

Ricklefs R E. Patterns of growth in birds. *Ibis* 110:419-51, 1968.

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Sigmoid growth equations were fitted to the post-hatching curves of weight increase for 105 species of birds. Time required to achieve mature size increased with the 1/4-1/3 power of adult body weight. Among birds of similar size, additional variation in growth rate was related to ecological factors and the developmental state of the neonate. [The SCJ® indicates that this paper has been cited in over 130 publications since 1968.]

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"This paper, which was part of my doctoral dissertation, reported a comparative survey of rates of growth in birds, and attempted to explain variation among species as adaptations to their particular environments. During the mid-1960s, ecologists became interested in life-history patterns and, following up on the work of British ornithologist David Lack,¹ proposed evolutionary interpretations for variation among species in number of offspring reared, age at first reproduction, and intensity of parental care, among other traits. One of the most influential of this generation of 'evolutionary ecologists' was my adviser at the University of Pennsylvania, Robert H. MacArthur.

"My interest in growth rate came about directly from Lack's papers^{2,3} on the characteristic number of eggs laid by each species of bird. Reasoning that food is required in direct proportion to growth, Lack supposed that in species which fed their young, parents could rear more offspring having slow growth than rapid growth. Balancing such selection favoring slow growth were factors, such as nest predation, which selected in-

dividuals that passed through the vulnerable development stage quickly.

"My thesis was stimulated, in part, by the relationships between offspring number, mortality rate, and growth rate predicted by Lack's theory. Lack was unable to test these predictions because he did not have a suitable measure of growth rate: he relied primarily on time between hatching and leaving the nest, which we now know to be quite variable with respect to rate of weight gain. At the suggestion of MacArthur, I worked out a simple method for fitting sigmoid equations to growth curves.⁴ As I began to apply the technique to published data, my attention was drawn away from testing Lack's ideas and toward problems suggested by emerging patterns in growth and development.

"This paper is cited frequently, probably because it described a new set of life-history relationships. Curve-fitting allows one to distinguish mature size and time taken to achieve mature size, thus providing an unambiguous measure of growth rate amenable to comparative study and revealing a variety of correlations between life histories and environmental factors.

"In this paper, I suggested adaptive interpretations of variation in growth rate, but these could not be tested directly and many issues were left unsolved. I have continued to work on these problems, concentrating on determining how growth rate and other life-history traits are interrelated through both physiological constraints and the expression of growth-rate variation in the evolutionary fitness of the individual.⁵ An opposing viewpoint has been presented by T.J. Case.⁶ Growth-rate variation continues to provide a useful focus for interpreting aspects of life-history patterns because of the large role development plays in the allocation of time and energy during the reproductive cycle."

1. Lack D. *Ecological adaptations for breeding in birds*. London: Methuen, 1968. 409 p.

2. The significance of clutch-size. Parts 1 & 2. *Ibis* 89:302-52, 1947.

3. The significance of clutch-size. Part 3. *Ibis* 90:25-45, 1948.

4. Ricklefs R E. A graphical method of fitting equations to growth curves. *Ecology* 48:978-83, 1967.

5. Adaptation, constraint, and compromise in avian postnatal development. *Biol. Rev.* 54:269-90, 1979.

6. Case T J. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quart. Rev. Biol.* 53:243-82, 1978.