Book Reviews

Evolutionary Genetics: Wright's Treatise Continued

Evolution and the Genetics of Populations. Vol. 3, Experimental Results and Evolutionary Deductions. SEWALL WRIGHT. University of Chicago Press, Chicago, 1977. viii, 614 pp., illus. $35.

"It is with books as with men: a very small number play a great part, the rest are lost in the multitude." Voltaire's dictum applies to Sewall Wright; within the field of population genetics he is one of the very small number who have played a very great part. The mathematical theory of population genetics, which accounts for evolutionary processes in genetic terms, arose in mature form around 1930, primarily through the efforts of three men: R. A. Fisher, J. B. S. Haldane, and Wright. The special characteristic of Wright's contribution was, besides the use of some novel mathematical methods, the importance attached in evolution to variations in gene frequencies due to sampling accidents through the generations—a process known as "random genetic drift," "sampling drift," or simply "drift." The role of sampling drift in evolution was much debated, particularly by R. A. Fisher, E. B. Ford, and other British population geneticists, but is now duly acknowledged in textbooks and research papers. Sampling drift is also the fundamental process underlying the "neutrality theory of molecular evolution," developed by Motoo Kimura and others, which is probably the single most stimulating development in the field of theoretical population genetics in the last decade.

Evolution and the Genetics of Populations is Sewall Wright's comprehensive view of population genetics. Volume 1 of this work, which appeared in 1968, is devoted to the genetic and biometric foundations of population genetics. Volume 2, published in 1969 with the subtitle "The Theory of Gene Frequencies," contains the core of Wright's theory of population genetics. The "experimental evidence" was to be examined in a third volume, but has now been distributed into two volumes, the present one and a fourth one, scheduled for publication in the spring of 1978, dealing with variability within and among natural populations.

The early chapters of the present volume are largely a review of inbreeding experiments. Particular attention is given to experiments with guinea pigs started in 1906 by G. M. Rommel and after 1915 continued by Wright himself for many years. Other experiments with animals as well as plants are also extensively reviewed. The characters studied in inbreeding experiments are very diverse, ranging from morphological traits, through fitness components such as viability and fecundity, to variations in temperament, intelligence, and resistance to disease. The results in general agree with the expectations from theory. There is a tendency toward random fixation of one or another allele at each variable locus, with the consequence of considerable differentiation of all characters among inbred lines.

In the case of relatively neutral traits the available evidence indicates that the actual progress toward fixation occurs at the rate expected, so that any given degree of homozygosity can be achieved by different systems of inbreeding, but the number of generations required is inversely related to the theoretical amount of inbreeding accomplished per generation. Thus, for example, the number of generations required to accomplish a given degree of fixation is 3.27 times greater under sib mating than under self-fertilization.

The evidence concerning heterosis, or hybrid vigor, is carefully evaluated. Wright's tentative conclusion is that heterosis is for the most part due not to single-locus overdominance but to the covering up of different sets of deleterious genes that have become fixed in different inbred lines. The extreme heterosis observed in crosses between inbred lines of maize is interpreted as overwhelming evidence in favor of such an interpretation. However, selection in favor of heterozygotes would tend to delay or prevent fixation and, as Wright points out, experiments with rats have shown that fixation may be delayed at least fourfold under sib mating owing to strong selection for vigor.

Two chapters (7 and 8) are devoted to artificial selection. The most important conclusion is "the practically invariable success of directional selection in bringing about drastic changes even from the narrowest foundation stocks." Artificial selection has been successful in the most diverse organisms—mammals, birds, insects, hydra, protozoans, and so on—and for very diversified traits. The unavoidable inference is the pervasiveness of genetic variation for all sorts of phenotypic characters in all sorts of organisms. Wright points out the difficulty of predicting the course of selection, which is due to wide heterogeneity in degrees of dominance, pleiotropy, linkage relations, and initial allelic frequencies.

Studies of natural selection in the laboratory (chapter 9) have provided considerable insight into the process. But the course of selection is not generally quantitatively predictable even when side experiments are used to determine the genetic parameters with respect to viability and fecundity. The conditions of the selection experiment are usually not reproducible in the side experiments.

The general conclusion derived from the experimental studies of mutation, sampling drift, inbreeding, and selection is that phenotypic evolution results from natural selection of variability provided ultimately by mutation of Mendelian genes. Wright dedicates two chapters (12 and 13) to "theories of evolution." He clarifies and defends his own "shifting balance theory" of evolution, in which selection relates to the adaptiveness of genetic systems as wholes. This reduces the limits on rates of evolution imposed by the "cost" of evolution. In particular, with respect to the evolution of a large species consisting of subdivided populations, Wright defends his claim advanced in 1929 that "there is a continually shifting differentiation among the local races, even under static conditions, which through intergroup selection brings about indefinitely continuing, irreversible, adaptive, and much more rapid evolution of the species as a whole." Changing environmental conditions further contribute to the acceleration of evolutionary processes through "a usually slight and reversible shift of gene frequencies to new equilibrium points." There is a "cost" that limits the rate of establishment of superior adaptive peaks in a local successful population, but

there is little cost in the diffusion process that establishes superior systems throughout the species.

This volume is a masterly review of experimental population genetics. Like the two previous volumes of *Evolution and the Genetics of Populations*, the present one will become an indispensable reference for investigators, teachers, and graduate students in population genetics. One noteworthy feature is that concepts and lines of research are traced back to the first relevant contributions, many of which have been completely forgotten in current literature. For example, I presume that most population geneticists are unaware that H. J. Muller's 1950 thesis that every mutation contributes substantially the same amount of damage to a population in the long run, independently of the severity of its effects on individuals, had been proposed by C. Danforth 27 years earlier; or that the theory that accounts for the prevailing recessiveness of mutations by postulating evolution toward dominance at loci with initially intermediate heterozygotes, usually credited to a paper published by R. A. Fisher in 1928, was first advanced in 1919 by E. M. East and D. F. Jones.

In a few places, Wright brings in recent work in molecular biology that is relevant to population genetics. One instance is the experiment of Mills, Peterson, and Spiegelman showing selection in favor of smaller molecules in self-replicating RNA from the bacteriophage $Q\beta$. Of wider implication is the calculation of the maximum number of genes in a variety of organisms, based on measurements of the amount of DNA per nucleus. Wright observes that the numbers of genes obtained in such calculations are much too high. In his calculations, Wright takes into account that a fraction of the DNA consists of highly repetitive sequences, but he ignores recent evidence indicating that only about 10 percent of the DNA transcribed leaves the nucleus and becomes associated with polyribosomes and translated into polypeptide chains. When this additional consideration is taken into account (as well as the fact that the number of nucleotides per structural gene may be greater than the 1000 assumed by Wright), the numbers of structural genes calculated on the basis of the amount of DNA per nucleus are, for many organisms, not very different from estimates based on other evidence.

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Dealing with Retardation

The Mentally Retarded and Society. A Social Science Perspective. Proceedings of a conference, Niles, Mich., April 1974. MICHAEL J. BEGAB and STEPHEN A. RICHARDSON, Eds. University Park Press, Baltimore, 1975. xx, 492 pp. $17.50. NICHD Mental Retardation Research Center Series.

Writings having to do with mental retardation can be traced back to antiquity. But scientific concern with the subject is probably best dated from the publication of Itard's *The Wild Boy of Aveyron* in 1798. With the exception of the great debate concerning the nature-nurture issue, the early attempts to deal with mental retardation were almost completely atheoretical. Discussion revolved around the problems of defining and measuring intelligence, the problem of differential diagnosis, and individual case histories and family pedigrees such as those of the Jukes and the Kallikaks. Some of these efforts today strike us as quaint, but attempts to understand and ameliorate the effects of mental retardation led to developments of considerable importance. Particularly noteworthy in the history of the subject are the commitment to mental orthopedics of Binet, the moral training efforts of Seguin, and the rise of the asylum movement. As researchers began to discover the etiology of certain organic forms of mental retardation, we learned how very heterogeneous a phenomenon mental retardation is. Simple classification seemed out of reach, and the area became a disputatious one. Many workers took refuge in the view that mental retardation was too complex a phenomenon to permit the sort of basic theorizing that could lead to more promising research. If the experts were befuddled through this period, laymen, often challenged by unavoidable interchanges with retarded individuals, were totally at sea.

In 1958, in a book entitled *Mental Subnormality*, three distinguished scientists, R. L. Masland, S. B. Sarason, and T. Gladwin, reviewed what was then known about mental retardation. While some impressive efforts on the biological front could be documented, the psychological and anthropological work was considered to be thin in quantity and poor in quality. In general, the field appeared mysterious and unpromising.

The two decades since the effort by Masland *et al.* have witnessed a vast improvement in mental retardation research. This success story has involved certain institutional forces, certain individuals, and finally a Congress that had the wisdom to realize that our ability to help any group of individuals can never outdistance the verified knowledge we have about them. The concern of President Kennedy with mental retardation should certainly be noted, as well as the commitment to utilize research to improve the lives of retarded persons made by the National Association for Retarded Citizens and the Kennedy Foundation. In 1962 Congress took the pivotal step of legislating the existence of the National Institute of Child Health and Human Development (NICHD), which has spearheaded research efforts in this area.

And now, in *The Mentally Retarded and Society*, we have a new milestone book. The book deals with most of the important issues in the field's past and present and appears to anticipate many important questions of the near future. These issues are not presented in any unitary manner but run as themes from chapter to chapter and from section to section. Although the reader will have to work hard to extract the many important messages contained in the book, the effort will be worthwhile for almost everyone interested in mental retardation, including research workers, clinicians, social workers, educators, administrators of programs for the retarded, and those at every level of government involved in the construction of social policy concerning the retarded. Mental retardation costs our society approximately $5 billion annually and it is imperative that a book speak to all of these audiences simultaneously. The book under review makes a vital contribution by demonstrating how the efforts of scientific research workers can guide and assist those who must deal with the social problem of mental retardation.

The editors have not limited the book to contributions by those whose central concern is with mental retardation. We find very fine chapters on general problems of communication, attitude change, compensatory education, and the treatment of juvenile delinquency. In the reviewer's opinion this decision on the part of the editors was astute, for a major problem in work on mental retardation has been its parochial nature, with investigators too often speaking only to each other. What the field needs rather than "retardationologists" or "defectologists" is biologists, psychologists, sociologists, and anthropologists, whose efforts can enrich our understanding of mental retardation.

As the title indicates, the book is limited to social science issues and does not include the biological perspective. It is