population growth. Although there are unsolved problems, incorporation of these factors into the genetical models has been so extensive that a review of the subject is badly needed. This is the purpose of Charlesworth's book.

The author begins with the basics of demography. The presentation is too condensed to serve as a first introduction to demographic theory, but those with some previous exposure to demography will profit from the treatment, since this is one of the few places where the basics are presented in an evolutionary perspective. The middle of the book is devoted to genetical evolution in age-structured populations, and an extensive final chapter surveys the theory of life-history evolution.

Charlesworth develops age-structured analogues to many of the traditional concepts in population genetics: Hardy-Weinberg equilibrium, inbreeding, effective population size, and so on. However, most of the genetical material concerns the study of selection, to which Charlesworth has contributed much. The chapters dealing with selection (3 and 4) are basically a redevelopment of Charlesworth's earlier work and, although clearer, contain almost as much mathematical detail as the original papers. The central question addressed is to what extent a single statistic can predict gene frequencies in an age-structured model, as individual fitness does in the discrete-generation models. The problem is a difficult one and was first addressed by Norton in 1928. Norton, Charlesworth, and others have found that the genotypic intrinsic rate of increase summarizes much of what is of interest concerning selection in an age-structured population. However, there are some exceptions, which Charlesworth's work points out. Rather than wallow in these exceptions, Charlesworth goes on and utilizes the intrinsic rate of increase as a sufficient parameter to study life-history evolution. It is fashionable among certain population geneticists to dwell upon the technical restrictions involved in deriving evolutionary concepts from first principles, and this tendency is represented in Charlesworth's book. The strength of his approach, however, lies in the balance between rigorous deduction of evolutionary concepts and their use in explaining organisms and their phenotypes. Charlesworth realizes that concepts that appear fragile when cast in the rigid deductive framework of population genetics can have great heuristic utility in evolutionary ecology.

Because the shift to life-history evolution in the last chapter is well motivated genetically, the theoretical underpinnings of such standard techniques in evolutionary ecology as maximizing the intrinsic rate of increase are made explicit. Such connections between evolutionary ecology and population genetics are crucial links in a synthetic theory of evolution. This chapter is the best review of life-history theory available. There has been so much loose theorizing and speculation in this area (Charlesworth is quick to point out where) that it is important to have all the correct concepts presented in one place. Some effort is made to discuss the data, but only as they bear on the theoretical points. In this regard it is disappointing how few data there actually are that bear directly on the theory, especially the reproductive-effort model.

Charlesworth's book will be a useful reference for serious students of evolutionary biology. The subjects covered are intricate, and the logical and detailed presentation will be satisfying for readers who already possess a certain amount of fascination with theory. Others may become bogged down in the mathematical technicalities and lose sight of the general points. Nevertheless, this book exemplifies both the logical development and the creative use of theory on the interface of population genetics and evolutionary ecology.

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An Ethological Problem

Olfaction in Mammals. Proceedings of a symposium, London, Nov. 1978. D. MICHAEL STODDART, Ed. Published for the Zoological Society of London by Academic Press, New York, 1980. xvi, 364 pp., illus. $63.50. Symposia of the Zoological Society of London, No. 45.

The study of olfaction in mammals is full of challenging problems, a prime example being simply to describe the message produced and to analyze its function in any communicatory act involving the use of scent gland secretions, urine, or feces. In the study of auditory communication, the sounds of an animal can be described accurately with respect to numerous parameters with equipment that is easily available to and usable by an ethologist. Sounds can then be categorized on the basis of their major characteristics, and the classical ethological questions of function, ontogeny, motivation, and evolution can be explored. In the study of olfactory communication, however, the first step, that is, the description of the presumed "signal," requires both equipment and expertise in chemistry that are unavailable to most ethologists. Thus the presumed communicatory information is usually unstudied while the behavior patterns (for example scent marking) used in the production of the message are emphasized. This is analogous to concentrating on the singing bird rather than the bird song, an approach that would be considered bizarre in studies of auditory communication.

A further factor complicating studies of olfaction is the lack of a clear correlation between an odor as perceived by the human olfactory system and the structure of the compound responsible for it. A competent student of bird song can usually look at a sonagram and know what the song sounds like. Even a chemist cannot necessarily predict the odor from the chemical structure, a problem addressed early in this volume by MacLeod.

Despite the problems it presents to researchers, olfaction is a subject of active study, as evidenced by the number of compilations of papers dealing with it that have appeared in the last decade. Yet as this and other volumes indicate, techniques of study are only slightly more advanced than they were 20 years ago, and the major problems have yet to be tackled.

This volume exemplifies some of the recent trends in mammalian olfaction research, with some authors concentrating mainly on reviewing particular topics, including the structure and distribution of scent-producing areas (Adams), olfactory influences on reproductive physiology (Milligan), the structure and function of the olfactory system (Dodd), and the chemistry of odors (MacLeod). There are also chapters specifically devoted to particular mammalian groups or species, such as carnivores (Gorman, Macdonald), ungulates (Gosling), pigs (Booth), primates (Schilling, Keverne), and lagomorphs (Bell), although these chapters vary greatly in the proportions devoted to review and to the authors' own research findings. Most of the chapters regarding particular mammalian groups are implicitly (or explicitly) concerned with the function of the various odors produced, although there are no real theoretical advances and several of the authors persist in synonymizing causation (motivation) and function, a long-standing problem in ethological research.

There are several advancing research areas that are represented in this volume. First, there are careful descriptions of when and where mammals deposit scent in nature and a fascinating attempt to correlate habitat type, phylogeny, and ecological niche with at least some aspects of the olfactory signal in a closely related group, the nocturnal prosimians (Schilling). Second, there have been some advances in understanding the chemistry of biologically important odors (Booth, Gorman) and in determining the discriminatory abilities of individuals for species-specific odors (Schilling, Gorman). But certain interesting and important advances in mammalian olfaction are barely represented, for example concerning the involvement of the vomeronasal organ in reproduction. Also, there is no summary of the available information on the chemistry of mammalian glandular secretions (the presumed "signals"), although there is a review of scent glands. Thus, although this volume contains some new and interesting research findings and several solid reviews of problems in olfaction, it does lack discussion of some major research areas.

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Seabirds

Behavior of Marine Animals. Current Perspectives in Research. Vol. 4, Marine Birds. JOANNA BURGER, BORI L. OLLA, and HOWARD E. WINN, Eds. Plenum, New York, 1980. xx, 516 pp., illus. $45.

Marine birds, though taxonomically diverse, have a lot in common. Of greatest importance is the fact that they have to breed on land and forage at sea. Natural selection may yet produce an ovoviviparous murrelet, outdoing those real species in which the chicks go to sea when two days old, but for now such a murrelet must remain in the company of Hardy's swift (D. Lack, *Bird Notes* **30**, 258 [1963]) and seabirds must nest, often colonially, on islands or coastal sites protected from terrestrial predators. There, they are accessible for the kind of studies of reproductive behavior that dominate the present book.

There has been a tardy realization that oceanic birds are an integral element in marine ecosystems, and this is reflected at the start by the stimulating though brief review by Richard Brown of seabirds as marine animals (in which, incidentally, figs. 1A and 1B have been interchanged). Further insight is provided by Bernice Wenzel, who reviews evidence indicating that albatrosses and petrels, constituting the most oceanic group of birds, really do use olfaction extensively in finding food.

Almost the whole of the rest of the book, however, relates to seabirds on their breeding grounds. The scope is further restricted by the strong emphasis on the gulls and their allies and on the temperate zone and by the lack of representation of the "British school," whose long-term population studies have made seabirds better known demographically than, perhaps, any other group of organisms apart from humans.

Many recent workers have focused on seabird reproductive behavior from the point of view of evolutionary ecology rather than ethology. Although there is surprisingly little discussion here of the adaptive value of coloniality, there is an extended treatment of reproductive synchrony by Michael Gochfeld, which left me wondering whether Fraser Darling's hypothesis on the role of social stimulation within colonies still merits so much attention. There are timely and competent reviews of breeding habitat selection (Francine and Paul Buckley), adaptive functions of development (Roger Evans), and mate selection and mating systems (George Hunt), although in the last paper the author perhaps tries rather too hard to find field data conforming to contemporary evolutionary theory.

The outstanding contribution, in my view, is Joanna Burger's long, hard look at the data and ideas relating to the transition to independence and postfledging parental care. Becoming independent is clearly a hazardous step for young seabirds competing with adults in unproductive environments; this paper, together with John Ryder's on the effects of age on breeding, leaves one in little doubt that the failure of many seabirds to breed until they are several years old, which has long intrigued ecologists, reflects the difficulty encountered by a relatively unskilled and inexperienced bird in reaching prime condition, and acquiring a mate and nest site, early enough in the season to have a reasonable chance of successful breeding.

A reflective essay by C. G. Beer on communication in gulls is of particular value as a reminder that the conclusions of rigorous ethological analysis can be conveyed in clear and elegant language; some other contributions, such as Montevecchi and Porter's study of parental investment in gannets, suffer by comparison. The final paper, William Southern's analysis of distribution and orientation of North American gulls, is flawed by presentation of banding recovery data mainly in the form of indigestible computer maps and by omission of the potentially interesting analysis of movements by age-class.

The editors of the volume have adopted a low profile, not attempting to achieve the kind of uniformity of presentation that one takes for granted in a journal, for instance in treatment of scientific names. Furthermore, they have apparently not read the proofs, with the result that the incidence of typographical errors varies wildly among the papers, reaching a peak on p. 325, where four out of eight scientific names are misspelled; my review copy is rapidly taking on the appearance of a corrected galley proof.

The reader finishes the book knowledgeable about North American seabird work and related studies elsewhere. One is left with the curious impression, however, that for most of the contributors the sea and its characteristics are almost irrelevant. It is especially striking, at a time when the economics of foraging forms a major strand in the literature of animal behavior, to find so little in this book on feeding behavior. Ways must be found to focus more precisely on the interactions of the birds with their marine resources if seabird biology is not to languish in the doldrums.

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