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### Growth-curve Analysis: A Critical Reevaluation

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Growth-curve analysis (Ricklefs 1967) has long enjoyed an ardent following. Recently, Brisbin et al. (1987) predicted a bright future for this methodology, but failed to address critical shortcomings of growth-curve analysis and of the Richards (1959) model in particular. They also completely ignored alternatives. Growth-curve analysis is a tool only, and not an end in itself. The main question is not which model to use, but whether to use growth-curve analysis at all. For many studies growth-curve analysis is inappropriate, and alternatives, such as simple observed-growth statistics, may be more effective growth indicators. Although the Richards model with its variable sigmoid shape is intuitively attractive, other simpler models can be superior for studying growth.

There are many reasons growth-curve analysis may not be an ideal methodology. Growth-curve analysis is labor intensive because numerous data are required to satisfy models with several fitted parameters. For passerines, with their short nestling time, this usually means daily measurement on a rigid schedule so that each nestling is always measured at about the same time. Alternatively, variable time must be taken into account during curve fitting. Growth-curve analysis requires numerous precise data. Small changes in only a single measurement can profoundly affect parameter estimates. Sensitivity depends on the type of model employed, however.

High data requirements of growth-curve analysis can stress both parents and nestlings. Frequent disturbances can cause nest abandonment and consequent loss of data. During cold, wet weather it is often difficult to keep small nestlings warm and dry; hence, handling alone can significantly affect growth (Zach

and Mayoh 1986a). Subtle stress from disturbances and handling is difficult to detect and confounds interpretation of treatment effects.

A consistent finding is large variation in growth among broods, commonly exceeding 50% of the total variation (Ricklefs and Peters 1979, Zach and Mayoh 1982). Consequently, statistical power to test for treatment effects is low unless a large number of broods is studied. Unfortunately, growth-curve analysis requires much effort per brood, making it difficult to study many broods simultaneously.

For many passerines, growth-curve analysis is difficult to apply because fledging occurs well in advance of growth completion. Meaningful fitting of growth curves requires precise estimates of final size. Body-mass recession may also occur before fledging (Ricklefs 1968a). There seems to be little agreement on how to deal with this phenomenon. We have used data up to, and including, the highest body mass before fledging, but this may not be entirely appropriate. Actually, adult body mass is difficult to define because the mass of most passerines fluctuates seasonally.

To summarize, growth-curve analysis is unsuitable when resource limitations prevent collection of sufficient and precise data, when disturbances lead to brood abandonment or growth depression, and when adult sizes cannot be unequivocally measured. Fortunately, there are viable alternatives to growth-curve analysis.

Our studies have consistently indicated that several simple observed growth statistics are equal, or better, growth indicators than fitted model parameters (Zach and Mayoh 1986a, b). These statistics are body-mass asymptote, and body mass, primary-feather length, and foot length at or near fledging. They are consistent with each other and with fitted model parameters. Further, they are more readily determined than fitted parameter values because fewer measurements

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are required, precise data can be secured more easily from large nestlings, disturbances are reduced, and statistics can be readily defined and measured. Fewer measurements per brood allow study of more broods to quantify properly variation among broods and to compensate for unforeseen losses. When measuring observed growth statistics, such losses do not represent much wasted effort. Finally, observed growth statistics are biologically meaningful and can be readily interpreted.

Like growth-model parameters, observed growth statistics are powerful stress indicators because they integrate growth performance throughout the nestling period. Growth in passerines seems to follow a rigid and rapid schedule, leaving little opportunity for compensation. Thus, stress at any time in, or throughout, the nestling period reduces the body-mass asymptote and is reflected in the size measurements at or near fledging.

Growth usually follows a sigmoid pattern in birds (Ricklefs 1968b, 1973). Of the sigmoid growth models, the von Bertalanffy, Gompertz, logistic, and Richards models are commonly used. The first three have a fixed shape and involve three parameters ( $A$  = asymptote,  $K$  = growth-rate constant,  $c$  = constant of integration); the Richards model has a flexible shape and four parameters ( $A$ ,  $K$ ,  $c$ ,  $n$  = shape parameter), and in essence includes the other three models. Given sufficient data to justify a four-parameter model, the Richards model seems to be most desirable; however, there are several difficulties with this model.

Perturbation studies have shown that the Richards model is particularly sensitive to small changes in the input data. Thus, these data must be precise to obtain good parameter estimates. In fact, some fitting procedures (White and Brisbin 1980) require that data be measured without error. The high sensitivity may be related to the fact that  $K$  and  $n$  are not independent. These parameters seem to be consistently correlated, with a coefficient,  $r$ , exceeding 0.9 (Bradley et al. 1984, Zach et al. 1984). This is a well-recognized problem (Davis and Ku 1977, Ricklefs 1983). Thus, although the Richards model has four parameters, it effectively has only three, like the models with a fixed shape, because of the close correlation between  $K$  and  $n$ . Another problem with the Richards model is parameter interpretation. It is difficult to attribute biological meaning to the shape parameter,  $n$ , and a priori state whether, or how, it will be affected by a growth stressor. Unfortunately, because of the correlation between  $K$  and  $n$ , and the variable shape of curves, the growth-rate constant,  $K$ , is also difficult to interpret and unsuitable for strict comparisons (Ricklefs 1983, Bradley et al. 1984). Fortunately, there are useful, proven alternatives to the Richards model.

With only three parameters, the von Bertalanffy, Gompertz, and logistic models require fewer data for meaningful fitting than the Richards model. These models are also less sensitive to changes in data and,

therefore, less demanding in terms of data precision. Further, their parameters have clear biological meanings and can be readily interpreted (Pruitt et al. 1979). In our studies the Richards model usually failed to explain a significantly larger proportion of the variation in the data than the best-fitting three-parameter model (Zach et al. 1984). This is not surprising because the best-fitting three-parameter model commonly explained more than 99% of the variation. Clearly, three-parameter models can have several distinct advantages over the Richards model.

Future studies involving growth should select the best tool for evaluating growth performance. In many cases this means the use of simple observed growth statistics rather than growth-curve analysis, or simple growth models rather than the complex Richards model.

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