A METHOD FOR CONSTRUCTING NESTLING GROWTH CURVES FROM BRIEF VISITS TO SEABIRD COLONIES

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We present here a technique for constructing an average growth curve for a population by combining as few as two successive measurements of large numbers of chicks of unknown age. The technique provides an accurate relative chronological age scale for a population during the study period, and it may also be used to construct a tentative true chronological age scale for a population on the average. Although many applications are possible, this method should be especially useful for colonial oceanic species. Seabird growth has been studied in few localities, and even more rarely in the absence of established field research stations, due to the difficulties of arranging the time and logistical support necessary to measure chicks throughout their long development periods. Growth rates of colonially nesting seabirds are valuable data because the young appear to be sensitive to regional, seasonal, and annual variations in feeding conditions. Furthermore, growth rates of seabirds are often discussed in terms of the significance of clutch size and development rates of birds.

Our method consists of deriving a relative age criterion for the population from wing growth increments of individually marked birds of various but unknown ages. Weights of individuals can then be plotted against their relative ages estimated from wing length to obtain an average body weight growth curve for a group of young birds. We use wing growth to age young because wing length can be measured consistently and easily on live birds. Furthermore, the wing grows continuously from hatching to fledging in most species, and wing length is less sensitive than body weight to short-term nutritional deficiencies. During the earliest phase of development, when wing growth is low, tarsus and culmen growth may be helpful in estimating ages. Body weight is not useful in aging birds because it varies too much over short periods; flight and contour feathers are not useful because they do not appear until the young are partly grown.

The technique for constructing an age scale utilizes the lengths of the wing, tarsus, and culmen obtained for the same birds at the beginning and end of an interval of several days. The method depends on banding a sample of chicks on the first visit and finding the same chicks on the second visit. Calculations are facilitated and accuracy improved if the sample of banded chicks represents the full range of developmental stages. This can often be achieved by two well timed visits to a seabird colony. The visits should be made at the same time of day to eliminate errors caused by diurnal fluctuations in weight.

A scale of relative chronological age is constructed by the following steps. The initial wing length of each individual is plotted on the horizontal axis versus its final wing length on the vertical axis. Figure 1 shows a completed graph prepared by randomly

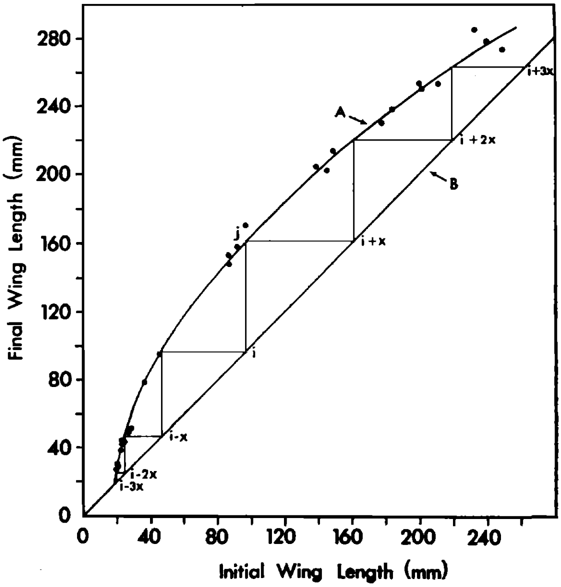

FIGURE 1. Relationship between initial and final wing lengths of Sooty Terns (curve A). To obtain these data, 25 intervals of 10 days were selected at random from measurements obtained by David L. Burckhalter throughout the period of growth on 12 chicks from 5 June to 20 August 1968 on Manana Island, Oahu, Hawaii. The diagonal line (B) represents equal, final and initial wing lengths, and the vertical distance between lines A and B, for example the line from i to j, represents the increment of growth over 10 days. Points i + x, i + 2x, etc., on line B represent wing lengths at successive intervals of x days obtained by the method described in the text.

selecting 25 ten-day growth increments for the wing lengths of 12 Sooty Tern (*Sterna fuscata*) chicks (Burckhalter, unpubl.). A smooth curve is fitted by eye to the points (curve A.). A diagonal line (B), representing equal initial and final wing lengths (hence zero growth), is added to the graph.

The wing length of a composite "individual" at successive intervals equal to the interval between visits is estimated in the following way: a point (i), representing some arbitrarily chosen wing length, is picked on the diagonal line (B). During the period between visits (x days), wing length increases by the vertical distance between the diagonal and curve A (the line from i to j). The wing length at point j is the initial wing length for the next time interval and is placed on the diagonal at point i + x by extending a horizontal line from point j to line B. Continuing in this way, wing lengths at successive intervals of x days (i + 2x, i + 3x, etc.) are estimated. Wing lengths may be extrapolated in the opposite direction (i.e., i − x, i − 2x, etc.) by drawing a horizontal line to curve A followed by a vertical line to B.

The wing lengths at points i, i + x, i + 2x, etc., on line B may be replotted on a graph of wing length as a function of time. Figure 2 shows the composite curve derived from the data in Figure 1

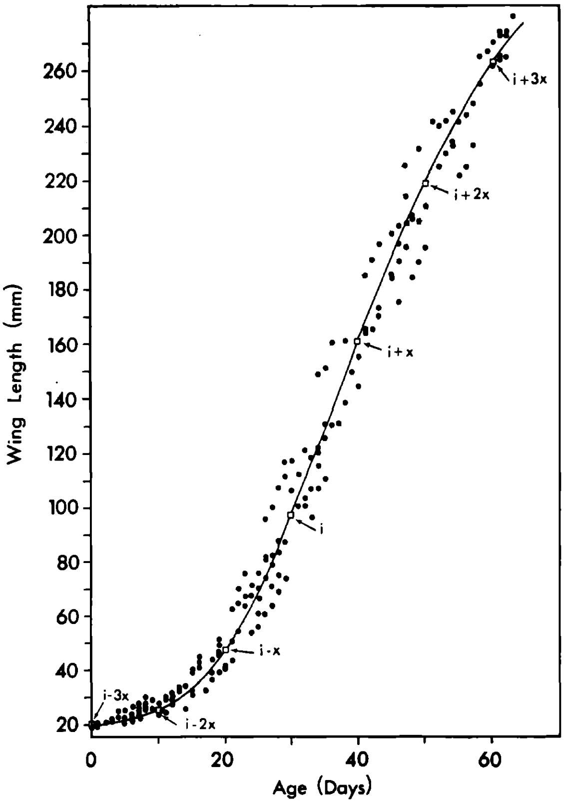

FIGURE 2. Wing lengths of 6 Sooty Tern chicks from hatching (age 0) through fledging. The growth curve was estimated from 25 random 10-day intervals in Fig. 1, and the time scale was adjusted to correspond to the true chronological growth data. Points i, i + x, i + 2x, etc., correspond to the same points in Fig. 1.

compared to wing growth data for 6 Sooty Tern chicks of known age. A weight-time curve may now be drawn using this composite curve to estimate the relative age of each chick.

In Figure 2, we superimpose the composite wing length curve to match the known wing length-age relationship. In the absence of complete growth data for individuals, hence where our technique is of use, true chronological age is difficult to establish. An absolute age scale is not needed for the calculation of growth rates (Ricklefs, *Ecology*, **48**: 978-983, 1967; *Ibis*, **110**: 419-451, 1968; *Ibis*, **115**: 177-201, 1973). But if a true chronology is needed, for example to establish the age at onset of behavioral traits, wing length at age 0 may be estimated from measurements of newly hatched (i.e., wet) young if such are present at the initial visit. This estimate must be made carefully because the wing grows slowly before primaries have erupted and wing length exhibits considerable variation among young. Small errors in estimating the wing length at hatching can displace the growth curve of the wing length several days. For the Sooty Tern data presented in Fig. 1 and 2, an initial wing length of 19 mm at age 0 results in a reasonably accurate aging criterion. An initial value of 20 mm at age 0 displaces the wing-length-age curve 4 days to the left. Such errors can by minimized by considering such appendages as the tarsus or culmen that grow rapidly during the early part of the nestling period. For example, 25 growth increments of culmen length of Sooty Terns at 10-day intervals are shown in Figure 3. If we assume that the average length of the culmen of newly hatched chicks (day 0) is 12 mm, lengths after successive intervals of 10 days are estimated to be 17.5 mm (10 days), 22 mm (20 days), 26.5 mm (30 days), 30 mm (40 days), and 33 mm (50 days). The growth rate of the culmen in the Sooty Tern decreases uniformly during the nestling period from about 0.5 mm/day to about 0.3 mm/day. Errors in estimating culmen length at age 0 will not alter the age scale as drastically as an error, of similar relative magnitude, in estimating wing length. An error of 0.5 mm in culmen length (about 3% of the total growth increment) would displace the culmen length-time curve about 1 to 1.5 days. As we have seen, an error of 1 mm in wing length (about 0.4% of the total growth increment) displaces the wing length-curve by 4 days. If we now plot wing length versus culmen length for a sample of birds (Fig. 4), we can find the wing length that corresponds to a particular age determined from increments in culmen length. This comparison is then used to adjust the age scale of the wing length growth curve. A culmen length of 22 mm corresponds to an age of 20 days (Fig. 3) and a wing length of 50 mm (Fig. 4).

The technique described in this paper may be used most readily when (1) hatching is spread over a period nearly as long as that of nestling development, (2) the initial visit is timed so a complete range of chick sizes is available, (3) the interval between visits is long enough to obtain significant growth increments but short enough to divide the growth period into at least 5, preferably 10, segments, and (4) sample size is as large as possible to reduce the influence of individual variation on the repeatability of the result. If these conditions cannot be met, the composite growth curve will be diminished in scope, or reliability, or both, but it nonetheless may be useful for comparative purposes, especially if the same species, or a close relative, has been studied elsewhere. Moreover, this technique can be applied not only to seabird colonies, but wherever a reasonable sample of young is to be found.

The composite growth curve constructed by the technique described in this paper differs from the growth curve of an individual throughout its development period in that the ecological conditions for which growth is described are representative of only a brief segment of the whole breeding season. These conditions may vary considerably from the average conditions of weather and food availability experienced by a young bird throughout its development. The composite growth curve is therefore a biological indi-

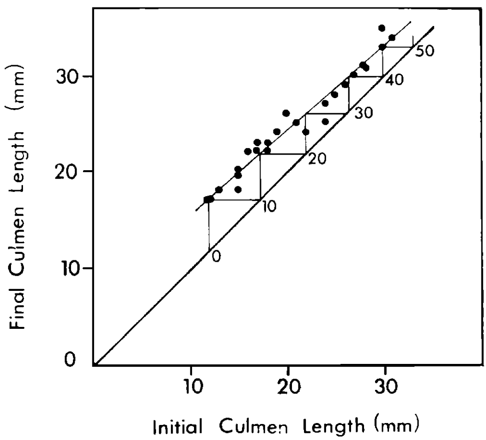

FIGURE 3. Initial and final culmen lengths for Sooty Terns, measured over 25 random 10-day intervals. Culmen length at hatching (day 0) is assumed to be 12 mm, and culmen length at successive intervals of 10 days is estimated by the method described in the text.

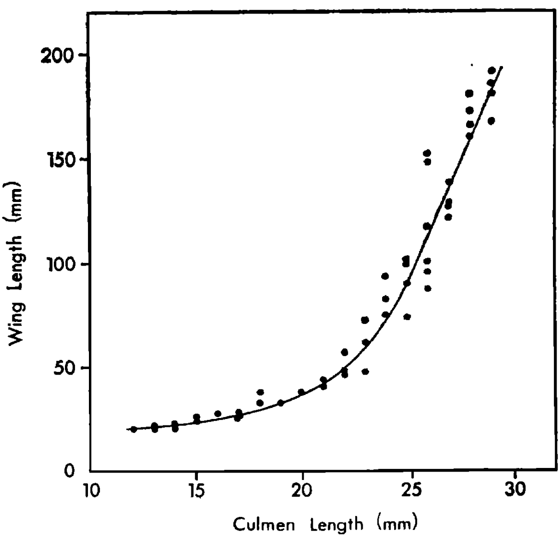

FIGURE 4. Relationship between wing length and culmen length in Sooty Tern chicks. The line was fitted by eye.

cator of the environment at a particular time. As such, it may be used as a simple assay for regional, seasonal, and annual variation in ecological conditions that influence the growth of young.

ACKNOWLEDGMENTS

We are grateful to David L. Burckhalter for providing a table of measurements of individual Sooty Terns, and to two anonymous reviewers for providing helpful criticism of the manuscript. This study was supported by National Science Foundation Grant GB 31554X.

Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19174. Received 12 August 1974, accepted 24 February 1975.