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This Week's Citation Classic®

Charlesworth B. *Evolution in age-structured populations*. Cambridge, England: Cambridge University Press, 1980. 300 p.
[School of Biological Sciences, University of Sussex, England]

Populations of many species are age-structured, and the study of their ecology and evolution presents many theoretical difficulties. This book reviews most aspects of the ecological dynamics, the theory of natural and artificial selection, and the genetic effects of finite population size, as they apply to age-structured populations. It applies the results to the general biological problem of the evolution of life-history phenomena such as senescence and age-specific patterns of reproduction. [The *SSCI*® and *SCI*® indicate that this book has been cited in over 285 publications.]

Age and Evolution

Brian Charlesworth
Department of Ecology and Evolution
University of Chicago
Chicago, IL 60637-1503

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The subject of my book is the application of concepts of demography to population genetics and evolutionary theory, allowing the development of models of evolutionary processes in populations where individuals are differentiated by age and in which matings can occur between individuals of widely different ages. Why should anyone care about this esoteric topic enough to cite, if not read, the book? The reason is that many kinds of living creatures, including man, have populations that are structured with respect to age. Evolutionary biologists have been intrigued by the question of how natural selection and other evolutionary forces mold the way in which fertility and survivorship change with age in such species. Why, for example, should senescence (the decline with advancing age in survival and fecundity) be an apparently universal property of multicellular organisms, apart from those that reproduce exclusively vegetatively? Why should there be such a diversity of patterns of reproduction and survival as functions of age among different species, ranging from the century plant that waits scores of years before flowering and then dies after a prodigious bout of reproduction to flies that develop over a few days and then reproduce continuously over a few more?

Answers to such questions can only be obtained if we have a properly worked out theory of the way in which evolutionary processes work in age-structured populations. The unit process of evolution is change in frequencies of alternative forms of the same gene within a local population,[1] and much of the book is devoted to describing the mathematical theory of such change. Research on this topic required the prior development of demographic models that allowed the description of the age composition and dynamics of age-structured populations without reference to genetics. This research was pioneered by Leonhard Euler in the eighteenth century, but its great development came in the early twentieth century, particularly in the hands of Lotka and Leslie. Population genetics was first introduced into demographic models (or vice versa) by J.B.S. Haldane[2] and H.T.J. Norton[3] in the 1920s.

After that time, the subject largely languished until the 1970s, when a number of workers, including myself, started to reexamine the questions originally explored by Haldane and Norton. In part, this work was motivated by dissatisfaction with the apparently elegant and simple solution to the problem of dealing with selection with age-structure, known as the Malthusian parameter method, and introduced by R.A. Fisher in his 1930 book.[4]

The firm quantitative basis for thinking about selection in age-structured populations provided by this work, reviewed in the first four chapters of my book, provides the starting point for theorizing about the ways in which natural selection can shape life history. This is the subject of the final chapter. One result of wide general significance is the fact that the intensity of natural selection is a function of the age at which genes affecting the trait are expressed. Other things being equal, genes with early acting effects are more strongly selected than genes with equivalent but late effects. The significance of this in relation to the evolution of aging was first perceived by P.B. Medawar,[5] whose formulation was qualitatively sound but quantitatively wrong. It is now clear that the phenomenon of decline in performance of most components of multicellular organisms with age is the evolutionary by-product of this decline with age in the efficacy of natural selection.

The theoretical literature on the evolution of life-history characteristics has grown considerably since 1979, the time at which my review of the literature was completed. In addition, there is now a large body of empirical evidence, both from comparisons of different species and from genetic and ecological studies of variation within species, against which the theory has been tested.[6] The general perspective presented in my book (which was a summary of the work of many biologists) seems to have survived this scrutiny well and helped (I hope) to stimulate this research.

1. **Crow J F & Kimura M.** *An introduction to population genetics theory*. New York: Harper & Row, 1970. 591 p. (Cited 1,065 times.)
2. **Haldane J B S.** A mathematical theory of natural and artificial selection. Part IV. *Proc. Camb. Philos. Soc.* 23:607-15, 1927. (Cited 20 times since 1945.)
3. **Norton H T J.** Natural selection and Mendelian variation. *Proc. London Math. Soc.* 28:1-45, 1928. (Cited 25 times since 1945.)
4. **Fisher R A.** *The genetical theory of natural selection*. Oxford, England: Oxford University Press, 1930. 291 p. (Cited 1,565 times since 1945.)
5. **Medawar P B.** *An unsolved problem of biology*. London: Lewis, 1952. p. 26. (Cited 90 times.)
6. **Partridge L & Harvey P H.** The ecological context of life history evolution. *Science* 241:1449-55, 1988.

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