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Models of Adaptive Behaviour: An Approach Based on State.—Alisdair I. Houston and John M. McNamara. 1999. Cambridge University Press, Cambridge, England. viii + 378 pp. ISBN 0 521-38480-X. Hardback, $80.00 ISBN 0-521-65539-0. Paper, $34.95.—There are two types of review book written by long-time experts in a field. The first emerges when the resident experts synthesize their accumulated (and typically prolific) work into a unified whole. That process involves cutting across domains of their original articles to create a new work in which all the relevant work is revisited and reworked holistically in light of their accumulated experience. Done well, such books often preempt the need to read and cite the original articles, for the most relevant material is available in the synthesis. Such books are often ideal for graduate courses: the purchase of the book provides the student with access to the field as a whole. The alternative type of review book emerges when the experts in question collate summaries of their accumulated works into an organized whole, with the organization revealing the structure not apparent in the original stream of publication of works in progress. That latter approach necessitates continued reliance on the original articles, with the book, in effect, providing an annotated road map to the location in the literature of the key ideas. Such is this latest work from the long-time collaboration of the theoretical biologist Alisdair Houston and the mathematician (and biologist) John McNamara.

State-based modeling considers the behavior of an organism to be characterized by a set of state variables that track body size, energy reserves, quality of territory, and so on, variables that collectively quantify the quality of the organism. In many ways, the concept of state is to the organism what the Hutchinsonian hyper-dimensional niche is to the species, and state variables impose constraints and determine costs and benefits of particular courses of action for the organism. In evolutionary terms, an organism should have a strategy that guides its response to every set of circumstances in which it finds itself, with the optimal strategy being that which maximizes fitness. The problem is that, among organisms following the optimal strategy, there will inevitably be differences in many state variables that may limit their potential for future offspring. One must resort to the concept of reproductive value to index that potential for each state. In other words, the organism (and researcher) must determine what strategy yields the maximum pay-off for a given state (i.e. the pay-off from performing any particular action as the sum of the reproductive values of any offspring that directly result from the action, plus the expected reproductive value of the organism after it has performed the action). This may be a simple task for a single action but the value of a current action usually depends on future actions. Hence one has to somehow determine a suitable outcome point in the future and work backwards to assess the value of the current action, often via a numerical approach known as "dynamic programming." Solving state-dependent dynamic models is hard work, by anyone's standards, particularly if one wishes to generalize the resulting findings. This book addresses analytical and computational procedures available in making those determinations, using simple state-dependent models along a spectrum from simple to complex. Those models in turn may either be, by themselves, sufficient to solve simple problems or they may provide greater understanding of more complex situations requiring full dynamic programming and generalized models. That is an area of research in which Houston and McNamara have been preeminent, in a collaboration that has yielded more than 75 publications on state-based behavioral modeling over the last 20 years.

The present work is organized into 10 chapters. The first is a short introductory chapter that introduces three key ideas—the concept of state, the utility of reproductive value as a common currency in evaluating merits of alternative behavioral strategies, and necessity of dynamic programming in evaluating actions whose fitness will be affected by other actions yet to be taken. The rest of this chapter outlines the authors' thinking about models. It describes the structure of the book, and sketches three areas where the writing of the book reveals a pressing need for more work to be done (namely physiology, interactions between animals, and determining the problem each animal is built to solve).

Chapter 2 takes a quick sweep through the components of behavioral decision modeling—state variables, reproductive value, actions, optimal decision, and the nature of trade-offs (in life histories, between energy and time, and between foraging and predation). This sets the scene for the third chapter in which the notion of dynamic optimization is developed. The first half of this chapter is very clearly written but mid-way through it an exasperating truncated style sets in. In essence, the authors' strategy is to provide clearly written summaries of previous work (often, and appropriately, their own), but all too often omitting technical details for which the reader is given a citation to the original paper. That is an adequate strategy if a book is to summarize the state of knowledge in the field; it is a major shortcoming if the book is intended to instruct the reader in the topic. As an example, consider the following paragraph:

> "McNamara et al. (1994a) show that not only the amount but also the type of stochasticity is important. In one class of models they allowed the amounts of food found in successive time intervals to be successively correlated. The resulting optimal daily routines of feeding and resting were very different from the routines obtained when food found in successive time intervals were independent."

This text, indeed, orients the reader towards further information on the influence of stochasticity. But it tells little about the class of models involved, or whether the conclusion was unique to this class or was tested only with that class! Neither does it tell one in what respect the routines changed, nor how the routines varied along a spectrum from uncorrelated to highly correlated patterns of food availability. A synthetic review would address such questions, and be the more valuable for doing so!

Chapter 4 turns to one of the classic problems of behavioral ecology, the maximization of the energy gained in foraging. What is most interesting here is the authors' use of mathematical theory to ensure rigor in generalization. Thus they visit the classic marginal-value theorem and its graphical solution by constructing a tangent to the mean gain curve. But because their approach follows mathematical logic to yield an iterative equation for the mean net rate of energy gain under a strategy, one can immediately deduce that the tangent construction will be in error where multiple patches are involved. It is such logical recasting of ecological problems into mathematical formalism with its immediate potential for generalization that has given theoretical biology its power (and Houston and McNamara their recognition). The same sparse elegance in dissecting behavioral problems permeates the book wherever the authors concentrate on presenting rather than providing synopsis. On the other hand, so many variants of problems are presented that their sheer diversity is intimidating! I would have liked to see the authors provide greater emphasis on the unity of thought and analysis that spans the array of problems they analyze. They do so comment, but too often only on an ad hoc basis rather than to highlight unifying principles. To some extent, one has to understand this broader phenomenon in order to recognize it in the text here—but perhaps that is why we have instructors as well as books!

Chapters 5 and 6 extend the approach used in Chapter 4 to the topics of risk-sensitive foraging (primarily the risk of starvation) and to the trade-off between energy acquisition and predation, respectively. To a large extent the dynamic models of other chapters are set aside here in favor of a simple conceptual model based on the two-dimensional space formed by axes for rate of predation and rate of energy intake. As noted earlier, exploring and documenting the value of relatively simple models was one of the key goals for the authors in writing this book. Even with that simplicity, however, the rigor provided by the mathematical analysis allows them to demonstrate that published conclusions in other related studies are definitely wrong. This use of mathematical rigor finesses the limit inherent in the inductive approach of much of ecology, that no matter how many case histories one accumulates in support of a pattern, there is no guarantee that the next case studied will not diverge from that pattern! Chapter 7 focuses on game theory, recasting several of the standard game-theoretic models, such as J. Maynard Smith's hawk–dove interaction, into state analyses. For avian biologists, the interesting elements of this chapter will be the treatment of mate choice and of brood care and desertion. Chapter 8 is a long chapter considering life-history phenomena, in particular developing rigorous approaches to the representation of fitness and reproductive value. For assistance in jump-starting their research, interested graduate students should turn to Houston and McNamara's list of four topics needing further investigation: sex dependence, the frequency dependence introduced by variation in the behavior of other individuals, kin selection, and senescence. Chapter 9 addresses the problem of analyzing behaviors dependent on environmental periodicity (daily, annual) which requires major modification of the standard dynamic programming approach to accommodate the requirement that the end point (of one cycle) be also a start point (for the next cycle). For anyone doubting the power of mathematics, the study of the elegant logic applied to this issue's successful resolution should be an eye-opener! A similar lesson can be learned in the authors' attack, in Chapter 10, of the problem of optimization in a fluctuating environment, particularly as it combines with periodicity imposed by annual cycles.

In the hands of a competent instructor, this book is a useful tool with which to inculcate important principles of mathematical biology into the next generation of graduate students. The book provides a comprehensive road map to state-variable analysis of behavioral decisions. At the same time, however, its reliance on citing the extant literature for many details of the problems reviewed poses a problem for students without access to a good instructor, probably demanding too much of the average graduate in terms of supplementary reading. Twenty-five years from now the authors' rigorous and mathematically sound approach is likely to have displaced much of the lightweight theory of current ecology. This will in no small part be due to researchers like Houston and McNamara opting for rigor and a small audience rather than bandwagon science and a large following. If Houston and McNamara are to drive that displacement effectively, however, they will need to revisit the contents of this book and recast them into a self-contained and truly synthetic version, cutting across the boundaries of their original articles and providing greater integration for those less familiar with the field. For those of us familiar with the field, this book underscores the tremendous contributions Houston and McNamara have made to the advance of behavioral ecology, in general, and to avian behavior in particular. As a teaching tool, though, it signals "This is a tough act to follow" rather than "You too can do this (even if standing on the shoulders of giants!)."—RAYMOND J. O'CONNOR, *Department of Wildlife Ecology, University of Maine, Orono, Maine 04469, USA. E-mail: oconnor@umenfa.maine.edu.*