Avian Ecology

Habitat Selection in Birds. MARTIN L. CODY, Ed. Academic Press, Orlando, Fla., 1985. xviii, 560 pp., illus. $69.50. Physiological Ecology.

Habitat selection in birds has a long and distinguished literature with major contributions from scientists as eminent as Charles Darwin, Joseph Grinnel, David Lack, and Robert MacArthur. It is curious therefore that the subject received rather little attention through the 1970's, despite the needs of wildlife managers and conservationists for better understanding of habitat needs. The present volume perhaps signals a resurgence of interest in the topic, appearing as it does soon after the October 1984 Wildlife 2000 conference on the modeling of vertebrate habitat relationships.

The book contains 18 chapters grouped (not very well) as an introduction and three other parts, two of which cover habitat selection in specific taxa and in specific habitat types and the third of which represents "a variety of approaches" from the perspectives of theory, physiology, morphology, behavior, diet, and island biogeography. Twelve of the 22 contributors are American, eight European, and two Australian. The British and Polish schools of ecology are the only significant omissions.

Cody contributes the introduction and two chapters on habitat selection by sylviine warblers and by birds of grassland and open country. All three contain much new material from Cody's own fieldwork, and all—especially the chapter on warblers—contain interesting insights and ideas. Unfortunately they all also suffer the complexity of diagrams familiar in Cody's publications, a feature that leads to a text too dense with information for easy reading. The density also hides a serious failing in some of the analyses, the confusion of levels of sampling. Many of Cody's protocols involve quadrat samples within habitats, and in some cases the use of these in quantitative analyses inflates apparent sample sizes and the statistical significance of the results. For example, Cody describes on pp. 101–102 an analysis of interactions between five *Sylvia* species at a site in Sweden, with results based on an impressive 1172 quadrats surveyed. Yet, according to p. 100, these results derive from only 17 pairs, two each of three species, five of one, and six of another. Where data for other censuses are presented, as in the appendix to the chapter on warblers, information on the number of territories involved is omitted. These flaws reduce many of Cody's analyses to illustrations of ideas.

John Terborgh's chapter on habitat selection in Amazonian forest, by contrast, is characterized by thoroughness and painstaking attention to detail and by the clarity of vision that often accompanies these. Terborgh's work over the last 20 years has shown South American forests to harbor the most diverse bird communities in the world, with over 500 species residing within regions as small as 10 square kilometers. Previous work detected nothing like this density and diversity, for two reasons. First, forest bird censuses depend critically on the ability to identify the songs and call notes of birds going unseen in the high canopy, and with few field guides and fewer recordings to aid them the investigators, newcomers to the region, were unprepared for the task they undertook. Second, the scale of territorial behavior of birds is an order of magnitude greater in Amazonian than in northern temperate forests. To sample 10 to 15 pairs—the sampling typical in North America—may require census plots of about 100 hectares, ten times larger than is usual in temperate zone censuses. Terborgh points out that the naive transfer of North American methods to Amazonia led to unnecessary disillusionment with the available census techniques. His conclusion should be learned by every would-be tropical ornithologist:

> The people who were studying tropical diversity . . . were in too much of a hurry. There were burning hypotheses to be tested, and quick results were desired. There was also the feeling that if one were armed with sharply focused questions, the answers could be obtained in a few weeks. The false assumptions behind this zealous attitude are now clearly apparent.

Terborgh's results suggest that the great diversity of Amazonian bird communities derives from at least four features: the greater structural diversity of the habitat, the presence of entire guilds not represented in temperate bird communities, larger guild niches supported by broader resource spectra, and tighter species packing.

An encouraging feature of the book is the convergence of ideas presented in several papers. In a number of recent papers John Wiens and John Rotenberry have emphasized how conclusions about avian habitat dependencies depend on the geographical scale of the analysis undertaken. Wiens restates these ideas in his chapter here, and they are also identified as crucial in the chapters by Burger (on marsh-nesting birds), Hutto (on migratory landbirds), Klopfer and Ganzhorn (on behavioral aspects of habitat selection), and Sherry and Holmes (on dispersion of territories in northern hardwood forests). Terborgh's conclusions also reinforce the common conclusion of multifactorial hierarchies in habitat choice.

A second recurrent theme is the scarcity of experimental manipulations of habitat and the importance of such manipulations for checking results based on correlational studies. The chapter by Alatalo, Lundberg, and Ulfstrand shows how the manipulation of nest box densities within breeding territories of the pied flycatcher *Ficedula hypoleuca* provided confirmation of the Fretwell-Lucas theory of density-dependent habitat use, and the theme also emerges in the papers by Wiens and by Sherry and Holmes and in Cody's introductory chapter and Morse's chapter on parulid warbler habitats in North America.

A third theme is a downgrading in the importance attributed to foliage height diversity and related features of habitat structure, whereas floristic diversity emerges as more important than was previously thought. This shift is in part related to the greater appreciation of the multiple demands birds make on their habitats: habitat features that are optimal at the onset of breeding may not be critical for choice of nest site or for feeding of young and may differ entirely from those that are critical in winter. The growing recognition of the complexity of habitat selection by birds is clear from this collection of chapters.

As a review of current knowledge of certain aspects of habitat selection by birds the book is broadly successful. Theoretical aspects are underrepresented, with only the final chapter by Rosenzweig going beyond presentation and synthesis of data. Similarly, the importance of temporal changes in habitat use hardly emerges, despite the dominance of the Fretwell-Lucas model in the conceptual arena. Third, few data on the relative fitness of populations in different habitats are presented and little attention is devoted to the selection of behavior of individual birds. The evolutionary *raison d'être* of habitat selection remains in need of review. Meanwhile Cody's book brings together many useful data and a wealth of ideas for future development.

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