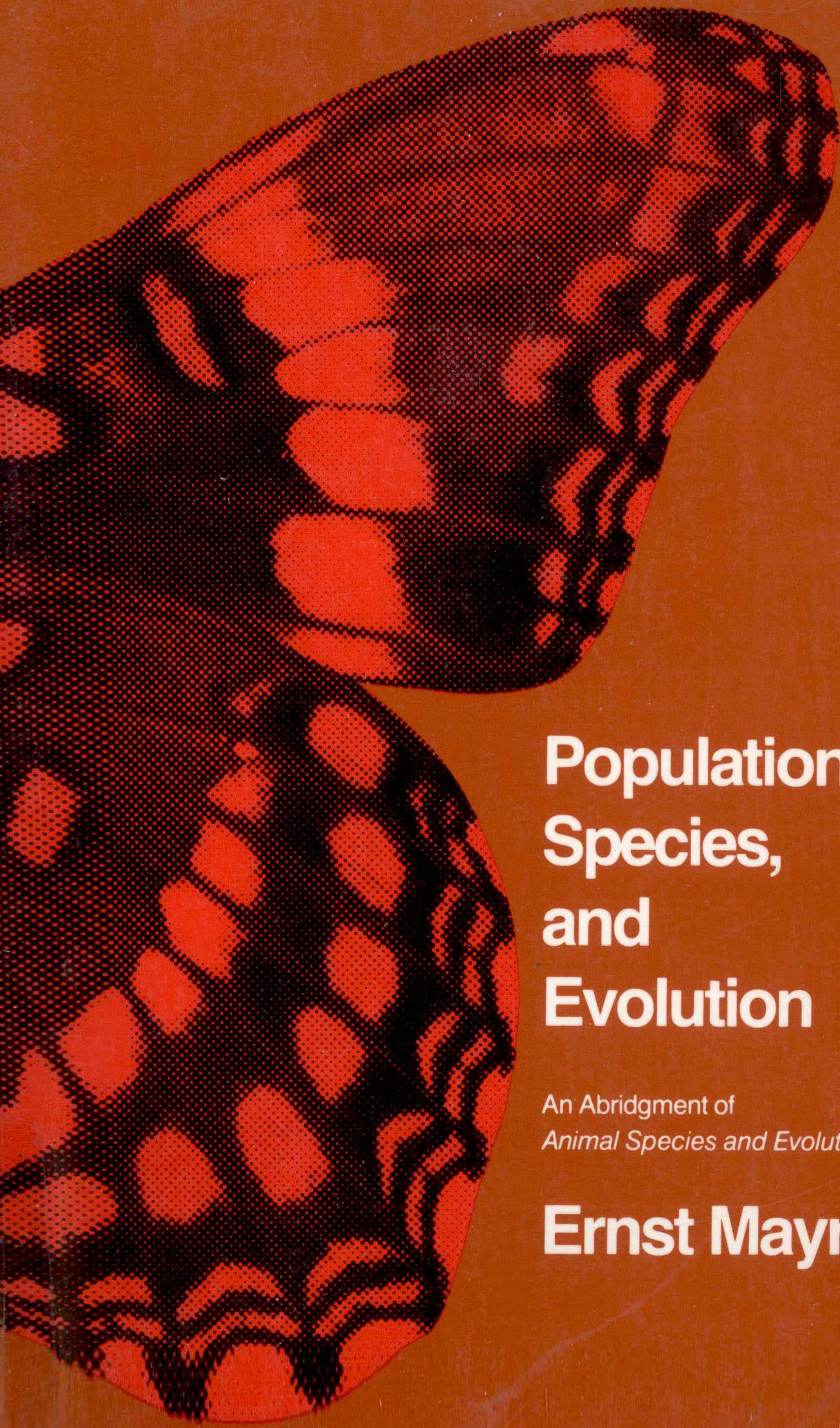

Populations, Species, and Evolution

An Abridgment of
Animal Species and Evolution

Ernst Mayr

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To my friend Theodosius Dobzhansky,
foremost architect of the
evolutionary genetics of today

Preface

In the Preface of *Animal Species and Evolution* (1963), I wrote that it was "an attempt to summarize and review critically what we know about the biology and genetics of animal species and their role in evolution." The result was a volume of XIV + 797 pages. Ever since its publication, I have been urged to provide an abridged edition that would be more handy for class use and for the reader who does not want the detailed documentation of the large volume. To satisfy this demand is the object of *Populations, Species, and Evolution.* The essential discussions of the original volume have been retained, but the massive citations of the literature and discussions of many peripheral subjects have been eliminated. The specialist as well as the teacher will still need the fully documented treatment in *Animal Species,* but the general reader will find the new volume easier to use.

At first, there was no intention to combine a revision of *Animal Species* with the preparation of this abridgment. Yet, during the work on many of the chapters a rather extensive revision became inevitable, and certain chapters, particularly 2, 8, 9, 10, 15, and 17 were almost completely rewritten. No conscious effort was made, however, to incorporate the entire literature published since 1962. To do so would have nullified the endeavor to provide an abridgment. Furthermore, a number of excellent books have been published recently that review current research. The present volume should be used in conjunction with such volumes as Verne Grant, *The Origin of Adaptations* (1963), E. B. Ford, *Ecological Genetics* (1964), B. G. Campbell, *Human Evolution* (1966), and Bruce Wallace, *Topics in Population Genetics* (1968).

Animal Species had three dominant themes: (1) the species is the most important unit of evolution; (2) individuals (and not genes) are the target of natural selection, hence the fitness of "a" gene is a nebulous if not misleading concept; and (3) the most important genetic phenomena in species are species-specific epistatic systems that give species internal cohesion. These three theses are now (in 1970) far more widely, or at least more

consciously, accepted than they were in 1963, and there was no need, therefore, to modify this basic platform in the abridgment.

A detailed typewritten criticism of *Animal Species*, prepared by Professor R. Alexander (Michigan) and a graduate class (D. J. Futuyma, D. L. Hoyt, R. J. Jehl, B. G. Murray, D. Otte, A. E. Pace, R. T. Vinopal, and M. J. West) was most helpful in eliminating errors and inducing me to tighten up loose arguments. In the Preface of *Animal Species* I thanked those who gave me most generous help in the preparation of the original volume. Mrs. Sara S. Loth undertook the preparation of the manuscript (typing, bibliography, illustrations, permissions, and so forth) in the most competent manner, and Mrs. Nancy Clemente devoted exceptional care to the editing of the typescript. The volume owes a great deal to their dedicated efforts.

E. M.

November 1969

Populations, Species, and Evolution

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1 · Evolutionary Biology

The theory of evolution is quite rightly called the greatest unifying theory in biology. The diversity of organisms, similarities and differences between kinds of organisms, patterns of distribution and behavior, adaptation and interaction, all this was merely a bewildering chaos of facts until given meaning by the evolutionary theory. There is no area in biology in which that theory does not serve as an ordering principle. Yet this very universality of application has created difficulties. Evolution shows so many facets that it looks alike to no two persons. The more different the backgrounds of two biologists, the more different their attempts at causal explanation. At least, so it was, until the 1930's, when the many dissenting theories were fused into a broad unified theory, the "modern synthesis." But even it has grown and matured since then.

Many of the earlier evolutionary theories were characterized by heavy emphasis, if not exclusive reliance, on a single factor (Table 1.1). The modern synthetic theory selected the best aspects of the earlier hypotheses and combined them in a new and original manner. In essence a two-factor theory, it regards the diversity and harmonious adaptation of the organic world as the result of a steady production of variation and of the selective effects of the environment.

Attempting to explain evolution by a single-factor theory was the fatal weakness of the pre-Darwinian and most nineteenth-century evolutionary theories. Lamarckism with its internal self-improvement principle, Geoffroyism with its induction of genetic change by the environment, Cuvier's catastrophism, Wagner's evolution by isolation, De Vries' mutationism, all tried to explain evolution by a single principle, excluding all others. Even Charles Darwin occasionally fell into this error, yet on the whole he was the first to make a serious effort to present evolutionary events as due to a balance of conflicting forces. The current theory of evolution—the "modern synthesis," as Huxley (1942) has called it —owes more to Darwin than to any other evolutionist and is built around Darwin's essential con-

Table 1.1. Theories of evolutionary change.

A. Monistic (single-factor explanations)
   1. Ectogenetic: changes directly induced by the environment
      (a) Random response (for example, radiation effects)
      (b) Adaptive response (Geoffroyism)
   2. Endogenetic: changes controlled by intrinsic forces
      (a) Finalistic (orthogenesis)
      (b) Volitional (genuine Lamarckism)
      (c) Mutational limitations
      (d) Epigenetic limitations
   3. Random events ("accidents")
      (a) Spontaneous mutations
      (b) Recombination
   4. Natural selection

B. Synthetic (multiple-factor explanations)
   1b + 2a + 2b = most "Lamarckian-type" theories
   1b + 2b + 2c + 4 = some recent "Lamarckian" theories
   1b + 3 + 4 = late Darwin, Plate, most nonmutationists during first three decades of 20th century
   3 + 4 = early "modern synthesis"
   1a + 2c + 2d + 3 + 4 = recent "modern synthesis"

cepts. Yet it incorporates much that is distinctly post-Darwinian. The concepts of mutation, variation, population, inheritance, isolation, and species, still quite nebulous in Darwin's day, are now far better understood and more rigorously defined.

The development of the modern theory was a slow process. Evolutionary biology was at first in the same situation as sociology, psychology, and other vast fields still are today: the available data were too voluminous and diversified to be organized at once into a single comprehensive theory. Looking back over the history of the many false starts gives a valuable insight into the process of theory formation. One important lesson is that some sets of data may not have significance until certain concepts are clarified or principles established. For instance, the true role of the environment in evolution could not be understood until the nature of small mutations and of selection was fully comprehended. Polygenes could not be analyzed and understood until the laws of inheritance had been clarified with the help of conspicuous mutations. The process of speciation (multiplication of species) could not be understood until after the nature of species and of geographic variation had been clarified. Discussions of variation among early evolutionists were utterly confused because they failed to make a clear distinction between geographical "variety" (geographical race) and

individual variety. The analysis of quantitative characters was futile until the principles of particulate inheritance were fully understood.

Genetics, morphology, biogeography, systematics, paleontology, embryology, physiology, ecology, and other branches of biology, all have illuminated some special aspect of evolution and have contributed to the total explanation where other special fields failed. In many branches of biology one can become a leader even though one's knowledge is essentially confined to an exceedingly limited area. This is unthinkable in evolutionary biology. A specialist can make valuable contributions to special aspects of the evolutionary theory, but only he who is well versed in most of the branches of biology listed above can present a balanced picture of evolution as a whole. Whenever a narrow specialist has tried to develop a new theory of evolution, he has failed.

The importance of eliminating erroneous concepts is rarely given sufficient weight in discussions of theory formation. Only in some cases is it true that the new, better theory vanquishes the old, "bad" one. In many other instances it is the refutation of an erroneous theory that vacates the field for new ideas. An excellent illustration of this is Louis Agassiz's neglect of what seem to us most convincing evolutionary facts because they were inconsistent with his well-organized, harmonious creationist world view. Darwin, who had started the voyage of the *Beagle* with views similar to those of Agassiz, began to think seriously about evolution only after he had found overwhelming evidence that was completely irreconcilable with the creationist explanation of the diversity of animals and plants. Or, to cite another example, as long as spontaneous generation and the instantaneous conversion of one species into another were universally accepted, even for higher animals and plants, there was no room for a theory of evolution. By insisting on the fixity of species, Linnaeus did more to bring about the eclipse of the concept of spontaneous generation than did Redi and Spallanzani, who disproved it experimentally. Indirectly, Linnaeus did as much to prepare the ground for a theory of evolution as if he had proposed such as theory himself.

More important for the development of the synthetic theory than the rejection of ill-founded special theories of evolution was the rejection of two basic philosophical concepts that were formerly widespread if not universally held: preformism and typological thinking. *Preformism* is the theory of development that postulates a preformed adult individual in miniature "boxed" into the egg or spermatozoon, ready to "unfold itself" during development. The term evolution is derived from this concept of