

commend the book as an account of the fundamentals of even the physiology, never mind the biochemistry, of the energetics of muscular exercise. However, as a fine account of what has "awakened the passion and interest" of Margaria, it is well worth reading.

Most of the book is based on simple measurements on human beings exercising at relatively high rates. A clear account is given of the major types of oxygen debt, of changes with exercise of cardiorespiratory function at sea level and at high altitudes, and of the "biomechanics of human locomotion." The problems of walking, running, and jumping on the earth's surface are presented and contrasted with the situation on the moon.

Perhaps the most important part of the book is a description of how, with a good stopwatch, some stairs, a chair, and the nomograms printed here, sufficiently accurate measurements can be made to estimate a person's maximum aerobic and anaerobic powers. Without doubt these powers should be much more widely known, not only to athletes, coaches, physiotherapists, and physicians, but to anyone who wants to monitor something closely related to physical fitness as it changes with the years.

It is refreshing to see an (albeit touched-up) series of photographs of what seems to be a woman sprinter on the book cover, but depressingly typical to see it described in figure 3.12 as "stroboscopic image of a running man."

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## Basic Ideas in Ecology

**Theoretical Ecology.** Principles and Applications. ROBERT M. MAY, Ed. Saunders, Philadelphia, 1976. viii, 318 pp., illus. \$13.50.

This book is intended to introduce simple ecological models and their applications to undergraduates and others who have had approximately one year of calculus. It succeeds well in this aim. The contributors—May, T. R. E. Southwood, M. P. Hassell, G. Gaughley, E. R. Pianka, J. M. Diamond, H. S. Horn, E. O. Wilson, S. J. Gould, J. E. Cohen, and G. Conway—are a distinguished group of ecologists whose specialties include theory, fieldwork, and applications. Often the writing style is uncommonly good, and the spirit of modern ecological

research is clearly and enthusiastically conveyed.

The book begins with two chapters on models for the population dynamics of single species, then offers three more chapters on models for two interacting populations, then four chapters on community-level phenomena, and finally a set of four chapters on the applications of theoretical ecology to allied fields. These concluding chapters discuss sociobiology, paleobiology, epidemiology, and pest control. The book is well balanced in its coverage of theoretical and empirical topics. Also, it is unusual in providing equal time to various predator-prey models and to competition models. I would like to point to several chapters that present material that is difficult to obtain from other sources. Hassell presents a useful synthesis of predator-prey models specially applicable to arthropods, Pianka pulls together a huge literature on niche theory and related field observations, May reviews empirical phenomena at the community level, Cohen summarizes the population dynamics of schistosomiasis parasites, and Conway presents an account of the biology of pest control.

The book is somewhat mistitled; it is an introduction to theoretical population ecology and not to the whole field of ecology. There are no chapters on the theory relating to the ecology of individuals, for example on models of foraging strategies, optimum leaf design, or daily activity cycles as a function of temperature. Nor are there chapters on ecosystem modeling. These remarks are not intended as a criticism, for the book is sufficiently long as it is and is well integrated. I predict that it will be well received and plan to use it myself in courses.

My principal reservation about the book has to do with its lack of chapters on evolutionary ecology and, more generally, an unfamiliarity with the relevant theory of evolutionary ecology on the part of many of the contributors. Consider three specific circumstances that illustrate this difficulty. First, the distinction between  $r$ - and  $K$ -selection is central to some of the chapters and is mentioned in most of the others. In recent years a lore has been fabricated concerning the life history traits that are supposed to evolve under  $K$ -selection as distinct from  $r$ -selection. The concept of  $K$ -selection and its extensions are well defined only in the context of density-dependent selection; to have a carrying capacity means there is some form of density dependence. Yet the actual theory of density-dependent selection is based on the standard dis-

crete-generation model of population genetics and simply does not address the relationship of life history characteristics to density-dependent selection because the models do not involve age-structured populations. On the other hand, the theory to date dealing with selection as it affects age-structured populations does not involve density dependence—it adds genetics to the standard density-independent model of demography. This theory does appear to be able to account for the observed correlations between life history traits and environmental disturbance—all without reference to density dependence and perforce  $K$ -selection. The lore of  $r$ - and  $K$ -selection is a separate matter from the actual theory on this topic and it stands or falls independently. In this regard the third chapter, on "bionomic strategies," should be read with particular caution.

A second illustration of the neglect of evolutionary ecology is to be found in the discussion of mutualism in the fourth chapter. It is known empirically that there are more mutualistic associations in the tropics than in comparable temperate habitats. The suggested explanation is that mutualistic interactions lead to a weakly stable equilibrium point for the coexisting species. Hence, it is suggested, such associations do not persist in strongly fluctuating environments. But it has been demonstrated that the condition for the evolution of a mutualistic strategy cannot be easily satisfied if the potential host species in the association has a high turnover. From evolutionary considerations there should not be any mutualistic associations in temperate or highly fluctuating habitats; and, if there is not, the issue of ecological stability can rarely if ever arise. Thus an evolutionary explanation appears to preempt one based on population dynamics alone. Incidentally, most ecologists are unaware of the important theoretical work on symbiosis, including mutualism, by Kostitzin in the 1930's.

A third illustration is the pointed remark by Graeme Caughley in concluding his chapter on plant-herbivore systems. He writes that he awaits the time when population geneticists "grow weary of their pivotal assumption that a population has no dynamics" and when population dynamicists "abandon the belief that a population has no genetics." One need wait no longer; there already is a rich and growing literature that has answered this challenge.

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