Book Reviews

Making Ecology an Applied Science

Ecology and Resource Management. A Quantitative Approach. KENNETH E. F. WATT. McGraw-Hill, New York, 1968. xii + 450 pp., illus. $14.50.

Kenneth Watt in this work treats resource management as an optimization problem: how to maximize a rate of harvest, or how to minimize the density of a pest. To "optimize" an ecosystem, we must know how it works and how to manipulate it to suit our purposes. Watt accomplishes this by making a mathematical model of the system and using the model to predict the effects of different management policies on its yield. The model usually takes the form of a computer program designed to simulate the system's behavior; we may then compare the effects of different management policies by simulating experiments on a computer, rather than carrying out their (far more expensive and time-consuming) counterparts on the real system. In sum, Watt would have us apply the techniques of operations analysis to resource management.

To learn how to make ecological models, one must know some ecology. Watt therefore devotes the first third of his book to a review of this subject. He illustrates ecological principles by concrete applications to resource management. The applications provide a cohesion, a discipline, that ecology lacks when practiced as a pure science; they demand hypotheses that work and that mean something, a benefit often overlooked by those who eschew "applied science."

For example, a consideration of a population's age composition provides four concrete criteria by which one can recognize when the population is being exploited ruinously. A discussion of the difference between weather-regulated and density-regulated species leads to an explanation of the stability of the North Sea fishery and the failure of California's sardine fishery. A study of "pest" dynamics tells us that most pests are weather-regulated species, and that fluctuating weather conditions usually play a greater role than insecticides in controlling pest populations. Some themes are familiar: the inevitable instability of single-species stands, the energetic advantages of cropping a lower trophic level rather than a higher one. But we are also told that insect species with a great many foods, or a great many predators, tend to have far less stable populations than species with more specialized feeding habits and those controlled by a single predator, respectively—quite a contrast with the usual belief that a more complex food web leads to greater stability. The near-platitude that an ecosystem evolves to maximize its productivity leads Watt to remark that a natural community is likely to be more productive than any (unfertilized) system we may substitute for it. Our short-grass prairie produced far more meat when it was cropped by buffalo than it does today, when it is cropped by cows; similarly, African game is more productive than the cattle replacing it. This conclusion appeals greatly to one who has compared the lush forest of the Amazon with the pathetic farms taking its place. Watt's review contains a wealth of such stimulating observations. The gap between his wise suggestions and present practice is depressing and terrifying.

Watt's primary concern is the construction of models. He believes that properly realistic ecological models will be workable only with the aid of computers—indeed, he thinks the sequential pattern of computation provides a natural simulation of the sequential development of a biological system. He therefore presents a chapter on computer programming, showing how conveniently one may express biological problems in Fortran language. Then he turns to the techniques for obtaining data. We learn how analyses of variance permit us to refine our sampling technique, making for less bias and greater precision in our estimates, and we encounter the complexities of estimating the sizes of populations whose members cannot be simultaneously exposed to view—the fish in a pond, say, or the deer in a forest. He discusses regression analysis, as a means not of making theories but of discovering which variables are most important—whether, for example, a population is primarily "density-regulated" or "weather-regulated." Finally, we learn how to estimate parameters of nonlinear models from a set of data (for example, to "fit" a logistic to an observed growth curve we must estimate the "carrying capacity" and the "intrinsic rate of natural increase"). The mathematics chapters do not presume to provide an algorithm for model-making; they are meant simply as useful aids in expressing and testing biological insights.

Watt takes a distinctly "reductionist" attitude toward model-making. In particular, his approach to population dynamics reminds one of a child's asking why something is so, and then insisting on an explanation of the explanation, in ever-ramifying series. First he asks about the birth and death rates of the population. Next he asks how birth rate relates to frequency and effectiveness of copulation. Then come "submodels" relating fertility and copulation frequency to the age composition of the population and the conditions of its environment (weather, past and present, degree of crowding, and the like). These in turn call for "sub-submodels" relating, for example, crowdedness to the numbers and age composition of this population and its competitors. If a predator figured strongly in the death rate, Watt might construct a "submodel" of the predator's feeding rate, incorporating, among other factors, knowledge of the behavior patterns of an individual predator. To guide us in the construction of such models, Watt provides a splendid chapter summarizing the mathematical generalizations about the effects of weather, population density, competition, feeding behavior, dispersal behavior, and other such factors on population growth. These generalizations are often sophisticated and effective, testifying abundantly to the value of childlike curiosity.

Finally, Watt describes how to find the optimum management policy for an ecosystem. Suppose we wish to maximize a system's annual yield. The yield will depend on the management policy we employ. Symbolically, we may express the yield as a function of several variables together representing the management policy. This construct is similar to Wright's "adaptive surface," which specifies the fitness of a population as a function of its genetic composition. Wright was interested in the "search strategy" by which the population could "find" the genetic composition of maximum fitness as quickly as possible; similarly, Watt requires a means for speedily finding the optimum management policy. If there were anything substantial to say on this subject, it would be of great interest, but the subject is hardly born yet, and Watt can only present abstractions unsupported by concrete applications. Our ignorance permits the contrast between Wright's emphasis on search strategies with a random component and Watt's emphasis on purely deterministic strategies.

The two most interesting aspects of this book are its reliance on computers and its reductionist approach. The reductionist attitude is very fashionable in biology nowadays, and quite possibly we can never claim to understand ecology until we can pursue a child's question why a lion eats zebras to an explanation of the chemistry of the lion's hunger and the more mysterious logic behind the events in the lion's brain. Before the time of computers, one could claim that such an attitude put the cart before the horse, for we would be busy explaining before we quite knew what to explain. A necessary prelude to the kinetic theory of gases was an empirical thermodynamics singling out pressure, temperature, and volume and, more generally, energy and entropy, as variables whose relations were important. Without such a theory, essays into molecular mechanics would have lacked purpose and direction; moreover, molecular mechanics has little to add to many of the predictions of "classical thermodynamics." Does Watt err by studying ecosystems through detailed analysis of their components? His specific objective, and his use of computers, vindicate this approach. He knows what he wishes to optimize, and to achieve this aim he has machinery to employ models as complex as our ignorance may demand. To learn what questions to ask first, he may make preliminary models of his system to test the relative importance of different variables. In no way does his investigation lack purpose.

Watt's reliance upon computers raises more interesting problems. There are three possible attitudes toward computers:

1) One may abstain from their use as a discipline to encourage simple and understandable thought. According to this attitude, a question so complex as to require computation is the wrong question to ask; one has to think further about what is really important, what constitutes the essence of the problem.

2) One may use them to simulate special cases, to learn what questions to ask of paper-and-pencil mathematics. According to this attitude, one seeks a theory simple enough to work out with paper and pencil, but a computer helps in the search.

3) One may view the computer as an extension of the mind, taking the attitude that we understand a system if we can construct a computer program that properly simulates its behavior. Watt thinks the last attitude is appropriate to the study of complex systems. Computation permits maximum interaction between model, experiment, and observation, for there is no need to gloss over biological complexities, and no obstruction to generating meaningful predictions.

Watt's reliance on computers is part of a phenomenon of very deep significance. In the past, a model or theory of a system usually served two purposes: it accurately predicted the system's behavior, and it was a description of the system substantially simpler than the system itself. The model helped us to understand "why the system behaves as it does" as well as to predict its behavior. The two requirements were really one: to predict a system's behavior one had to construct a model simple enough to understand, simple enough to let us work out the consequences of our assumptions. The bond between theory and application was that prediction required simple yet meaningful description. Computers disrupt this bond: one no longer needs *simple* theory for prediction. Indeed, for accurate prediction we quickly resort to models too complex to understand. This proliferating complexity may have strange consequences. After all, one can *predict* planetary motion quite accurately by introducing enough Ptolemaic epicycles. Yet, even though it makes no difference to the relativity theorist whether we center our world on earth or sun, we cannot "understand" the dynamics of planetary motion unless we do away with the epicycles by sending the earth round the sun. Many scientific revolutions, many advances of understanding, were brought about by the demands of simplicity. Since applications do contribute to such advances, the computer's dissociation of prediction and understanding may greatly affect the development of science. It is distressingly easy to see how such a dissociation could lead to a proliferation of abstract theory, no longer needed for, and therefore undisciplined by, application; and an applied technique more dependent than ever on elaborate machinery, and thus more a slave of circumstance.

Watt's book betrays some haste. The book is technically nearly self-contained (requiring only a little elementary calculus and statistics), yet many readers will find the mathematics quite difficult; a little more time and thought would surely have made the book far more accessible. In later portions of the book, many ideas are expressed in Fortran language; I hope others do not find the algebra as difficult as I did the Fortran. On the other hand, the book is well put together, the equations nicely displayed, and so on. I think the book is one of substance, perhaps the greatest to appear in ecology since the fundamental works of Elton, Gause, and Volterra.

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Responses to Light

Insect Photoperiodism. STANLEY D. BECK. Academic Press, New York, 1968. viii + 288 pp., illus. $12.50.

In both plants and animals many seasonal adaptations, involving growth pattern and timing of reproduction and dormancy, are mediated by responses to seasonal differences in the duration of daylight, that is, in day-length. The physiological mechanisms underlying such biological responses to day-length constitute the usual subject matter of photoperiodism. The vast literature in this area is generally dismaying to the student; the terminology is inconsistent and the concepts are often vague; the experimental designs are commonly confusing; and the distinction between hypothesis and experimental observation is seldom kept clear.