MEASURING GROWTH IN NESTLING GREY-CROWNED BABBLERS

The ability to age and sex birds in wild populations is often fundamental to field studies of social behaviour and ecology. All too often, simple techniques are not adequately tested or checked, sometimes because of lack of time, but often because repeating the experiments or observations of other researchers, though generally deemed of merit, is not considered the most valuable or creative use of scientific effort.

The Meandarra Ornithological Field Study Unit has long been interested in studying the behavioural ecology of the Grey-crowned Babbler, *Pomatostomus temporalis*, in southern Queensland. In 1976 we pioneered a method of ageing nestlings from a single weighing, based on fitting a logistic growth curve to a previous sample. For nestlings between one and 21 days, it probably indicated satisfactorily the approximate date of hatching or fledging. Because the method was so simple, we wondered if we could use it as a quick procedure for gathering data to characterise growth in a population, thus enabling us to compare populations or to compare the same one in different years.

Before using the method, as described by Brown (1979), we decided to test its repeatibility. In 1980 we were beginning a study of the growth of nestling Babblers, and so were in a position to compare our results with those of Brown (1979) and also to compare the method directly using subsets of our own, more complete, data.

Various models have been used to describe the growth of birds. The most appropriate method for describing growth as measured by weight in passerines is the logistic growth curve (Ricklefs 1968). Increase in weight of the hatchling begins gradually, becoming faster until reaching some maximum rate. Further increase in weight is more slow, gradually tapering off as it approaches an asymptote. Three parameters define a logistic curve. A point of inflection marks the age (in days) when the growth curve changes shape from being concave upward to concave downward. A line tangent to the curve at this point is taken as the growth constant (k), representing linear increase in weight over time. The asymptote (A) is the weight finally achieved, or approached, near the time the nestling may be expected to fledge. The position of the point of inflection on the X-axis is somewhat arbitrary, depending on assumptions about the age of a nestling on Day 0. The growth constant and asymptote are the parameters that have received most attention by researchers.

Given sufficient numbers of weighings throughout the nestling period, k and A can be calculated for each bird and a curve fitted. Overall population parameters can then be estimated by averaging these sampled values. Alternatively, the raw measurements from several nestlings can be lumped, and a single value of k and A calculated. Note that the latter method, although its mean should be similar to that from the former, provides no direct way of calculating the variance of an estimate.

Brown (1979), with a novel approach, found the best estimates for a logistic curve of weight for Babblers to be k = 0.348 and A = 56.0. From each nestling in a sample, he obtained two weights, several days apart, and successively fitted them to a series of specified growth curves using the well-known statistical method of least squares. That procedure was conceived by one of the present writers (DDD) to analyse the data presented by Brown, who was then working with MOFSU. Dow, using a PDP-10 computer at the University of Queensland, developed a FORTRAN programme (GROFIT - Version: July 1977) specifically for this project. Brown's published results were based on the programme option of setting a nestling's earlier weight on the growth curve under trial and calculating the deviation of the second weight from that curve.

Because the difference in time of a nestling's two weighings had been estimated as an integer, this procedure constrained the position of the second weight, on the X-axis, to an exact number of days from the curve. This was not a restriction of the original programme, which allowed placing the initial weight to the left of the curve and then minimised deviations from the curve of both first and second weights. This permitted a more accurate fit as the size of the iterative step could be varied, in practice down to 0.1 days, as the two points were moved in tandem along the X-axis until the best fit was found.

But Brown further modified the method by considering an additional two sets of weights from 'natural' and 'premature' *fledglings*, to which he assigned ages of 21 and 19 days. He computed the sum of squared deviations (SS) for these two samples and then assessed the overall best-fitting curve by finding the one yielding the minimum SS for these together with data from nestlings, i.e. *three independent samples added together*. There are technical problems with such an approach and we show that comparisons using his method are virtually impossible.

When a sampled measurement, Y, is from a fixed value of X (e.g. 19 or 21 days), the growth curve intersects that value at a point, i.e. at X it can be considered horizontal. Also, by definition, the best-fitting horizontal line is the arithmetic mean. Thus, the minimum SS for each of the two samples of fledglings

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will be found when the growth curve passes through their mean values. By fitting a line through any other position, say $\bar{Y} - d$, deviations from that line are not $[Y - \bar{Y}]$ but $[Y - (\bar{Y} - d)]$. It can be readily shown that the sum of the squared deviations from the position selected will be $SS_d = SS + n.d^2$, where SS represents the SS from the arithmetic mean and n the sample size. By varying the asymptote of the logistic curve between 54.0 and 58.0 g, as did Brown, the SS pooled from these two sources would vary from 532 to 788 (calculated from standard deviations and sample sizes given by Brown). On the other hand, fitting only the paired weights of nestlings to the curve generates SS in the range 200 to 350 and may change little as a precise fit is approached. Brown's data consisted of 20 such paired weights from nestlings plus 36 single weights in his two classes of fledglings, thus the latter would considerably mask the 'fine-tuning' of the former. It seems better to use data from fledglings to estimate the asymptote independently, as the growth constant (k) is not independent of the asymptote (Ricklefs 1968). Brown's curve is difficult to use because of the bias from the fledglings' SS and the unreported overall SS for the test. Thus, one could compare his results only if using samples of identical size and composition.

Because we were interested in comparing both Brown's estimates and the reliability of the method, we analysed the data again using the programme GROFIT. The programme makes use of the hatching weight, though variation in the range discussed here has virtually no effect on the results. Brown (1979) estimated the weight at hatching to be 3.85 g (the mean weight of four eggs close to hatching less the estimated weight of the shell). We found that seven nestlings on Day 0 (i.e. 0–24 hours old) weighed 3.0 to 3.9 g with mean 3.44 and SE 0.140. If Brown had first estimated the asymptote A = 56.0 and then fitted only the 20 sets of points, for k = 0.348 as reported, the SS = 323.5. If GROFIT is allowed to fit the best curve it can, without constraining the plot of each first weight to the curve itself as did Brown, then for his data k equals 0.350 (SS = 203.9). One of the values used by Brown was clearly an outlier, accounting for 33% of the residual variance in his sample. This nestling was the second youngest of five. The youngest died. Records suggest that this clutch may have been produced by two females. With this suspicious point removed, and A = 56.0 g and k = 0.348 as before, than SS = 173.2. If only the asymptote is fixed (A = 56.0), then GROFIT yields a best fit with minimum SS = 169.5 when k = 0.355. If no estimate of the asymptote is assumed and only the 19 sets of nestling weights used by Brown are entered as data, then GROFIT finds a minimum SS = 142.4 at k = 0.301 and A = 61.4. *These are the only comparable values available from Brown's (1979) data if his method is made reproduceable.*

To test the reliability of this method more directly, we compared the results of curve-fitting by GROFIT with those obtained using the complete set of weights from each of 13 nestlings (Dow & Gill, in press). We selected a random subsample of two weights from each nestling. These were selected so that the range of differences in age between weighings was the same as in the data reported by Brown. From our complete data set, we had previously calculated k = 0.349 and A = 54.4. Making no assumptions or estimates about parameters, we found for our random subsample k = 0.373 with A = 53.8 (SS = 67.1, n = 13). We selected a second random subsample from the same set of complete data and analysed it independently of the first. It yielded k = 0.442 with A = 52.0 (SS = 85.9, n = 13).

The discrepancy between estimated values of k (0.373 vs 0.442) and of A (53.8 vs 52.0) from two subsamples of the same growth data (with independent estimates of k = 0.349 and A = 54.4), viewed over the range shown by passerine birds, is considerable. We consider it so great as to preclude the use of the technique in this way. Although Brown's (1979) data showed more variation than ours, we think that the estimates yielded from his data by GROFIT of k = 0.301 and A = 61.4 are unrealistic. However, if an asymptote can be estimated independently and fixed (not contributing to the SS as in Brown's analysis), GROFIT appears to produce a much more precise estimate of k. Although the residual variances of our two subsamples differed considerably (SS 68.3 vs 90.5) with A fixed at 54.4, the least-squares fit yielded identical estimates of k = 0.351, not very different from the estimate using all our data (k = 0.349). With Brown's asymptote fixed (A = 56.0), the value of k = 0.355 calculated from his data also seems reasonable.

We set out to test whether the results of this method could be generalised to Babbler populations; to see how repeatable the results were within a population; and to see how useful the method was for its primary purpose, i.e. determining age and estimating weights. We conclude that the method as used by Brown (1979), even with our refinements, does not yield reliable estimates of population growth parameters. If the asymptote of a logistic growth curve can be independently and accurately estimated, e.g. by weighing fledging birds, then two weights from each nestling in a sample may well suffice for an accurate estimate of the growth coefficient, k, in the population. Further studies are needed to ascertain the variability of coefficients obtained by such an approach. Finally, as a method for estimating the age of nestlings, it is probably unnecessarily sophisticated. Babblers do not gain much weight during their final week as nestlings. Hence, at this time, weights are less useful as indicators of age. Other criteria, such as feather development, must be used to age them. Likewise, other criteria are available for birds in their first two or three days (Gill & Dow 1983). Nestlings between Day 3 and 13 can be aged - to the nearest day - just as reliably with a linear as a logistic growth relation.

However field ornithologists should also consider that growth parameters, and hence the slope of a growth curve, may not be the same in each year. Both growth rate and asymptote for weight were probably higher in 1976 than in 1980, perhaps because of the excellent growing conditions at the time of Brown's study compared with the drought when we collected our data.

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