studies have employed growth analyses to describe the growth of species (e.g., Beintema and Visser, 1989; Viñuela and Ferrer, 1997; Steinen and Brenninmeijer, 2002; Tjørve et al., 2007, 2008), to compare growth patterns of different biometrics within a species (e.g., Beintema and Visser, 1989; Tjørve and Underhill, 2009), to compare one biometric between populations (e.g., Redfern, 1983; Schekkerman et al., 1998), or to associate environmental conditions to growth and energy expenditure (e.g., Klaassen, 1994; Schekkerman and Visser, 2001; Schekkerman et al., 2003). Despite the large number of studies (see Starck and Ricklefs, 1998; Weathers, 1992; Tjørve et al., 2009 for reviews), there has been no single standardised method to describe or assess the growth of body mass or other biometric measurements across time. Ricklefs' (1967) method does not involve regression and is not discussed here.

Regression is usually performed as an ordinary least square (OLS) regression (McArdle, 1988). A simple linear regression may be applied after a linearisation (i.e., transformation) of the data (Ricklefs, 1967; Ricklefs and White, 1981; Redfern, 1983; Miller and Knopf, 1993) or a non-linear regression is used. The latter is the more common today (e.g., Oniki and Ricklefs, 1981; Reed et al., 1999; Viñuela and Ferrer, 1997; Arroyo et al., 2000), because computers and statistical software have facilitated the computations. These tools also allow for the use of models that are not easily linearised. Of course, a linearised regression does not produce exactly the same fitted parameter values as the non-linear regression since the data points never fit perfectly to the curve. For this reason a linearised regression may be preferable if the aim is to compare parameter values from linearised regressions found in the literature.

One may fit a regression to the whole data set (all birds and all observations) but this approach raises concerns of pseudoreplication, i.e., the lack of independence between data points (see Wilcox, 1996; Heffner et al., 1996). Some ways of avoiding pseudoreplication include performing a regression of average values for each day during the prefledging period (e.g., Reed et al., 1999), calculating within-clutch averages (e.g., Greeney, 2008; Merino and Potti, 1998), taking random samples from each individual (Pinaud et al., 2005), performing a regression for individuals (e.g., Hunt and Hunt, 1976; Tjørve et al., 2008), and applying Jackknife methods (e.g., Schekkerman et al., 1998; Beintema and Visser, 1989). Robust regression has become more available (in commercial software) and may be a good alternative (see Tjørve and Underhill, 2009 for use of robust regression) because it relaxes the assumptions of normality (Gaussian distribution) and homoscedasticity.

It is possible to fix parameter values or to estimate them from expected values or means of observed values. The parameter fixed before the performance of the regression is typically the upper asymptote. For the three (aforementioned) commonly applied regression models, a single parameter controls the upper asymptote.

This article reviews four candidate models, the logistic, Gompertz, Bertalanffy, and the extreme value function (EVF) model (Williams, 1995), and discusses their application and usefulness for modelling growth in birds. It also considers the curve shapes of the models in relation to expected and observed shapes of empirical growth plots of six biometric measurements. A single regression model does not necessarily fit all biometrics equally well. Tjørve

Table 1
Parametric interpretations for the candidate models showing the value (mass or length) at the inflection point and the value relative to the upper asymptote (A).

Model	Value at inflection (M_i)	Value at inflection in % of A
Bertalanffy	$8A/27$	29.63%
Gompertz	A/e	36.79%
Logistic	$A/2$	50%
EVF	$A(1-(1/e))$	63.21%

and Underhill (2009) noted, for instance, that the Gompertz model fitted growth in mass well but the fit for tarsus was less satisfactory. The aim of this study is thus not to demonstrate which model is superior, but to illustrate how growth curves from different species or from different biometrics may have different shapes and therefore require different regression models. We intend to show that characteristics other than, e.g., maximum growth rate or comparisons of growth rate constants are useful in describing growth patterns and differences between growth curves.

We will discuss the candidate models in relation to the position of the inflection point (because different models have dissimilar inflection points) and other parameters in relation to the expected and observed curve shapes of different biometric measurements. Furthermore, we discuss the usefulness of fixing the upper asymptote to the adult value, e.g., adult body mass.

2. Methods

Growth usually follows a sigmoid curve shape. Candidate models should also have an upper asymptote corresponding to adult size (of different biometric measurements). In addition, the hatching mass or hatching length (of different biometric measurements) is defined by the intersection between the fitted curve and the x-axis (i.e., at age 0). The point of the maximum growth rate is at the inflection point, which for each model discussed is fixed at a given percentage of the upper asymptote (Table 1).

2.1. The logistic model

The logistic growth curve is a three-parameter model, typically given as:

$$M = \frac{A}{1 + \exp(-k(t - T_i))}, \tag{1}$$

where M is body mass, A is the asymptotic body mass, k is the growth rate constant, t is age, and T_i is the age at the inflection point (Ricklefs, 1968; Tjørve and Underhill, 2009). This model is quite inflexible, because it is symmetrical around the inflection point, which is fixed at 50% of the upper asymptote. The value of M at the inflection point is found at $t = T_i$. The model thus reduces to $A/(1 + \exp(0)) = A/2$. Despite this limitation, the logistic model is one of the most useful and often applied models.

2.2. The Gompertz model

The Gompertz growth curve is usually (Ricklefs, 1968; Tjørve and Underhill, 2009):

$$M = A \exp(-\exp(-k(t - T_i))). \tag{2}$$

The Gompertz model is related to the logistic model, and behaves quite similarly. It too is inflexible in that the inflection point is fixed, but it is fixed at 36.79% of the upper asymptote. This is found at $t = T_i$, which reduces the model to $A \exp(-1) = A/e$. Therefore, the Gompertz growth curve is best suited for growth processes where the point of inflection is localised approximately at one-third of the