

### A New Paradigm for the Analysis and Interpretation of Growth Data: The Shape of Things to Come

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The process of growth is basic to all organisms, and studies of growth have long been a subject of concern to ornithologists. At a workshop held at the recent meeting of the American Ornithologists' Union (18–21 August 1986), a series of presentations and subsequent discussions laid the foundation for what we feel to be a new paradigm for studying growth. The strengths of this new paradigm lie in its potential for more detailed quantitative comparisons of growth in general and intraspecific comparisons in particular. It is our purpose to summarize the major aspects of this paradigm and to provide information on its development. The paradigm was derived mainly from studies of birds, but should have broad applicability to studies of a variety of organisms.

Growth was first studied qualitatively by describing developmental stages in chronological series. This was followed by quantitative formulations that considered growth as the net result of simultaneous anabolic and catabolic processes. Many of these early concepts (e.g. Huxley 1932, von Bertalanffy 1957) still influence current thinking. A third stage was introduced by Ricklefs (1967), based on a graphical method of fitting data to S-shaped or sigmoid growth models. This methodology, applied to interspecific comparisons, has contributed significantly to our understanding of the meaning of the patterns of variation in avian growth—particularly from an evolutionary point of view (Ricklefs 1983). The new paradigm is also based on the fitting of data to sigmoid models but is directed more toward questions that involve intraspecific as well as interspecific comparisons.

The Richards sigmoid growth function (Richards 1959) and its expression in terms of parameters with specific biological meaning (Bradley et al. 1984, Brisbin et al. 1986b) have been of basic importance to the new growth paradigm. These approaches now allow independent quantitative assessments of three biologically meaningful aspects of growth: (1) *size*, the upper or asymptotic limit; (2) *rate*, a measure of the time required for specified growth increments to take place; and (3) *shape*, a quantitative measure describing

the path or trajectory taken by the growth process. The parameters of size, rate, and shape in the Richards sigmoid model are, at least theoretically, free to vary independently of each other.

In the Richards model, growth-curve shape is quantified by the so-called "shape parameter,"  $m$ . When  $m$  has values of 0, 0.67, or 2.0, the Richards model is identical to the monomolecular (also known as the negative exponential), von Bertalanffy, or logistic sigmoid models, respectively, and as  $m$  approaches a value of 1.0 the Richards model approaches the Gompertz. In this sense the Richards model may be considered a generalized "parent" growth function, from which almost all of the other commonly used growth functions may be generated by changes in the value of the curve shape parameter,  $m$ .

The quantification of growth rate has been a particular problem in the past. In its original form the Richards model contained a growth-rate parameter,  $K$ , which became unstable statistically as the value of  $m$  approached 1.0. Recent reparameterizations of the Richards model, however, produced alternative means of describing growth rate that do not have this problem and that are more meaningful biologically (e.g. the parameter  $G$  of Bradley et al. 1984, or the parameter  $T$  of Brisbin et al. 1986b).

One important hypothesis tested within the new paradigm concerned the suggestion that growth-curve shape, as quantified by the Richards shape parameter  $m$ , is several times more likely to change in response to environmental stress than is either asymptotic size ( $A$ ) or growth rate ( $T$ ) (Brisbin et al. 1986a–c). These experiments dealt with a variety of species exposed to various stressors, with comparisons at the intraspecific level. The findings suggested that comparisons based on the use of models in which curve shape is set and not allowed to vary (e.g. Fendley and Brisbin 1977) may not be useful in understanding the effects of environmental stress on growth. Moreover, others (Pasternak and Shalev 1983) suggested that changes in growth-curve shape alone can reflect an alteration in the energetic efficiencies with which birds may grow to a specified size within a specified time. Considerations of changes of growth-curve shape, within the approaches outlined here, may thus be important to studies of basic bioenergetics, as well as to commercial interests of the poultry industry.

Fitting growth curves requires nonlinear least-squares curve-fitting techniques. These have now been adapted to nearly all of the standard statistical packages, and some can now be used on personal microcomputers. These tools simplify the fitting of the new growth equations. Procedures such as PROC NLIN

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of SAS (SAS Inst. 1982) or program AR of BMDP (BMDP 1983) permit the fitting of growth data (entered as dates or ages paired with corresponding body masses or measurements) without writing complex differential equations. As suggested by Ricklefs (1983), these nonlinear curve-fitting techniques can replace the graphical method of selecting and analyzing nonlinear growth models.

Along with these advances have come concomitant developments in readily usable statistical packages for testing the parameters estimated by the curve-fitting programs. This ease in detecting statistical differences among treatment groups encourages the use of growth data to rigorously test important hypotheses concerning the biology of birds and other organisms. In the case of the Richards model, for example, the parameters quantifying growth size, rate, and shape can now be tested for differences among such groups as males vs. females, birds maintained on different diets or exposed to different levels of some toxicant, or birds from different parts of the breeding range.

The procedures for fitting growth data to a model and then comparing statistically the results for size, rate, and shape will vary according to the type of data available. As pointed out previously (Ricklefs 1983, Bradley et al. 1984), several different experimental designs exist by which growth data can be collected. Each design imposes certain restrictions for fitting data to models and then comparing the estimated parameters. Three of the more important of these designs are:

(1) *Longitudinal data sets*, where individual organisms are weighed or measured repeatedly throughout the growing period, ideally until a size asymptote is reached. Because of problems introduced by autocorrelation and because successive data points from the same individual are not independent, such longitudinal growth data should be analyzed with a process-error model as described by White and Brisbin (1980) for the Richards function. In a process-error model, growth rate is considered a function of increasing body size or mass. Failure to use the process-error model approach for longitudinal data might produce excessively narrow confidence intervals and increase the likelihood that significance may be claimed erroneously between parameter estimates for different treatment groups (White and Brisbin 1980). Application of a multivariate analysis of variance (MANOVA) and then one-way analyses of variance (ANOVA) procedures can then be utilized to identify the parameters that differ between treatment group (Brisbin et al. 1986a-c).

(2) *Cross-sectional data sets*, where each individual is weighed or measured only once (as, for example, in the case of destructive population sampling). In such cases it is not possible to test for differences among individuals. Differences between treatment groups are tested with an *F*-statistic comparing "com-

plete" vs. reduced models (White and Brisbin 1980). Cross-sectional data cannot be analyzed with the process-error model approach but must be fit directly using the integrated form of the growth equation in which size or mass is considered as a function of age. Fitting the integrated form of the Richards model requires the addition of a fourth parameter to the three described earlier. This fourth parameter is usually the size or mass of the organism at birth (or hatching) and either may be entered into the equation as a constant (the value of which is determined from observations of the sizes or masses of newly born or hatched individuals) or may be estimated by the curve-fitting procedure. Further discussion of the analysis of cross-sectional data sets with the Richards model is provided by Bradley et al. (1984).

(3) *Mixed data sets*, where some individuals are weighed or measured only once while others may be weighed or measured several times. These include the interval data sets described by Ricklefs (1983) and Fabens (1965). Such data may be analyzed by curve-fitting procedures using a jackknife technique as described by Bradley et al. (1984).

One danger that accompanies these analytical tools is their use to analyze data sets that do not warrant their application. It is now possible to use curve-fitting procedures that will create an estimate of a final asymptote whether or not one exists in the data. Frequently, for example, growth data sets are truncated long before the subjects approach asymptote. One such situation is the growth data obtained for species whose young leave the nest (and thus can no longer be weighed or measured) before they reach adult size. In some cases, asymptotes estimated from such data sets are obviously unrealistic and are readily recognized as artifacts. The danger lies in cases where a realistic value is generated for the asymptote but must still be considered unreliable in light of the limitations of the data used for the estimate.

Each researcher must consider which growth parameters are to be estimated and what specific hypotheses the growth data will be used to test. The burden is also placed on the investigator to demonstrate that the data are sufficient to warrant the degree of model complexity used in their analysis and interpretation. Editors and referees should demand nothing less in evaluating such studies for publication.

Besides the need for data at and beyond the attainment of asymptote, consideration must be given to the total number of data points available and their spacing throughout the growing period. Data sets of only a few points determined at widely spaced intervals throughout the growing period cannot be expected to give an adequate estimate of the value of the shape parameter from any sigmoid model even if some of the data points are taken well after asymptotic size is attained. Practical considerations may thus often prevent the collection of sufficient data for a

sigmoid analysis. In such cases, or whenever adequate post-asymptotic data cannot be obtained, it may be necessary to choose a simpler model (e.g. linear or exponential) to test hypotheses. Such procedures, while failing to provide all the information contained in a sigmoid analysis, are nevertheless preferable to analytical procedures that are unwarrantedly complex with respect to the nature of the data available.

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### On Paradigms vs. Methods in the Study of Growth

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Paradigms provide models for restructuring our investigations. New paradigms allow us to answer questions that formerly eluded us. Because growth is both a universal biologic property and a complex, usually nonlinear phenomenon, new approaches to quantifying growth are highly desirable. The sigmoid curve, long heralded as the growth curve, reappears in many mathematical, economic, and scientific analyses. Accordingly, access to mathematical tools for analyzing

and characterizing sigmoid curves affords the opportunity to use parameters of the curve as discrete independent variables. Brisbin et al. (1987) detail new methods for approaching the study of the sigmoid growth function. With powerful statistical packages available to crunch the numbers, the iterative procedures for solving nonlinear function problems are now readily available.

Apart from lauding the introduction of such procedures, I want to call attention to the fact that Brisbin et al. (1987) do indeed offer a paradigm and not merely a tool. I emphasize that the availability of these procedures, by themselves, allows us to restructure our investigations and to ask new questions. In fact,

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