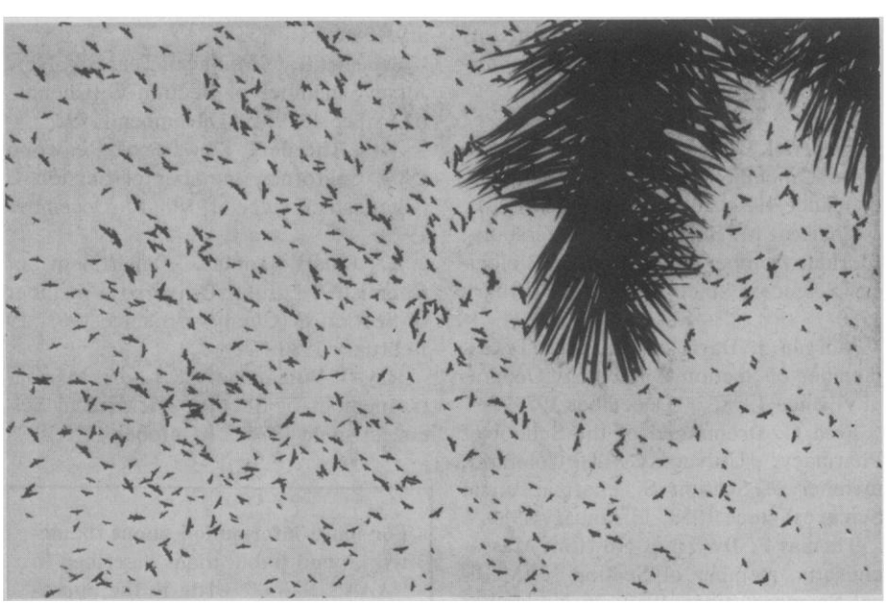
Book Reviews

Birds of Prey

Population Ecology of Raptors. IAN NEWTON. Illustrations by Jim Gammie. Buteo, Vermillion, S.D., 1979. 400 pp. + plates. $35.

In recent decades, raptor populations have become widely recognized as "ecological barometers" revealing perturbations in natural ecosystems. The misfortunes of species such as the peregrine falcon, osprey, and bald eagle played a key role in highlighting the dangers of chemical pollution, and evidence of the devastating effect that organochlorines and heavy metals could exert on raptor populations eventually led to restrictions on their use. Yet, for all the attention that has been focused on birds of prey as a result of the environmental movement, research on raptor populations has so far contributed surprisingly little to the mainstream of ecology. Perhaps because there has been no synthesis of the considerable information recently amassed by raptor biologists, the important contributions that studies of raptors can make have been overlooked. Ian Newton has filled this void with a volume that should inspire avian population ecologists to look more closely at raptors as potential subjects for certain types of studies and encourage raptor biologists to expand their horizons.

Relying on an extensive review of the raptor literature as well as his own impressive fieldwork, Newton has produced a balanced and well-organized synthesis that is reminiscent of the classic ornithological works of David Lack, who was Newton's teacher at Oxford. One possible limitation is that Newton rarely introduces comparative material from ecological studies of other birds, though the book clearly reflects his broader knowledge of avian population ecology. There are two chapters dealing with social organization and spacing behavior, two on density regulation, five on various aspects of breeding, two on movements, one on mortality, and three on the effects of human persecution and organochlorine chemicals and other pollutants on raptors. Finally, there are two chapters on conservation and management. An enormous quantity of information is condensed in 68 tables grouped at the back of the book, and 50 figures and 32 plates are scattered throughout the text. Unfortunately, the plates, which are of good quality and often illustrate pertinent points, are arranged without relation to the adjacent text.



"Broad-winged Hawks migrating over Ancon Hill, Panama. On their way between North and South America these birds form a concentrated stream, passing each October/November within 5 km of Panama City. Most Broad-winged Hawks pass this way, as do Swainson's Hawks; totals of 395,000 and 344,000 were counted in 1972." [Photo and details, N. G. Smith, from *Population Ecology of Raptors*]

Few raptor biologists can resist promoting their pet solution to the puzzle of why female raptors are larger than males and why the extent of this reversed size dimorphism is closely related to the diet of the species; Newton is no exception. In his opening chapter he reviews previous theories and then proposes his own. It is based on the argument that raptor species preying on agile, fast-moving birds (the most dimorphic raptors) have fewer competitors than those preying on slow-moving invertebrates and mammals. Reduced interspecific competition permits bird-eaters to exploit a wider feeding niche, which provides a greater opportunity for diet division between the sexes through the evolution of sexual size dimorphism. Why females should consistently be the larger of the sexes remains somewhat obscure, but the ecological consequences are well documented.

Newton's treatments of dispersion, fecundity, mortality, and population regulation are rather traditional. For the most part he has used raptors to confirm a wide variety of trends that have already been established with other animals. Nonetheless, I doubt that any other group of birds could have served to illustrate with such clarity so many principles of population ecology. Even as a raptor biologist, I was surprised by how much we actually know about these birds. Although Newton reveals nothing novel, he suggests that the study of raptor populations may contribute significantly to our understanding of population regulation.

Perhaps because he has written the book for a wide audience, Newton may frustrate some ecologists by avoiding widely accepted terminology. For example, nowhere in the book are "numerical and functional responses" or "compensatory and additive mortality" used, though the phenomena to which the terms refer are discussed in detail.

Newton's chapters on conservation provide a sobering chronicle of the relationship between humans and raptor populations. His documentation of the massive persecution that many raptors have withstood for centuries while maintaining stable populations underlines the resilience of certain species. It is remarkable, for example, that recovery rates for banded raptors in Europe are higher than for many game birds and waterfowl that

are exposed to regular hunting seasons. Newton also provides optimistic evidence that certain raptor populations decimated by persistent chemical pollutants are recovering now that the use of these chemicals has been curtailed.

Captive breeding and reintroductions of endangered raptors, especially the peregrine falcon, have been much in the news lately. Newton points out that the techniques involved, though still largely unproven, offer perhaps the only hope for certain endangered species. Falconry, perhaps the oldest relationship humans have with raptors, is surprisingly not discussed directly. A scholarly discussion of the negligible impact that falconry has on raptor populations might have helped quell lingering opposition to the sport.

Raptors enjoy an impressive following these days. For example, the 1979 meeting of Raptor Research Foundation, an organization of raptor biologists, attracted more participants than the combined attendance at the meetings of the three major ornithological societies of North America. This book is obviously essential reading for all raptor biologists and avian population ecologists, but Newton's lucid style makes it of value also to the growing number of naturalists who enjoy these impressive birds and wish to learn more about them.

STANLEY A. TEMPLE
Department of Wildlife Ecology, University of Wisconsin, Madison 53706

Population Biology

Theory of Population Genetics and Evolutionary Ecology. An Introduction. JONATHAN ROUGHGARDEN. Macmillan, New York, and Collier Macmillan, London, 1979. xii, 634 pp., illus. $24.95.

Over the last ten years, there has been much discussion of the need to integrate population genetics and ecology into one field, population biology, but few attempts have been made to do this at the level of a full-length book. For this reason, Roughgarden's book, which provides a self-contained treatment of population genetics theory, theoretical ecology, and evolutionary ecology, should attract considerable attention. The author has made many significant contributions to the application of population genetics techniques to evolutionary ecology and is thus well qualified to carry out the task.

Chapters 1 through 6 are concerned with the elements of population genetics. The treatment is clearly designed for those not previously acquainted with the subject, and much of the classical algebra associated with the Hardy-Weinberg law, selection at a single locus with two alleles, and other such topics is worked out in detail. I find it surprising that genetic drift is treated by means of stochastic matrices and diffusion theory (chapter 5), with no mention of identity by descent and the inbreeding coefficient. (Identity by descent is not introduced until chapter 10.) This necessitates a rather dogmatic style, with bald statements of the mathematical results needed, rather than the fuller presentation that the inbreeding coefficient approach would permit. Similarly, neutral allele theory is treated (in chapter 6) in terms of Ewens's sampling theory, without any mention of the Kimura-Crow formula for equilibrium heterozygosity. There is no treatment of the probability of fixation of mutant genes and no discussion of molecular evolution. Frequency-dependent selection is scarcely mentioned. These omissions limit the utility of this part of the book for someone wishing to learn basic population genetics, although the topics covered are mostly lucidly presented.

Chapters 7 through 10 cover more advanced topics in population genetics, such as selection with multiple alleles, multiple loci, and quantitative inheritance. Here again there is plenty of useful material, although one might question the emphasis placed on certain aspects of the subject and the omission of others. For example, in chapter 8 the fine details of the two-locus model are presented in such profusion that the basic principles underlying the interaction of selection and linkage are obscured. The effects of selection on quantitative characters are treated by means of the "segregation variance" introduced by Bossert, and there is no mention of the work of Bulmer and Lande that renders that approach obsolete.

Chapters 11 through 14 cover some special topics in population genetics and evolutionary theory, notably the evolution of genetic systems, evolution in varying environments, and the evolution of altruism. The treatment of genetic systems in chapter 11 is rather disappointing, as the coverage is highly selective. For instance, the possible evolutionary advantages of sex and recombination are treated largely in terms of their consequences for population properties such as the rate of evolution, with little reference to selection at the level of changes in the frequency of genes affecting parameters like recombination rates. On p. 201, the problem of the evolution of gamete size dimorphism is mentioned without any reference to the theory of Parker, Baker, and Smith. Similarly, the theory of mutation rate optimization is discussed in group-selectionist terms, without reference to Leigh's work on selection on mutator genes. Selection on the selfing rate is discussed without mention of Fisher's discovery of the intrinsic selective advantage of a gene that increases the rate of selfing. Sex ratio theory is only perfunctorily mentioned.

Chapters 15 through 20 treat the ecology and evolution of single-species systems. The basic concepts of density-dependent population growth and models of selection with density dependence are presented clearly and straightforwardly in chapters 16 and 17. Chapter 18 deals with the dynamics of age-structured populations, mostly by means of continuous-time models. Indeed, on p. 328 the Leslie matrix approach is (inaccurately) described as not allowing an easy calculation of population growth and age distribution. Chapter 19 includes a treatment of selection in age-structured populations, using the Von Foerster differential equation approach to modeling continuous-time populations. This seems an unnecessarily complex method of attack. There is also a useful account of life-history evolution, although the attempt on pp. 369–370 to explain the inverse relation between reproductive value and mortality rates in children, in terms of a trade-off between reproduction and survival, overlooks the fact that human infants do not reproduce.

Chapters 21 through 24 are concerned with multispecies systems, both from the point of view of pure theoretical ecology and from the evolutionary viewpoint. Chapter 23 in particular contains an elaborate discussion of the consequences of selection for interactions between species, based largely on Roughgarden's own work. The book ends with appendixes on elementary statistics, computer programming, and stability theory. The last should be especially valuable to biology students interested in theoretical problems.

As the author states in the preface, the book contains material for two very different audiences: beginning students of the subject and advanced students and professionals. I suspect that it would have been wiser to separate this material. Both audiences will find themselves being forced to pay for material they cannot use, and the style of the book suffers