Book reviews 647

## Basic Theory, Plain and Simple

A review by Michael Doebeli

**Population Biology – Concepts and Models.** By Alan Hastings. Springer, New York, 1997. xvi + 220 pages. ISBN 0-387-94853-8.

Surprisingly few basic concepts and models form the foundation of the large body of literature in population biology. In this beautifully clear book, Alan Hastings introduces most of these concepts and models at an undergraduate level. Familiarity with the material covered in this book is a prerequisite for anybody who is going to work in population biology and evolutionary ecology. For empirical research, the theory is essential for clarifying the assumptions underlying experiments and interpretations of data. For theoreticians, the models presented in this book are the key to understanding the ramifications of these models that constitute most of contemporary population biological theory. In the present text, Hastings has integrated his experience of teaching in an environment renowned for both empirical and theoretical research. The result is an excellent textbook for introductory classes in theoretical population biology.

The book has ten chapters, one introductory, four on single species models, ranging from density-independent and age-structured models over basic population genetics and models for density-dependent population growth to elementary life history theory, and five chapters on models for interacting species, ranging from Lotka-Volterra competition and predation to host-parasite interactions and elementary epidemiological models. Most of the material is standard, but in contrast to many ecology textbooks, the exposition is crisp and clear, conceptual rather than enumerative, and as simple as possible, yet at the same time complete and self-contained. A particularly convincing example is chapter 8, in which mathematical stability analysis, experimental data, and various extensions of the basic Lotka-Volterra model are woven together into a very succinct introduction to the theory of predator-prey interactions. Throughout, important mathematical concepts are set apart and explained in boxes, which is a very useful way to present more difficult technical points in a textbook. Another nice feature are the frequent marginal notes, which give additional information and generally keep the reader aware and thinking. In addition, the exercises at the end of each chapter (an indispensable ingredient of any textbook in theoretical biology) are well chosen and often engage the reader in conceptual thinking, rather than merely giving numerical examples.

At times, the logic of the mathematical development seems to dictate the flow of the book, which leaves some of the biological concepts a bit stranded. For example, chapter 2 ends with an explanation of reproductive value, to no apparent avail at that point. Similarly, some game theoretical concepts are introduced at the very end of chapter 3 on population genetics, and then abandoned for the rest of the book. On the other hand, metapopulation theory is introduced in chapter 4, and then nicely reappears in the context of competition and predation. This is very useful and important, given the prominent role that spatial structure has played in ecological and evolutionary theory in recent years.

Book reviews

One might have expected a bit more emphasis on evolutionary concepts in a textbook on population biology. The traditional ecological view seems to be that ecology matters for evolution, but no so much vice versa. I disagree, and I think that the chapter on the evolution of life histories is informative, but short, and that concepts such as selection, optimization and frequency-dependence could have received more discussion. Specifically, one important and influential model that is missing is the Prisoner's Dilemma game. The conceptual clarity of the book would probably not have suffered from a final chapter presenting, just as an appetizer, a synthesis of some of the ecological and evolutionary concepts by means of a few examples combining population genetics and frequency dependent selection with ecological and life history models.

There are two other recent books with similar scope and length as Hastings' book, reflecting a growing interest in the theoretical foundations of population biology. Bulmer (1994) addresses more advanced readers and puts more emphasis on specific topics in evolutionary ecology. Thus, Bulmer (1994) covers more ground, but where they overlap, Hasting' book is more conceptual, easier to read, and better suited as a textbook for undergraduates. The overlap between Hastings' book and Gotelli (1995) is larger. Gotelli (1995) contains more biological examples, but is also more enumerative, while Hastings' book is more concise, conceptual and self-contained. In contrast to Hastings' book Gotelli (1995) is a purely ecological textbook and contains topics such as demographic stochasticity and island biogeography, but does not discuss population genetics, life history evolution, or evolutionary game theory. In sum, I highly recommend the present book to anybody who wants to learn fundamental concepts and models in population biology, or who wants to make sure that her or his undergraduate students obtain a good theoretical and conceptual education in this field. I would not be surprised if Hastings' book became the most widely used textbook for these purposes.

## References

Bulmer, M. 1994. Theoretical Evolutionary Ecology. Sinauer, Sunderland. Gotelli, N. J. 1995. A Primer of Ecology. Sinauer, Sunderland.

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