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Book review

Charnov, E. L. 1993; **Life History Invariants**. Oxford University Press, Oxford. xv + 167 pp., £13.50 (pbk). ISBN: 0-19-854072-8 (cloth). ISBN: 0-19-854071-X (paper).

There is an enormous literature that examines the allometric relationship $\log(y) = c + b \log(x)$, where a and b are constants. This literature tends to focus on the slope b. In his book, Life History Invariants, Charnov seeks those relationships in which b is ± 1 and then asks how the intercept c varies. Thus, the central interest in this book is the equation $y = cx$, rearranged as $c = y/x$, where x and y are some life history characteristics and c is a constant. Thus, for example, c could be sex ratio, the ratio annual clutch size/adult mortality rate or the ratio clutch size/age at maturity.

The book is divided into six major chapters: 1) the evolution of the sex ratio, 2) alternative life histories, 3) the evolution of life history characteristics in indeterminate growers, 4) the evolution of life history traits in determinate growers, 5) population dynamics and 6) senescence. No significant new results are presented, the book being an overview of papers previously authored by Charnov. However, it brings this body of work together within a particular framework. It is this framework that is the central motivation of the book. The most important question that arises when considering a particular way of viewing the world is "does the change in perspective give us new insights into the phenomena under study?". In some cases Charnov does demonstrate that his approach opens novel avenues of analysis, but in others I was not convinced that the approach produced new insights. This is most obvious in the case of the evolution of sex ratio and sex allocation (chapters 2–3). Charnov has made some extremely insightful advances in this area, and these two chapters summarize part of this work. But I cannot see how an emphasis on "symmetry" or "dimensionless numbers" in any way helps me understand more clearly these phenomena than the original approach that focussed on the phenomena themselves.

The approach is, however, very useful in the analysis of the evolution of life history traits in indeterminate (chapter 4) and determinate growers (chapter 5). Chapter 4 proceeds from the general growth function, $l_x = l_\infty(1 - e^{-kx})$, where l_x is length at age x, l_∞ the asymptotic length and k is a constant. It has long been known that in fish the ratios l_x/l_∞ and M/k, where M is mortality rate, are more or less constant for populations within a species and for species within a taxonomic family. Charnov reviews these data, noting both the general agreement in fish and the existence of data that do not conform. Additional data from aquatic invertebrates and reptiles also suggest a rough constancy in the aforementioned ratios. Following this review Charnov presents a theoretical justification for these observations. His argument is based on three assumptions: 1) that R_0 is a suitable fitness measure, 2) that the reproductive value at the age of maturity, $V(\alpha)$, is a power function of the length at maturity ($V(\alpha) \propto l_\infty{}^p$), where p is a constant, 3) there is a trade-off between l_∞ and k, this trade-off being described by the power function, $l_\infty \propto k^{-h}$, where h is a constant. From these assumptions Charnov shows how the ratios k/M and l_x/l_∞ are related to the power function exponents h and p. There is general agreement between the predictions and the observations, though some statistical gymnastics are required.

At the onset of chapter 5 Charnov reviews the literature demonstrating that, at least to a rough approximation, life history traits (primarily of mammals) scale to the $+0.25$ or -0.25 power of weight. He then gives an analysis that derives the relationship between mortality, M, and weight at maturity ($W[\alpha]$) from the assumption that 1) R_0 is maximized, 2) that the only cost to reproduction is the loss of growth and 3) that growth follows the rule $dW/dT = AW^{0.75}$. The derived equation, $M = 0.75AW(\alpha)^{-0.25}$ has, however, also been derived by Peterson and Wroblewski (1984) based upon alternate assumptions that make no reference to evolutionary theory. I note this, not to detract from the importance of Charnov's analysis, but to point out the care with which we must view analyses that are very broad in scope. By an algebraic manipulation of four allometric functions Charnov derives a table of the predicted signs of the correlations between life history traits when weight is kept constant. The predicted and observed signs agree, though we perhaps not be too surprised given the strength of the original relationships.

Chapter 6 discusses primarily various allometric relationships between body size and the rate of increase. It follows the same general approach as chapter 5, showing that the power relationship between r_{max} and body weight can be derived from a few simple underlying functions. In his final chapter Charnov opens with "I hope that I have convinced the reader of the utility of a *symmetry approach to life histories*" (p136). While I agree with the general approach of the book I am not convinced at the end that use of the term symmetry is particularly enlightening. However, this is perhaps a semantic quibble. Charnov takes a big brush to cover a broad canvas, and in so doing necessarily ignores many important details. That his approach is successful is testament to the power of the approach. The next challenge is to link those more accurate, particular life history approaches that concern themselves very intimately with mechanisms with this "grand" approach. While the many equations and algebraic manipulations make this book at times difficult, if not tedious, to read, it should be read by anyone interested in the evolution of life history variation.

Reference

Peterson, I. and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41: 1117–1120.

Derek Roff
Department of Biology
McGill University
1205 Dr Penfield Ave.
Montreal, Quebec
Canada, H3A 1B1