Book Reviews

The New Population Biology

Population Biology and Evolution. Proceedings of an international symposium, Syracuse, N.Y., 1967. RICHARD C. LEWONTIN, Ed. Syracuse University Press, Syracuse, 1968. x + 206 pp., illus. $8.

A science can be said to enter maturity when its theories become predictive. Slowly, in little steps, evolutionary biology seems to be approaching that vital moment. For the past 20 years it has stumbled along far behind molecular biology—not because populations are more complex than ribosomes and nuclei, not even because biochemists are churlish toward taxonomists, but rather because, as R. C. Lewontin points out in the introduction to this little volume of essays, evolutionary biologists have been too slow to take up the Cartesian method of simplification, analysis, and resynthesis. Molecular biologists have been able and bold enough to be Cartesian; evolutionary biologists have not. That is an oversimplification, of course, but it contains a generally unrecognized truth.

In the 1920's neo-Darwinism was born as a synthesis of Darwinian natural-selection theory and the new population genetics. Simultaneously Lotka, Volterra, and others were creating the foundations of mathematical population ecology. By 1930, when the publication of Fisher's *The Genetical Theory of Natural Selection* closed this pioneering decade, a respectable number of new ideas had been generated that formed an extensive, albeit untested, framework on which a mature science might have been built. But evolutionary biology did not and could not proceed in this straightforward manner. For reasons that are clearly exemplified in *Population Biology and Evolution,* and which I will attempt to summarize in this review, it was necessary for the science to pass through a period of about 30 years of consolidation of information, innovation in empirical research, and slow forward progress. This period is sometimes referred to as the Modern Synthesis and its achievements rather loftily as "the modern synthetic theory of evolution." Actually, very little theory in the strict sense was created between 1930 and 1960 beyond that already laid down in the 1920's. What really happened was that most of the several branches of evolutionary biology—systematics, comparative morphology and physiology, paleontology, cytogenetics, and animal behavior studies, to be exact—were reformulated in the *language* of early population genetics. The greatest accomplishment of this period was the elucidation, through excellent empirical research, of the nature of genetic variation within species and of the means by which species multiply. Other topics were clarified and extended, but some of the apparent new understanding of the Modern Synthesis was false illumination created by the too-facile use of a bastardized genetic lexicon: "fitness," "genetic drift," "gene migration," "mutation pressure," and the like. So many problems seemed to be explained by invoking these concepts, and so few really were. Stagnation inevitably followed. Reliance was placed increasingly on a few authoritative treatises in each of the respective fields that contained, in appropriately transmuted form, the magical genetic language. It thus happened that almost a whole generation of young evolutionists cut themselves off from the central theory. Having never grasped the true relation between theory and empiricism in the first place, they were willing to submit to authority rather than to advance the science by altering the central theory.

The new phase of evolutionary biology, in which an attempt is being made to produce theory that can predict particular biological events in ecological and evolutionary time, has taken upon itself such a great task, requiring such profound changes in attitude and working methods, that it can rightfully be termed post-Darwinism. Although not all of the 14 authors of *Population Biology and Evolution* are explicitly post-Darwinist in their philosophy, most are (Waddington even refers to his own contribution as "post-Neo-Darwinist"). Collectively their essays express better than any other recent publication the problems and the hopes of the new approach. The book consists of the proceedings of a symposium whose purpose was to bring together representatives of population genetics, ecology, and developmental biology, three fields that have hitherto been largely independent of each other. The contributors were well chosen from around the world, and in general the meeting was a success.

In an early chapter J. F. Crow shows how the most sophisticated methods of Mendelian genetics have led to measurements of the genetic load, the relative frequencies of genes in the several classes of varying deleterious effect, and the rate and effects on population fitness of new mutations. But, as Alan Robertson suggests, this information comprises only a small part of what is needed for a mature science of population genetics. The direct count of segregating loci in populations has only begun, having first been made possible through the separation of isozymes by starch-gel electrophoresis in 1966. Still largely unexamined are the basic questions of the number of loci involved in continuous variation, the modes of action of polygenes, and the degree of linkage among them.

Developmental biology, as its own practitioners admit, is even less up to the demands of population biology. Robertson and G. L. Stebbins perceptively sketch out the great unknowns in this field: the complexity of gene action, the lengthy and poorly understood epigenetic molecular sequences, the uncertain mapping of "phenotypes" onto cistrons, the relation of genotypes to fitness, and so on. Information of interest to evolutionists is being produced by Stebbins' studies of the pleiotropic modifications of flower parts in connection with selection for single characters, and his ideas on the role played by modified mitotic rates in early organogenesis offer an entree at the physiological level. The elegant use of probit analysis by J. M. Rendel to measure canalization has come the closest to actually linking population biology with molecular interpretations of development. Rendel persuasively accounts for the results of his experiments on selection of scutellar bristle number in terms of variable quantities of repressor substances and replicative activity by major genes.

The ecologists have had the greatest problem finding a common ground with other biologists. Their difficulty is due to the long period of isolation in which modern ecology has developed. Also, the

annectent field of ecological genetics is still in a primitive stage, largely, I suspect, because of the chance circumstance that *Drosophila* studies have dominated population genetics for so long. *Drosophila*, being sparsely distributed and elusive in the field, is one of the worst animals with which to study ecology. But the ecologists have begun to produce predictive theories on their own that are of great interest to the rest of evolutionary biology. R. H. MacArthur, after dismissing critics of his highly abstract method of theorizing with an impatient wave of his hand ("Think how physics would be without its frictionless pulleys, conservative fields, ideal gases, and the like"), reviews some of his well-known ideas on competition and species diversity. Time and again he produces intriguing predictions, some of them susceptible to testing by direct measurements, which contribute new insights concerning the foraging behavior of animals, properties of the niche, and competition among species. J. L. Harper, who has the distinction of being the first botanist to speak to animal ecologists in their own language, reviews progress in experimental plant ecology. The puzzling phenomena he describes in competition and synergism among plants, together with the lack of any visible laws relating competitive ability to biomass, growth rate, and seed production, make a unifying theory in botany impossible at this time. And there are too many differences between higher plants and animals to permit botany to borrow freely from zoology. Nevertheless, Harper and his co-workers have now demonstrated that plants are very superior material for such studies, and future progress should be rapid.

C. H. Waddington stresses the shortcomings of classical selection theory and outlines a method for the study of selection of simple allelic systems in heterogeneous environments. The same subject is taken up by Richard Levins, who uses his powerful fitness-set method to predict the consequences for genetic variation of varying such parameters as developmental flexibility, degree of inbreeding, and amount of environmental heterogeneity. Levins' exposition is as hurried, brilliant, and hypercondensed as in earlier papers; one gets the feeling he is receiving secrets of the universe from a space visitor anxious to be on his way. Th. Dobzhansky provides a thoughtful essay on the intuitive meaning and the methods of measuring adaptedness, Darwinian or reproductive fitness, and persistence (fitness in the Thoday sense), three of the general properties of populations. Bruce Wallace, in his meticulous manner, develops an original method of graphical analysis in which the complex interactions of population size, density-dependent mortality, and frequency-dependent fitness are visualized. The method promises to predict not only the equilibrial frequencies in a two-allele case but also the equilibrial population size.

Speciation theory is still the least analytic branch of evolutionary biology. In the book the multiple consequences of episodes of rapid population growth on species-level evolution are considered in detail by H. L. Carson, but still largely in terms of verbal imagery. Speciation is also pondered from a novel viewpoint by G. E. Hutchinson, who suggests that the phenotypic limits of "good species," in other words, species that taxonomists find easy to distinguish, are set by discontinuities in the environment, regardless of whether the organisms are bisexual metazoans or such parthenogenetic groups as the bdelloid rotifers. The means are discussed, in a still tenuous fashion, by which taxonomic characters and niche dimensions might be mapped onto one another. Finally, in the closing chapter, L. B. Slobodkin remains, as in his earlier writings, sternly cautionary about the prospects of a predictive evolutionary theory. He allows that one is possible in principle, provided a way is found to relate homeostatic ability, which Slobodkin regards as the single most important quality of organisms and populations, to the persistence times of species.

It is clear from these contributions that the grip of the neo-Darwinist savants on evolutionary biology is at last loosening, and that the subject is being turned into a creative, chancy, young man's game. There is a refreshing quality in Lewontin's frank protest:

> It is unhappily true that there are population biologists who reject the analytic method and insist that the problems of ecology and evolution are so complex that they cannot be treated except by holistic statements. The influence of these people has held up progress in population biology for many years and, in addition, has tended to degrade population biology as a science. They are the stamp collectors of biology who, because they themselves are unable to analyze the complex problems of ecology and evolution, try to convince the rest of us that nothing but "objective description" of nature is possible.

Even so, I hope that the revolt will proceed at the right pace and not get out of hand. The analytic cutting edge is not all of evolutionary biology. I fear (and think I even see in some departments of biology in this country) the beginnings of an unholy alliance between the population model builders and molecular biologists to exclude systematists and descriptive ecologists. In their understandable desire to press on down the mainstream of biology together, let them not forget that evolutionary biology cannot exist without the substantive knowledge being carefully built by descriptive biologists. More than anywhere else in science, their expertise takes long periods of time and concentration to acquire, and once lost it is not easily retrieved. If they go, post-Darwinism will eventually become as sterile as neo-Darwinism did in its most antitheoretic moments.

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The Evolution of Reproductive Rates

Ecological Adaptations for Breeding in Birds. DAVID LACK. Methuen, London, 1968 (U.S. distributor, Barnes and Noble, New York). xii + 409 pp., illus. $15.

As there have been few breakthroughs in population ecology only a few ecologists stand above the others in eminence. David Lack is one of these few; his approach and ideas collected in *The Natural Regulation of Animal Numbers* (Oxford University Press, 1954; reprinted 1967) have been, and for many continue to be, an immensely profitable source of inspiration and frame of reference. Since the publication of this first major work, two more large volumes, *Population Studies of Birds* in 1966 and that under review, have appeared. These deal, respectively, with the two most general and important aspects discussed in the earlier book, population regulation and the evolution of reproductive rates. Both books, as a primary concern, attempt to uphold earlier hypotheses with the help of and in some instances in spite of more recent evidence.

All students of the subject will doubtless find *Ecological Adaptations for Breeding in Birds* useful. Its two stated aims, to provide a handbook of data on breeding birds and to interpret and interrelate these data, are sufficiently