The Evolution of Population Biology

This is the third of three volumes published by Cambridge University Press in honor of Richard Lewontin. The first volume, Evolutionary Genetics from Molecules to Morphology, honors Lewontin’s more technical contributions to population and evolutionary genetics, and the second volume, Thinking about Evolution: Historical, Philosophical, and Political Perspectives, honors Lewontin’s contributions to the history and philosophy of biology and to the controversial field of sociobiology. This volume honors his contributions to population biology: the nexus between population genetics and ecology.

This unique collection of essays deals with the foundation and historical development of population biology, and its relationship to population genetics and population ecology on one hand and to the rapidly growing fields of molecular quantitative genetics, genomics, and bioinformatics on the other. Such an interdisciplinary treatment of population biology has never been attempted before. The volume is set in a historical context, but it has an up-to-date coverage of material in various related fields. The areas covered are the foundation of population biology, life history evolution and demography, density- and frequency-dependent selection, recent advances in quantitative genetics and bioinformatics, evolutionary case history of model organisms focusing on polymorphisms and selection, mating system evolution and evolution in the hybrid zones, and applied population biology including conservation, infectious diseases, and human diversity.

The volume brings out the central role of population biology in all aspects of its connection to population genetics and population ecology and it is a must for all graduate students and researchers in population genetics and ecology.

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The Evolution of Population Biology

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Preface

Scientists earn their reputation by making special contributions in a variety of ways. Some become known for a discovery that revolutionizes their science. Others are respected as intellectual leaders for significant contributions leading to sustained progress in their field. Still others become known for providing guidance, opportunity, and uniquely inspiring rapport with a large number of graduate students, writers, and research colleagues. A rare few do all the above, and remarkably enough still find time to deal with the broader issues of epistemology, philosophy, history, and sociology of science. Richard Lewontin is one of these rare scientists.

If we are to attach a major discovery or a conceptual breakthrough to Lewontin’s name (like Haldane’s cost of natural selection, Fisher’s fundamental theorem of natural selection, Wright’s shifting-balance theory, or Maynard Smith’s game theory applications), then the successful completion of the genetic variation research program of the Chetverikov–Dobzhansky school will be known as the outstanding highlight of Lewontin’s career. Dobzhansky and his students and collaborators pursued the twin problems of the amount and the adaptive role of genetic variation for nearly 25 years without a satisfactory solution. All estimates of genetic variation were indirect or inadequate as there was no reductionist research program that could allow the study of genetic variation at the level of the gene. Lewontin’s pioneering success in the application of protein electrophoresis to the problem of genetic variation changed the scene radically. The estimation of electrophoretic variation was direct and more useful than anyone had expected. The technique also removed the experimental limitations imposed by genetic incompatibility among species and allowed reliable comparisons of genetic variation among populations and species without any need to make genetic crosses. The impact and the anticipation of the avalanche of future results from the use of electrophoresis were discussed in his well-known book, The Genetic Basis of Evolutionary Change (1974). This book sets out the problem of population genetics in a rationally constructed historical context and is required reading for all aspiring population geneticists.
Evolutionary research requires broad interest and versatility in modeling experimental design, statistics, field biology, and much more. Such breadth allowed Lewontin to be successful, time and again, in designing new experimental systems or suggesting key concepts to answer old questions or pursue new ones. Lewontin became interested in the uniqueness of the phenotype—and the genotype–environment interactions inspired mainly by the Russian biologist I. Schmalhausen’s book *Factors of Evolution*. His doctoral thesis studied fitness as a function of genotype frequency and density and showed that “viability of a genotype is a function of the other genotypes which coexist with it, the result of any particular combination not being predictable on the basis of the viabilities of the coexisting genotypes when tested in isolation.” This was followed by studies of interlocus epistatic interactions in fitnesses and the evolution of naturally occurring inversion polymorphism in *Drosophila*. His mathematical work on linkage disequilibrium provided a new direction for research and results from a series of papers on multilocus fitness effects anticipated discussion on the units of selection. His experimental work on norms of reaction in *Drosophila* was exemplary in exposing the problem of the genetic determination and led to a new appreciation of genotype–environment interaction and phenotypic plasticity. He pointed out the importance of developmental time in fitness, something which is usually forgotten when describing fitness components. His 1972 paper on “Apportionment of human diversity,” pointing out that any genetic difference between races has to be compared with genetic variation within population and races, is a landmark in human genetics and evolution. More recently his laboratory has been a major center for studies of DNA sequence variation. Lewontin has provided training and guidance to a large number of graduate students and postdoctoral fellows. The number is well over one hundred! Many more have worked in Lewontin’s laboratory but have not necessarily coauthored publications with him.

But what makes Lewontin known more in the wider circle of evolutionary biology and in science in general is his role as a critic of how science is done, on the one hand, and his passionate engagements with the issues of science and society, on the other. He has made important contributions and has influenced research workers in the history and philosophy of science and in areas of science and society such as agriculture, social health problems, bioethics, and genetics, and IQ. If you drop Lewontin’s name in any group of biologists, an animated discussion is sure to follow! These discussions are not about science but about its relevance and applications to human affairs. His concern about social issues springs directly from his unique perspective of evolutionary biology. Lewontin’s research program may be reductionist but he is not. He has encouraged and challenged evolutionary biologists to find the most desirable combination of Platonic and Aristotelian traditions in studying nature. Accordingly the mathematical rigor of early population biology must be extended to accommodate interactive, hierarchical, probabilistic,
and historical factors as learned empirically in the field. To him “Context and interaction are of the essence” (Lewontin 1974, p. 318), whether one is talking about interactions between hierarchical levels, between organisms and the environment, or between causes and effects. A reductionist approach to science does not necessitate a reductionist view of the world. No level of analysis is specially privileged for a general understanding of causality. Genetic and environmental effects are interdependent and the phenotypic variance cannot be partitioned into fixed components. Organisms do not fit in preexisting ecological niches but create their own niches. History and contingencies are so important in evolution that looking for adaptive explanations for all organismic traits undermines the role of natural history. These ideas essentially follow from his belief that relationships between organisms and their environments, and likewise, those between groups and hierarchical levels, are governed by forces so weak that the outcomes are neither fixed nor predetermined.

John Maynard Smith has written (first volume of this series, pages 628–640) that “Richard Lewontin has contributed to science not only by his own work on evolutionary theory and molecular variation and by his influence on the many young scientists who have worked with him but also by asking us to think about the relationships between the science we do and the world we do it in.” While you may not agree with Lewontin on all issues (he would be surprised if you did!) one thing is sure – Lewontin has been a colorful personality who has made evolutionary biology rigorous and interesting at the same time. We affectionately dedicate this volume to him.

We sincerely thank Subodh Jain for his encouragement and valuable contribution in the early planning of this volume. At Cambridge University Press, we express our sincere thanks to Ellen Carlin for her enthusiastic support and early work on this project and to Maria Murphy for her supervision in the completion of this project. Thanks are also due to Aaron Thomson, McMaster University, who did the maddening job of checking up references and preparing the manuscripts for final submission.