A View of Population Genetics

Mathematical Population Genetics. WARREN J. EWENS. Springer-Verlag, New York, 1979. xii, 328 pp. $32. Biomathematics, vol. 9.

Population genetics is surely a strange field. It contains the most developed body of theory in biology, with an 80-year history of mathematical treatment. But experimental population genetics has remained poorly developed and in only fragmentary contact with the theory. Experimentalists have remained second-class citizens within the field. This situation has not been improved by the entrance into population genetics of applied mathematicians, bringing with them notation, terminology, and concerns distant from the experience of experimentalists.

Ten years ago, a sudden flood of electrophoretic data on protein polymorphisms promised to bring theoretician and experimentalist into fruitful contact at last. The neutralist-selectionist controversy focused attention on population genetics, and the resolution of the controversy was regularly promised and occasionally announced. After a decade of frustrated hopes, it seems likely that our observations have insufficient power to discriminate between many hypotheses, particularly ones involving weak selection or neutrality. It is a tribute to the immaturity of the theory that it has taken us so long to suspect this and that we still cannot prove it formally.

We need both more data and more theory. More data are coming, in the form of population samples of DNA sequences and samples from an increasing range of species. It is fairly clear that the theory is not up to the challenge.

At this uncomfortable juncture, Warren Ewens has produced an advanced-level treatise on theoretical population genetics. Ewens intends his book as a graduate-level account of the mathematical theory, with no pretense of covering the results of experimental population genetics, or even of treating theoretical topics that have been dealt with by highly approximate and nonrigorous arguments.

Those familiar with Ewens's 1969 book *Population Genetics*, to which this is a successor, will expect a simple, clear, graceful style and will not be disappointed. Ewens seems incapable of writing badly. Clarity is admirable in any other author, given its rarity in this field. In Ewens it is to be expected.

The opening chapter, "The golden age," gives a quick summary of the basic work of Wright, Haldane, and Fisher. Ewens's respectful treatment will be a useful antidote to the view held in some quarters that theoretical population genetics was invented in California about 1970 and that the preceding half-century of work was done by sloppy thinkers who could not get their mathematical notation right.

The titles of the chapters will convey the flavor of the rest of the book: "Technicalities and generalizations," "Discrete stochastic models," "Diffusion theory," "Applications of diffusion theory," "Two loci," "Many loci," "Molecular population genetics," "The neutral theory," and "Generalizations and conclusions."

The two topics covered most completely are the neutral mutation theory, with the diffusion methods used to analyze it, and the theory of natural selection in infinite populations with two loci. In the former, Ewens is much concerned with developing the machinery for formal statistical testing of the neutrality hypothesis. Ewens has himself been the major pioneer in bringing formal statistical testing to bear on the neutral hypothesis. His treatment is fully up to date, certainly the best available summary of this highly complicated area. We are nowhere near a satisfactory test of neutrality versus selection, particularly since the behavior of various test statistics is known under some variants of the neutrality hypothesis, but only under a few rather implausible kinds of balancing selection.

With respect to two-locus theory, Ewens places some emphasis on Fisher's "fundamental theorem" and its failure to be true in virtually all interesting cases. Ewens correctly emphasizes that even though the mean fitness of a population may either decline or increase as a result of natural selection, in model systems it seems to increase a great deal more often than it declines. If this were not true in nature, evolution would never have allowed population geneticists the opportunity to write papers implying that fitness usually decreases as a result of natural selection.

It is well to keep in mind that Ewens is not attempting a survey of theoretical population genetics but intends to concentrate on those areas that have been invaded most successfully by sophisticated mathematical theory. Even within these areas, the treatment tends to concentrate on matters in which he is interested, and though he has broad interests some bodies of successful theory are slighted. Noticeably absent is treatment of the rapidly expanding application of quantitative genetic models to ecological and evolutionary questions, in particular the work of Lande, Slatkin, Bulmer, and Roughgarden.

To his credit, Ewens does make an effort to point out some areas of future expansion of mathematical theory in population genetics. He is ahead of most of his colleagues in appreciating the importance of work on methods of estimating evolutionary trees and testing hypotheses using them. As DNA sequence data become available over a range of related species, these kinds of macroevolutionary applications of population genetics will grow in importance. Other macroevolutionary concerns such as models of speciation are the focus of much current work, but Ewens provides little coverage of them, either from lack of interest or because their theory is so complex that it does not lend itself to exact mathematical methods.

This is an idiosyncratic work, but a very good one. It comes at a time when theory and data are too immature to attempt a post-neo-Darwinian synthesis, so that we can benefit from idiosyncrasy, particularly when it is elegantly, concisely, and knowledgeably presented.

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A Medical System Examined

Health, Medicine and Mortality in the Sixteenth Century. CHARLES WEBSTER, Ed. Cambridge University Press, New York, 1979. xiv, 394 pp., illus. $39.95.

This collection of interdisciplinary essays on Tudor times is dedicated to the memory of Sanford V. Larkey (1898–1969), a Johns Hopkins researcher who pioneered the historical analysis of medical systems. A medical system includes a natural environment, diseases and crop failures, the economy, institutions, competing medical theories, various types of medical practitioners, and, of course, the patients who provide the prerequisite for the existence of medicine. The essays