BOOK REVIEWS

Microbial Evolution

Population Genetics of Bacteria. S. BAUMBERG, J. P. W. YOUNG, E. M. H. WELLINGTON, and J. R. SAUNDERS, Eds. Published for the Society for General Microbiology by Cambridge University Press, New York, 1995. xii, 348 pp., illus. $110 or £55. Symposia of the Society for General Microbiology, vol. 52. From a symposium, Leicester, U.K., Jan. 1995.

The bacteria display an amazing diversity of metabolic activities and life styles. Comprising two of the six kingdoms of living organisms, they define the limits of the biosphere, being found in the uppermost reaches of the Earth's atmosphere and in its deep subsurface and prospering at temperature as high as 250°C and at pH as low as 2, conditions under which most self-respecting proteins would denature and DNA double helixes fall apart. Although numerous books on bacterial genetics and on the population genetics of higher eukaryotes are published every year, volumes on bacterial population genetics and evolution have been few. The present collection of papers is only the third to appear in the last two decades, following *Evolution in the Microbial World* (M. J. Carlile and J. J. Skehel, Eds.; Cambridge Univ. Press, 1974) and *Microorganisms as Model Systems for Studying Evolution*, R. P. Mortlock, Ed.; Plenum, 1984). This might suggest that there is no interest in the field or that nothing has changed since the last volume was published in 1984. Neither conclusion is correct. A Gordon Conference devoted to the field has been meeting biennially since 1987, and almost all other conferences concerned with population genetics and evolution now include some speakers working with microbes. So what's new? A lot, it turns out from reading this book. The field has been growing healthily, and the chapters in this volume provide an excellent overview of it.

Perhaps the most significant conclusion that emerges from the book is that bacterial populations are clearly not the homogeneous entities that classical models of evolution in asexual populations would have us believe. Rather, natural populations of a variety of species have been shown to contain abundant levels of variation (Sharp *et al.*; Whittam) and to possess a wide range of population structures. The immense power of the *Escherichia coli* experimental system has allowed mechanisms for the generation of this variation to be analyzed in considerable detail. Thus, certain regions of the bacterial chromosome have been found to be highly mutable as a result of small chromosomal rearrangements (Saunders), and overall mutation rate can increase drastically under inclement conditions—the phenomenon now widely known as "adaptive mutation" (Foster). As the variability generated by these systems can significantly increase the ability of a cell and its descendants to survive, they can be thought of as adaptations to life in an inconstant and hostile environment.

Although it is true that bacteria reproduce primarily asexually, horizontal transfer of DNA, and therefore recombination, can occur by means of transformation, phage-mediated transduction, and conjugation. These processes can generate very different population structures, as is illustrated in several chapters in this book. At one end of the range, the naturally transformable *Neisseria gonorrhoeae* possesses a completely panmictic population structure—being apparently as promiscuous as its human host (Maiden and Feavers; Spratt *et al.*). At the other extreme, even the lowly *E. coli*, with a predominantly clonal population structure, shows patterns of sequence variation among strains that reveal a history of recombination (Milkman and McKane).

One issue that repeatedly surfaces in the book is, What constitutes a species in bacteria? Maynard Smith addresses this question head-on in the opening chapter—a particularly provocative and enlightening one—entitled "Do bacteria have population genetics?" He concludes that "no species concept could be devised [for bacteria] that would carry the heavy load of meanings and theoretical implications" that the concept has regarding higher organisms. Yet strains of *E. coli* are similar to each other and can be distinguished on the basis of DNA sequence divergence from strains of, say, *Salmonella*, which also can be grouped together. Clearly there are clusters of prokaryotic organisms, but what maintains them as units and how did they arise? We are perhaps closer to answering these questions and to identifying "speciation genes" in prokaryotes than in any other group of organisms. We now know a considerable amount about barriers to recombination in the Enterobacteriaceae, erected by the numbers and diversity of restriction-modification systems (Barcus and Murray), as well as by the mismatch repair enzymes (Radman, an invited speaker at the conference that gave rise to the book but unfortunately not a contributor to the book). On the other hand, the SOS system acts as a positive regulator of interspecific recombination, and so-called "promiscuity genes" that allow cross-species transmission across wide boundaries have been identified in R-plasmids (Wilkins).

One of the fascinating aspects of microbial evolution is the seeming ease and speed with which bacteria can evolve new functions. This is a second theme of the book—adaptive evolution. The rapid acquisition of antibiotic resistance, covered in two of the chapters (Bennett, Levin), is but one spectacular example. Meanwhile, in the laboratory, the short generation times of bacteria allow experiments to be carried out that can last as many as ten thousand generations (Lenski)—a time span approaching an era for many higher organisms! Evolutionary changes and the sequence in which they occur can thus be determined directly, without resort to the inferential procedures that are usually required in evolutionary biology.

Who should read this book? Although it contains little information that has not already been published, it provides an overview of the advances in microbial population biology over the last 11 years or so. It should therefore be useful for workers in the field. It should also be a valuable introduction for the vast majority of evolutionary biologists not working with microorganisms. They will not fail to be impressed by the power of microbial systems for the analysis of evolutionary changes and to be fascinated by the peculiarities of microbial populations.

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Island Reptiles

Anolis Lizards of the Caribbean. Ecology, Evolution, and Plate Tectonics. JONATHAN ROUGHGARDEN. Oxford University Press, New York, 1995. xiv, 200 pp., illus., + plates. $59.95 or £45; paper, $29.95 or £20. Oxford Series in Ecology and Evolution.

From the title one could be misled into thinking that this little book is a field guide for the identification of the most exuberant

A male *Anolis marmoratus*, from Guadaloupe, shown with yellow dewlap extended during a display to another anole. [From the dust jacket of *Anolis Lizards of the Caribbean*]

group of lizards occupying the Caribbean (indeed the world). Though such a book is needed, this decidedly is not it. Those more familiar with the author and his work on theoretical community ecology, and particularly the coevolution of interacting species as applied to the anoles of the Lesser Antilles, may be equally misled into thinking that it is just another review of his illuminating research program pursued over the last two decades. While such a review is definitely here, much more is novel, representing exciting new directions.

Anolis lizards occupy a special place in the disciplines of ecology and biogeography. They are diverse, with over 300 species in the New World. They are conspicuous, often coming in bright colors and active during the day; they are abundant, and particularly so on islands in the Caribbean, where they fill the insectivorous-vertebrate niche preempted by birds in more speciose continental faunas. Finally, they illustrate several important phenomena in evolutionary ecology—they are prime examples of adaptive radiation on the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico).

The ecology, evolution, systematics, and biogeography of anoles of the Greater Antilles have been studied by Ernest Williams and his students and colleagues and are reviewed in this book. The proliferation of *Anolis* species in the Greater Antilles has resulted in a diversity of niche occupations, yet these can be usefully categorized as "ecomorphs" by specifying only three niche dimensions: body size, perch type, and climatic preference. The remarkable feature of this radiation is that, while the niches are easily ordinated along these three axes, only particular combinations of the three features are realized, and roughly the same combinations occur on all the islands even though niches identical to one another are filled by unrelated forms on the different islands.

The overall impression is that the unusual regularity of niches has been molded by the persistent selective force of interspecific competition between anoles and a large and habitat-rich playing field on these large islands. On the smaller islands in the Lesser Antilles, Roughgarden and students were struck with another regularity, this time in *Anolis* body sizes. Islands either have two anole species, in which case one is large and the other small, or have a single species, which is nearly always intermediate in body size. Since these islands are old (Miocene or older), colonized by more than one stock of *Anolis* ancestors, and since one- and two-species islands do not differ systematically in area or isolation, Roughgarden (like Williams and Thomas Schoener before him) suspected that the differences between islands are generated by interactions among the lizards themselves. In this book we get to see the genesis of this idea in many possible manifestations, each with testable, albeit sometimes difficult-to-measure, consequences.

After all is said and done, and after one theory is pitted against another, some falling by the wayside, it is the biogeographic pattern that remains, and so it is important that it be explained in factual detail. Over the years, Roughgarden has been active in chronicling the relevant facts, developing theoretical explanations, and experimentally testing them where possible. His views on the models' adequacy have changed over time, and it is interesting to read his account of the problems that exist with theories that he earlier supported. His careful effort to bring all the observations and experiments together to answer the questions is refreshing. Every step of the way there is a crystal-clear logical development with succinct prose.

"*Anolis pogus*, male and female, from St. Martin, the smaller species [on this two-species island] now found only in the hills in the center of the island, having become extinct on Anguilla." [From *Anolis Lizards of the Caribbean*]

Chapter 1, "The sentient forager," is for me the most exciting, both because it contains heretofore unpublished models and data on *Anolis* foraging behavior and because it represents a novel approach to understanding the evolution of adaptive behaviors. It begins with a typical optimization approach. If you were a lizard sitting on a perch, how far would you be willing to run to catch an insect landing on the ground around you? All else being equal, insects nearby will be easier to see and cost less in energy expended in pursuit. A big lizard may be able to run faster than a small lizard. Big insects will be worth more effort than small insects. Such considerations all go into a mathematical stew along with actual data on insect settling rates, caloric content of insects, and other such parameters and out come predictions of the cut-off point beyond which pursuing insects will, in general, be a colossal waste of time (or energy—two versions of the model are developed). What is unique, at least for evolutionary ecology, is the next step that Roughgarden takes. He now asks, What is the simplest algorithm that a thinking lizard might adopt that would lead to the same answer without its having to do the mathematics? This mechanistic approach bridges many fields—those in computational science will be interested in seeing how genetic algorithms fare compared with a more comparative-psychology approach based on simple, blindly followed rules of thumb. Each step in the development of the synthetic models involves a comparison with data on anoles. The remarkable result is that optimal foraging behavior as predicted by an omnipotent mathematical model can be attained by a lizard that learns by a very simple but biologically plausible rule of thumb.

This fascinating chapter will surely stimulate much more research. It took me a long time to get through it because I kept going off on tangents extending the model in new directions. This task is made easy because Roughgarden supplies the source code (in Scheme) for all the programs in the book.

Chapter 3 explores the phylogenetic origin of the *Anolis* of the Lesser Antilles. How much of the body size pattern, along with associated niche differences in habitat and microclimate preferences, is simply a historical remnant from the primordial *Anolis* that originally occupied the land masses that now form the several islands? Roughgarden puts on his geologist's hat and reconstructs a historical scenario for the origin of the islands and their founding *Anolis* populations. His figure 3.5 encapsulates a bold and detailed exposition of his version of the geological facts—facts scanty enough that there is still much room for alternative interpretation. One controversial point will be his interpretation of the geological evidence that would give St. Lucia, in the southern Lesser Antilles, a common origin with Bonaire, which nearly hugs the north coast of Venezuela. The anoles of Bonaire and St. Lucia seem to have a common ancestor on Roughgarden's phylogenetic hypothesis for the group. While both the phylogeny and the geological evidence remain controversial, Roughgarden is applauded for standing out on a limb with a detailed and testable hypothesis. Additional sea-floor information, along with application of molecular and biochemical markers for phylogenetic reconstruction of anoles and co-occurring reptiles (such as the geckos and snakes) whose ages bracket the time of origin of the Caribbean islands, will provide support or refutation of Roughgarden's reconstruction.

The final chapter of the book builds a food web starting with anoles in the center. The resulting web is notable because, like several others emerging in the literature, it does not exhibit supposed regularities in structure that have been the subject of recent theoretical generalizations. Roughgarden takes this as a point of departure to review the adequacy of food web theory and the empirical facts that support it. This is a short but thoughtful chapter (summaries of entire research programs can be distilled in a single rich footnote), and Roughgarden's views of the nature of generality in ecology will be found provocative.

The production of the book is generally first-class but suffers from a few annoying problems. Some of the variables referred to in the text are not evident in the listing of the Scheme programs in the accompanying tables of chapter 1. Table 3.2, which gives a useful listing of all the amphibians and reptiles on each of the Lesser Antilles islands, has many entries out of alignment for St. Lucia, St. Vincent, and Grenada. Fortunately, with Roughgarden's copious notes it is possible to reconstruct the correct entries. More maps of the region with different overlays illustrating the various biological and geological features discussed in the text would have been welcome. Finally, it would have been nice to compare and contrast the *Anolis* system with similar lizard systems such as the *Phelsuma* geckos of the Indian Ocean, the *Rhacodactylus* geckos of New Caledonia, the endemic genera of viviparous geckos on New Zealand, and the endemic skink genera of New Guinea. The ecological relationships and phylogenetic affinities of these groups await study, and we will all be much better off if they attract investigators with the genius, clarity, and perseverance of Roughgarden.

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