Book Reviews

Plant Populations

Perspectives on Plant Population Ecology. RODOLFO DIRZO and JOSÉ SARUKHÁN, Eds. Sinauer, Sunderland, Mass., 1984. xviii, 478 pp., illus. $45; paper, $27.50. From a meeting, Oaxtepec, Morelos, Mexico.

For many years, plant population ecology was a discipline in which hypotheses developed from animal ecology were passed down to students at the first trophic level. This volume resulting from a symposium held in Mexico on the centennial of Darwin's death establishes clearly that times have changed. The volume contains 19 papers organized in four sections: New and Contrasting Approaches to the Study of Plant Populations; The Interface between Ecology and Genetics; Plants as Integrated Ecophysiological Units; and Agronomic Implications of Plant Demography. The varied approaches and interests of the contributors illustrate the present good health and rich future of plant population ecology.

The book successfully identifies future directions for research on a number of important issues, among them competitive interactions in local neighborhoods (Turkington and Aarssen), the effects of herbivores on plant growth and survivorship (Dirzo), the evolutionary significance of sex (Antonovics), population genetic consequences of migration (Levin), and the evolution of gender allocation (Lloyd).

Several themes emerge repeatedly. Most prominent of these, at least in terms of frequency, is the ecological and evolutionary significance of plant metamerism, that is, the serial repetition of unit structures, or modules. In the foreword, Harper focuses exclusively on this topic, suggesting that modular growth provides "at least the theoretical potential for exponential increase in size (and of fecundity) and for infinite life." Dirzo and Sarukhán echo these sentiments in the introduction. In the first chapter, White traces the history of the concept of metamerism and speculates that the metameric structure of plants is under relatively simple genetic control. He concludes that small genetic changes could promote major changes in shape. In the second chapter, Bell illustrates how metamerism and clonal growth may allow plants to explore their local environments. Several other authors briefly discuss metamerism. Venable suggests that metameric construction provides greater variation in life histories, and Jefferies, Bazzaz, and Dirzo identify various factors influencing the age structure of modules within a plant.

The interest expressed in plant metamerism may signal a prominent role for this topic in future studies of plant population biology. Where it will take us is unclear. Its applicability to ecological and evolutionary problems is, at this point, rather vague. Two particular questions must be addressed in future work. First, what is the genetic basis of growth form? Rapid phenotypic change in metameric organisms following slight genetic changes (White) is not well documented. Second, what is the role of metamerism with respect to plant demography? Harper suggests, "In modular organisms demography is a science to be applied both *of* organisms and *within* organisms." This clearly depends on the kind of question one asks. There is a growing trend of applying demographic techniques developed for whole organisms to parts of organisms. For instance, Bazzaz calculates the reproductive value of ragweed leaves, with the photosynthetic rate per leaf equivalent to birth rate. Further development of the theory and methodology of within-plant demography is necessary to evaluate this kind of approach.

Demography has long played a central role in plant population ecology, and it receives considerable attention here (Sarukhán *et al.*, Dirzo, Bazzaz). The emphasis is on stage-specificity of demographic parameters, for example, survivorship as a function of size (Sarukhán *et al.*) and the causes of intrapopulation variation in demographic status, for example seedling size hierarchies resulting from asynchronous emergence of seedlings (Bazzaz). The addition of physiological links (Bazzaz, Mooney and Chiariello) provides an important glimpse of how mechanistic approaches can contribute to our understanding of plant life history. One disappointment is that the demographic data presented for perennials do not encompass the entire life history, and consequently questions concerned with the growth and dynamics of populations are not addressed. Only by identifying the contributions of particular life-history paths to population growth can the importance of life-history variation be estimated.

To complement the phenotypic analysis of plant life history, there are also discussions of the genetic basis of life-history traits (Venable, Schaal). The conclusion is that natural populations regularly contain significant genetic variation for life-history characters. This in itself is not a new finding. What is exciting is the new emphasis on determining the evolutionary significance of such variation through carefully designed field experiments (Venable). Several papers (Sarukhán *et al.*, Turkington and Aarssen) call for a stepped-up commitment to genetic demography, a field that is poorly represented at present but that is sure to play a significant role in the future.

One question raised by much of the current work in plant population biology is in full view in this volume. What evolutionary processes contribute to the genetic differentiation of populations? Through the years an intellectual schism has developed between those who stress the likely joint effects of natural selection, migration, and genetic drift and those who favor a primarily selectionist view. Most of the discussion in this volume is focused on natural selection (Bradshaw, Turkington and Aarssen, Snaydon), with little attention to other possible forces (but see Levin). This emphasis is surprising in light of the widely held belief that, because of restricted gene flow, inbreeding and drift should often play a major role in determining the genetic structure of plant populations. That view may be wrong. But I suggest that the current status of natural selection as the primary mechanism of evolution in plants comes, in part, from the uncritical interpretation of experiments that, by their design, inflate the apparent intensity of selection. For example, reciprocal transplants used to study the degree of local adaptation are often conducted on a spatial scale far surpassing the boundaries of genetically effective populations, that is, neighborhoods. This will serve to bias upward the estimated importance of local selection. Approaches that emphasize evolutionary processes within populations (Antonovics) are likely to provide the most useful information on the origin and maintenance of genetic variation.

This book had ambitious goals: to take stock of the present and to look toward

the future. It is more successful at posing problems than at solving them, and in their ambition to point the way the contributors may have made some errors in emphasis, interpretation, and methodology. Such is the case in an evolving science. This book marks the beginning of an exciting era in population biology, with an emerging role for tropical studies and an expanding link between ecology and genetics.

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Ground Squirrels

The Biology of Ground-Dwelling Squirrels. Annual Cycles, Behavioral Ecology, and Sociality. JAN O. MURIE and GAIL R. MICHENER, Eds. University of Nebraska Press, Lincoln, 1984. xvi, 459 pp., illus. $25.95. From a symposium, Banff, Alberta, Canada, Oct. 1982.

This collection of symposium papers is the first synthesis of investigations bearing on sociality of the ground-dwelling sciurids—ground squirrels, prairie dogs, and marmots—of western North America. These animals have been the subjects of many long-term investigations, which have begun to generate the basic data on kinship, spacing, dispersal, and asymmetries of behavior that are needed to test hypotheses in sociobiology. Of the 20 chapters in the volume, nine are primarily reviews; the remainder are based on original data, generally from intensive studies of individual species. The volume is an empiricist's delight. The reader is given a clear idea of what is known and what is not known about ground squirrels. All the chapters give honest critiques of existing data, and the authors frequently make suggestions for future research and call for consistency in the gathering and analysis of data (as is particularly appropriate in the case of spacing behavior, as reviewed by McLean). Although adoption of the comparative method is a strength of the volume, one deficiency is a lack of consistency in cross-referencing among chapters.

Because an understanding of sociality within any group depends on knowledge of many other aspects of its biology, Murie and Michener chose to include papers on phylogeny (Hafner), behavioral ontogeny (Ferron), life history (Heaney), and physiological ecology (Phillips, Joy, Bintz). The chapters by Ferron and Heaney compare aspects of the biology of tree squirrels and ground squirrels. In his treatment of the evolutionary relationships of the Nearctic Sciuridae, Hafner concludes that, although phyletic components may in some cases help explain interspecific differences in behavioral patterns, in sciurids there is a lack of concordance between degree of sociality and phyletic position. This sets the stage for explaining sociality in sciurids in terms of socioecological or energetic parameters.

Sociality in ground-dwelling sciurids is the major concern of the remainder of the volume, which is organized into sections on annual cycles, communication, mating systems, dispersal and dispersion, and kinship and sociality. The mix of review and data papers is effective in highlighting the questions asked by ground squirrel biologists and the results of attempts to answer them. The reviews of annual cycles (Michener), mating systems (Dobson), and dispersal (Holecamp) clearly define the limits of sociality in ground squirrels and should serve as the starting point for an understanding of their behavioral ecology. Communication is presented as the mechanism by which social cohesion is maintained, and the reviews on vocal and visual communication (Owings and Hennessy) as well as the thorny subject of olfactory communication (Halpin) are interesting and provocative.

The seven papers that report data on sociality cover a wide range of the levels of sociality found in ground-dwelling sciurids and demonstrate the rewards of long-term field investigations of single species. Here the most important theme is the role of individuals within social groups, whether the matter at issue is the ecological basis of monogamy in hoary marmots (Holmes), the functional basis of multiple mating in 13-lined ground squirrels (Schwagmeyer), settlement patterns in Columbian ground squirrels (Murie and Harris), or behavioral asymmetries based on kinship in Richardson's ground squirrels (Davis). By far the most important paper in this group is the presentation by Armitage (the dean of active ground squirrel researchers) of data collected over 20 years on patterns of residency, recruitment, and immigration in discrete populations of yellow-bellied marmots. Although it requires some effort to decipher and interpret these marmot genealogies, a fascinating tale of individual variability and its effect on population processes makes the effort worthwhile.

The volume appropriately ends with a retrospective comment by King on the importance of burrows to the biology of ground-dwelling sciurids. It was King's classic 1955 paper on social organization in a black-tailed prairie dog town that showed what could be learned by studying sciurids. Now, nearly 30 years later, with publication of this volume, we have a timely update on progress in the field. This volume will be valuable not only to mammalogists and vertebrate sociobiologists but indeed to all of those interested in the adaptive nature of sociality.

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Physiological Ecology

Seabird Energetics. G. CAUSEY WHITTOW and HERMAN RAHN, Eds. Plenum, New York, 1984. xii, 328 pp., illus. $55. From a symposium, Honolulu, Aug. 1983.

The utilization of energy by organisms is of interest to both ecologists and physiologists. As J. Wiens notes in a chapter of this volume, physiologists are concerned with how the environment influences the quantity of energy and nutrients available to an organism and how these resources are apportioned among requirements for such activities as maintenance, growth, and reproduction. Ecologists, on the other hand, wonder how metabolic requirements create demands for energy and nutrients from the environment and how the balance between supply and demand influences individual fitness. This book uses both these approaches by considering environmental relations to energy acquisition and expenditure and by using this information for the development of ecological models.

The book focuses on seabirds, a group defined on the basis of habitat rather than taxonomy. Seabirds range over about two-thirds of the world's surface, yet comprise only about 3 percent of all avian species. Representing four orders—Procellariformes (tube-nosed birds such as albatrosses), Pelecaniformes (pelicans and relatives), Charadriiformes (shorebirds such as gulls and terns), and Sphenisciformes (penguins)—these birds breed in some of the harshest environments on Earth, including Antarctica. The susceptibility of population size and distribution to regional variation in abundance of oceanic food and to periodic disturbance in availability of food, such as that caused by the El Niño