BOOK REVIEWS

Sperm Competition and Sexual Selection.—T. R. Birkhead and A. P. Møller, eds. 1998. Academic Press, San Diego, CA. 826 pp. ISBN 0-12-100543-7. \$59.95 (cloth).

Sperm competition occurs when the sperm from two or more males could fertilize the ova of a single female. Parker (1970) was the first to focus directly on this topic, and the subject received a major boost from R. L. Smith's edited volume Sperm Competition and the Evolution of Animal Mating Systems in 1984. Smith's book predated by a year the advent of DNA fingerprinting (Jeffreys et al. 1995), which has subsequently revolutionized the study of sperm competition in many taxa, especially birds. In Sperm Competition and Sexual Selection, T. R. Birkhead and A. P. Møller update and expand upon Smith's earlier volume. In keeping with the advances that have been made in the intervening 14 years, this edited book is a monster, containing 826 pages of intriguing information about sperm competition in a wide range of taxa.

"Wide-ranging" is an apt description. Only 43 pages of the 826 are explicitly about birds. Two other chapters, Møller's chapter (no. 2) on sperm competition and sexual selection and Wright's chapter (no. 4) on paternity and paternal care, include many bird examples, but the rest of the book focuses on other organisms. There are chapters on plants, mollusks, spiders, insects, fishes, amphibians, reptiles, two chapters on mammals, and three chapters that cut across taxa but emphasize organisms other than birds (e.g., one on external fertilizers, one on simultaneous hermaphroditism, and one on female roles in sperm competition, in which insects dominate). So why should ornithologists bother to read this book, let alone buy it?

It depends on what kind of ornithologist one wants to be. It is my, entirely biased, opinion that the study of sperm competition has led to the most important revolution in ornithology in the past 20 years. Our view of the ways in which male and female birds interact over breeding has been radically altered during this time. Studies of birds and the ideas of ornithologists are a conspicuous part of the general literature on sperm competition. And yet, our understanding of sperm competition in birds is limited in some odd ways in which comparisons with other taxa may be instructive. A conspicuous example-to date, there is no evidence in birds of the type of complex morphological adaptations to sperm removal by males (e.g., spines on penises) or of sperm manipulation by females (e.g., muscle control of sperm storage affecting sperm displacement) that occurs in many insects (Chapter 10). Why not? Knowledge of sperm competition in other organisms may help to suggest answers to such questions.

The non-bird chapters in this volume present an array of interesting approaches to sperm competition. Geoff Parker opens this book with a summary of a general ESS model of how sperm competition shapes allocation of resources to the number of sperm released per mating. This chapter takes some considerable effort to read, and some occasional errors make the meaning even harder to grasp. For example, a sentence in the legend to Figure 1.1 claims that selection favors values of sperm allocation higher than a particular value $[x_2]$. Unfortunately, the figure clearly indicates the opposite; values lower than $[x_2]$ are favored. Nevertheless, a number of fascinating ideas on conflicting demands emerge from these models, as well as insights about how mechanistic constraints (e.g., the amount of information males have about female mating history) can influence optimal allocation of sperm.

Parker's chapter is focused on males (but contains the structure to include females in the game). Eberhard (Chapter 3) counters with a conceptual and empirical argument focusing on females. The major thesis here is that female reproductive tracts, at least in species which fertilize eggs internally, provide the environment in which sperm competition takes place. Thus, females seem likely to influence the process and outcome of sperm competition, and a body of circumstantial evidence supports this view. Eberhard also acknowledges that in this game between the sexes, both sexes can exert influence, and the interaction may be complex. For example, Eberhard argues that females can sometimes benefit if male traits lead to a direct cost to her because her sons will also have those traits. However, Eberhard tends to use metaphors (e.g., females are the playing field on which male games are played out) too often when illustrating his ideas, and so he never develops a suitable paradigm that fully captures the intricacies of male-female conflict and produces clear, quantitatively testable predictions. That framework lurks between the lines, both in this chapter and throughout this book, but remains incompletely formed.

By reading chapters on a diverse set of taxa, I found I began to think on broader terms, and to have insights about birds that might not have occurred otherwise. Don Levitan's chapter on external fertilizers (Chapter 6) is a case in point. Fertilization is a different process when it occurs out in the environment. Described in this chapter is an interesting result from studies of sea urchins; larger eggs tend to be fertilized more quickly than smaller ones, presumably because larger eggs are a bigger target for sperm that have been dissipated in the environment. Birds, of course, are internal fertilizers. Yet sperm limitation, via either occasional male infertility or depletion from frequent copulation, might occur in birds. It seems unlikely that in birds this sort of sperm limitation would exert similar pressures to increase ova size, but the possibility makes one wonder. Another example comes from studies of the accessory components of semen in mammals (Chapter 16). Besides containing the products which form copulatory plugs, semen in some mammals, including humans, contains hormones which might influence the action of muscle contractions within the female reproductive tract. Such glands appear absent in birds. Why? And, does this mean birds have no components in their ejaculates other than sperm? This book is full of additional examples of how research in other taxa can lead to novel ideas about birds.

Comparisons aside, what can we learn directly about birds in this book? Three chapters contain considerable information on birds. In the first, Chapter 2, A. P. Møller folds sperm competition into a general theory on sexual selection. The basic premise of this chapter is excellent. Sexual selection is composed of a number of components, all having to do with the process by which males and females encounter one another, transfer gametes, and combine them. Sperm competition fits directly into this sequence. However, there is room for confusion in Møller's broader view of sexual selection, summarized in Figure 2.1. The possibility that some components are under natural selection or covary (e.g., Arnold and Wade 1984) is not mentioned. In addition, Møller ignores the fact that traits such as parental investment confound fitness and heritability, a problem that quantitative geneticists have been wrestling with for some time. Nevertheless, Møller's general approach is useful, and he presents a wide variety of evidence, dominated by birds, to support the idea that sperm competition leads to sexual selection. This chapter contains a good survey of exciting hypotheses about the ways multiple mating can influence males and females. In most cases, only data supporting each hypothesis are presented, whereas examples of inconclusive or opposing data are not. Hence readers should view this chapter as a survey of neat ideas rather than a critical and balanced review.

A distinctive feature of birds is the preponderance of biparental care. It is therefore natural that studies of birds would dominate the literature on how paternity affects paternal behavior. In Chapter 4, J. Wright reviews the ideas and evidence for an effect of paternity. Any ornithologist interested in mating dynamics or parental care should read this chapter, as it summarizes nicely how this topic has benefited from integrating theory and empiricism, and how intriguingly complicated is the relationship between paternity and paternal care. While I might argue with a few of the details here, by and large the chapter demonstrates clearly that paternity could affect paternal care. This effect also depends on the circumstances, and we do not know yet what circumstances prevail among most birds. Wright gives a sufficient review of theory to illustrate that empirical studies will have to collect a great deal of contextual data in order to test details of hypotheses about paternity and paternal care. A review of empirical work, both correlative and experimental, reveals that we are nowhere near to adequately testing theory. In addition, the reader will see that the paternity-paternal care issue cuts across other areas of study, such as kin recognition (relevant to whether or not males can detect non-descendants), sensory-hormone integration of parental care behavior (relevant to how cues of paternity might influence patterns of care), and life history studies (relevant to age-related patterns of paternity and paternal care). Using this chapter as a guide, students of avian parental care should have no trouble finding new types of data to collect about this important trait in birds.

Finally, in Chapter 14, T. R. Birkhead describes the mechanisms and function of sperm competition in

birds. Birkhead focuses on two major questions: (1) why do females copulate with multiple males? and (2) what are the mechanisms that determine how copulations translate into fertilizations? The chapter covers a number of other topics as well: male and female reproductive tracts, paternity guards, techniques of determining paternity, and data on patterns of paternity. One emergent result is that there is tremendous variation among bird species in almost every aspect of sperm competition. Why do species differ so much in the types of paternity guards, the intensity of particular behaviors, whether females seek or merely accept copulations from other males, and in the patterns of multiple matings? This chapter raises these functional questions, but is not sufficiently critical of much of the material it presents. An example is illustrated by Table 14.2, which is titled "Studies in which females do and do not prefer better quality males as EPC partners." In about two-thirds of the studies listed, there is no direct evidence in cited, or related papers, that females are "preferring" anything-the patterns could come from differences among males in the ability to harass females into engaging in EPCs. In addition, no study in birds has demonstrated that EPCs all occur in the same way. So, in species like the Blue Tit (Parus caeruleus), in which females have been seen initiating EPCs with males (Kempenaers et al. 1992), we do not know that all EPCs are achieved that way. House Sparrows (Passer domesticus) and Red-winged Blackbirds (Agelaius phoeniceus) show tremendous variability in how EPCs occur (Møller 1987, Westneat 1992)-variation which suggests that the fitness consequences of extra-pair behavior for both males and females are far more complex than presented here.

Birkhead's review of mechanistic issues is more complete. Alternative models of sperm dynamics and female control are described. The available data support a passive loss model of sperm competition, in which sperm numbers slowly decline within the female oviduct, and hence give rise to last male precedence through a numerical advantage. These studies have led Birkhead to question the popular idea of an "insemination window" after egg-laying in birds. In addition, Birkhead reviews the evidence for cryptic female control of fertilization in birds and finds no support for that possibility. As a whole, these studies are exciting, but I would quibble with Birkhead on one point. Early on, he states that we are reaching a reasonable understanding of the dynamics of insemination and fertilization in birds. In fact, we have good information on only 3-4 species, none of which have the mating patterns of rampant extra-pair paternity which is causing such a stir within ornithology. Given the variation within and among species in male traits linked to sperm competition (e.g., cloacal protuberances; Sax and Hoi 1998), I will not be surprised if new female mechanisms are uncovered in the future.

Despite some words of caution, I heartily recommend this book to any ornithologist who wants to understand how sperm competition has shaped the reproductive traits of birds, and is willing to find new ideas about birds in the studies of other taxa. It is my view that only by comparisons with other taxa can our studies of birds be made more relevant and our understanding of their unique features made clearer. All scientific libraries should have a copy. Individual ornithologists interested in reproductive traits should too, although there is a cost; carrying it around in public places (e.g., barber shops and airport lounges) with the title conspicuously displayed can generate some odd looks.— DAVID F WESTNEAT, Center for Ecology, Evolution, and Behavior, T. H. Morgan School of Biological Sciences, 101 Morgan Building, University of Kentucky, Lexington, KY 40506-0225, e-mail: biodfw@pop.uky.edu

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Population Limitation in Birds.—Ian Newton. 1998. Academic Press. San Diego, CA. x + 597 pp., 110 text figures. ISBN 0-12-517365-2. \$79.95 (cloth). ISBN 0-12-517366-0. \$49.95 (paper).

In 1954, David Lack published The Natural Regulation of Animal Numbers marking the beginning of the modern approach to understanding what factors control animal populations. Lack stood at the juncture of two paradigms: the earlier emphasized natural history and description, the latter focused on quantitative analysis within an evolutionary framework. In Natural Regulation, Lack intertwined good natural history with just enough quantitative theory to develop a rational argument of how populations of animals were regulated. His theory was multifaceted: animal populations are kept in check by the interaction of numerous environmental forces, including available food, weather, predation, and disease. Darwin's fundamental observation that populations could not grow without bound emerged under Lack's influence as a full-fledged field of ecological research.

The large share of data cited by Lack in support of his arguments were from bird populations. Since Lack, ornithologists have attacked the problem of population regulation with zeal. Drawing upon the wealth of data published since Lack's days, Ian Newton has carefully attempted to flesh out the details of the rough outline proposed by Lack. The synthesis that emerges from Newton's treatment is grounded on two major premises. The first is that behavioral attributes of birds directly determine how bird populations react to changes in resources. Within a population, individual birds interact with one another to establish dominance hierarchies. Existence of dominance hierarchies allows dominant individuals to claim territories in the best habitat or the safest positions within a flock or colony. Prime spaces make dominant individuals less likely to encounter extreme conditions. When densities rise above those that can be supported by a given environment, dominant individuals tend to survive, whereas subordinates suffer death or must move elsewhere. The second major premise is that, given such socially structured populations, many environmental conditions interact to limit populations to a subset of individuals that could otherwise survive. Like Lack, Newton individually considers the major regulating processes: food supply, nesting habitat, predators, and pathogens. Unlike Lack, Newton adds important chapters on human-generated regulation processes: hunting, pest control (yes, some people actually consider birds to be pests), and introduced environmental toxins. Such chapters could not have been written by Lack: the problems they identify have emerged only in the last few decades as important forces capable of controlling bird populations.

Most sobering is Newton's final chapter on extinction. He estimates that 127 (phenetic) species of birds have gone extinct since 1600. Over 90% of these were island endemics. Some of the most striking examples of avian adaptation and evolution have been lost due to human alterations of fragile island ecosystems. Newton examines the significance of recent trends in habitat fragmentation from a metapopulation perspective to underscore the importance of island extinctions. Human activities not only directly impact bird populations, but by preempting so much of the earth's productivity, humans have created vast expanses of habitat archipelagos within which bird populations are more vulnerable to the vagaries of environmental change.

Newton provides an excellent review of European literature regarding population limitation. Much of what we know about bird populations has come from the many long-term population data sets obtained from carefully conducted research in western Europe and Great Britain. Less adequately covered are studies from North America, though long-term data sets are less common here. Studies of Australian bird populations are also under-represented. Perhaps the greatest disappointment is coverage of literature from tropical regions, particularly the Neotropics. Admittedly, literature on avian populations in the Neotropics is scant compared to the wealth of information from temperate regions, but some mention of this discrepancy would be in order. From a different perspective, the paucity of information on tropical bird populations indicates that there is ample opportunity to develop tests of Newton's general model of population regulation in birds. Tropical bird populations may be ideal for such tests because so many species of tropical birds have evolved elaborate behavioral mechanisms to sort out dominance both within and among species.

In summary, *Population Limitation in Birds* provides an extremely valuable resource for libraries of all sorts. Its synthetic view of the role of dominance behavior in the regulatory process should stimulate further research on the interaction between individual behavior and population dynamics. Such cross-scale thinking is vital if we are to develop a more sophisticated understanding of bird populations. And there is little question in the minds of most ornithologists that such a sophisticated understanding is necessary given the increasing pressures that human populations are placing on avian diversity.—BRIAN A. MAURER, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, e-mail: maurer@ msu.edu

A Guide to the Birds of India, Pakistan, Nepal, Bangladesh, Bhutan, Sri Lanka, and the Maldives.—Richard Grimmett, Carol Inskipp, and Tim Inskipp. 1999. Illustrated by various artists. Princeton Univ. Press, Princeton, NJ. 888 pp., 153 color plates, numerous drawings, tables, and range maps. ISBN 0-691-00687-3. \$85.00 (cloth).

Bird watchers in the Indian subcontinent have long awaited a well-illustrated, comprehensive yet concise guide to all 1,300-odd species. This book finally appears to have met that need, albeit its size $(25 \times 17 \times 5.5 \text{ cm})$ and weight (>2 kg) hardly conform to the conventional concept of field guide. Although illustrations of Indian birds in field guide style have appeared before, this is the first time a detailed text focusing on field identification has been combined with a comprehensive set of high-quality illustrations, and, as such, this book represents a milestone in South Asian bird literature.

The taxonomic sequence and scientific and English names follow An Annotated Checklist of the Birds of the Oriental Region (Inskipp et al. 1996, Oriental Bird Club, Sandy, Bedfordshire, U.K.). An introductory section deals briefly with criteria for inclusion of species, descriptive terminology, climate and bird habitats in the region (including conservation issues) and more. and includes lists of birds-related organizations and a glossary. The color plates are grouped together separate from the main descriptive text and a list of references and an index of bird names are given at the end. About two or three species are covered per text-page, but some species (e.g., Yellow-legged Gull Larus cachinnans, Booted Warbler Hippolais caligata) are allocated more space, while certain others (e.g., Andaman Hawk Owl Ninox affinis, Persian Shearwater Puffinus persicus) are dealt with briefly, reflecting differences in complexity of identification of different species. Following the English and scientific names (with alternate names used in selected works listed on p. 11) and plate reference, each species account covers identification, voice, habits, habitat, breeding, distribution and status, and references (some omitted by oversight in the references list). The identification section draws attention to diagnostic features, differentiates clearly between similar species, and discusses subspecies of polytypic species. However, not all subspecies are indicated in some cases (e.g., Black-rumped Flameback *Dinopium benghalense*, Greater Flameback *Chrysocolaptes lucidus*), which may cause some confusion. A range map faces each species account. Those maps, unfortunately, have been reduced in size almost beyond the point of practical value. Some distribution/ status symbols cannot be distinguished without mag-infication.

All but three species included in text are illustrated in color. The plates are the work of 12 well-known bird illustrators and are of exceptional quality overall. Most species are illustrated with at least two or three figures and many species (e.g., raptors) with considerably more. Captions facing figures summarize key features and distribution. Some errors are noticeable: comb in male Sri Lanka Junglefowl Gallus lafevetii (plate 5) should be larger; gloss on cormorants Phalacrocorax spp. (77) exaggerated and too pale; legs of Black Ibis Pseudibis papillosa (81) should be red; dippers Cinclus spp. (95) are disproportionate; Brachypteryx major major and B. m. albiventris (99) switched in caption; black head of Black-headed Bulbul Pycnonotus atriceps races (117) too restricted; and Sand Lark Calandrella raytal (138) should show white outer rectrices.

The precursor of this book is the Inskipps' A Guide to the Birds of Nepal (1985; C. Helm, London) and evidently the authors are most familiar with Himalavan avifauna. However, the book is relatively weak in coverage of southern forms. Many birds occurring in the Chennai (obsoletely indicated as "Madras" on p. 8) area are shown absent (e.g., Clamorous Reed Warbler Acrocephalus stentoreus, Zitting Cisticola Cisticola juncidis, Lesser White-throat Sylvia curruca, Chestnuttailed Starling Sturnus malabaricus, Thick-billed Flowerpecker Dicaeum agile) or shown present though absent (Brown-headed Barbet Megalaima zeylanica). Similarly, common birds here are deemed scarce (Brown and Blue-throated Flycatchers Muscicapa dauurica and M. rubeculoides) and rarities indicated common (Red-necked Phalarope Phalaropus lobatus); Yellow-throated Bulbul P. xantholaemus range in text omits Kerala; breeding range of Honey Buzzard Pernis ptilorhyncus and Grey-headed Fish Eagle Ichthyophaga ichthvaetus should include the Anaimalai Hills (R. Kannan, 1998. J. Bombay Nat. Hist. Soc. 95:193-214); and description of Eurasian Thick-knee's (Burhinus oedicnemus) call (p. 488) is incomplete.

The range maps accompanying the species accounts are a welcome feature. Unfortunately, many of those maps are marred by errors. Some status symbols (two different asterisks) or shading (passage migrant and former distribution) are similar and have been switched frequently or used inappropriately (e.g., some seabirds); some maps indicate solid dots, a symbol which is not keyed on p. 15. In a number of cases, maps contradict information in text or plate captions, with the text appearing more reliable than maps. Apparently, the different authors worked on different sections and failed to cross-check for consistency. Examples of such discrepancies relating to Sri Lanka include Black-capped Kingfisher Halcyon pileata (visitor), Changeable Hawk Eagle Spizaetus cirrhatus (resident), and Spot-winged Thrush Zoothera spiloptera (endemic resident). Sri Lankan and Andaman/ Nicobar endemics are mapped on larger scale, but some ranges are incorrect (e.g., Sri Lanka Junglefowl G. lafeyetii, Sri Lanka Grey Hornbill Ocyceros gingalensis, Sri Lanka Hanging Parrot Loriculus beryllinus).

The authors have used museum specimens, personal field experience, and published and unpublished observations of others. In some cases undue weight has been given to stray sight records. At least one species (White-winged Scoter Melanitta fusca, p. 377) is included based on an unpublished sight record, yet, p. 11 states some species were omitted because "no details have been published." Similarly, the Great Hornbill Buceros bicornis (p. 397) is erroneously shown in c. India, far from its known range and appropriate habitat, and the Little Pied Flycatcher Ficedula westermanni (p. 638) described as wintering in "plains south to Tamil Nadu," both based on questionable single sightings. The reference list includes many unpublished survey reports and trip lists. Until local birdrecords committees are established to evaluate sight records, it would be wise to exercise caution in their interpretation. It is not clear how unusual sight records were evaluated before their acceptance.

Some incorrect past records have been re-evaluated and expunged (e.g., Black-nest Swiftlet Collocalia maxima, p. 424), and records attributed to R. Meinertzhagen are justifiably treated with caution. However, in some cases the book diverges from generally held position (e.g., S. Ali and S. D. Ripley's Handbook of the Birds of India and Pakistan, Oxford Univ. Press, Oxford, 1967–1974), without adequate explanation for the change. For example, the Handbook indicates breeding populations of the Black Baza Aviceda leuphotes in south India, yet here it is regarded as winter visitor only. References to unlisted works "in preparation," as in this particular case, do not offer much clarification.

The change in scientific name of White-faced Starling *Sturnus albofrontatus* (G. F. Mees 1997, *Bull. Brit. Ornithol. Club* 117:67–68) evidently appeared too late for inclusion. The incomplete entry for Moluccan Scops Owl *Otus magicus* (p. 431) suggests it was added late in the book's production, which is puzzling since its inclusion is based on a 1980 publication. Many alternate names listed under individual species are incorrectly attributed to works listed on p. 11 (e.g., D. P. Wijesinghe 1994 [not 1991!], *Checklist of the Birds of Sri Lanka*, Ceylon Bird Club, Colombo, Sri Lanka).

Despite the plethora of minor errors, this is an outstanding compendium and fills a long-felt need for a complete illustrated guide to Indian birds that focuses specifically on field identification. Its shortcomings only serve to highlight the difficult task of collecting, organizing, and presenting in one volume information on nearly 15% of the world's avifauna. The splendid color plates and detailed descriptions will make this indispensable to the further study of the subcontinent's birds. While Ali and Ripley's *Handbook* will remain the standard general reference to South Asian birds for many years, this new book will establish itself as the most useful work for their field identification.— RAGUPATHY KANNAN, Department of Biology, Westark College, Fort Smith, AR 72913, e-mail: rkannan@systema.westark.edu and D. P. WIJESINGHE, Department of Biology, City College/CUNY, New York, NY 10031, e-mail: dpwcc@cunyvm.cuny.edu

The Birds of St. Helena.—Beau W. Rowlands, Trevor Trueman, Storrs L. Olson, M. Neil McCulloch, and Richard K. Brooke. 1998. BOU Checklist No. 16, British Ornithologists' Union, Tring, U.K. 295 pp., 50 color plates, 3 text figures. ISBN 0-907446-20-5. \$38.00 (cloth).

This excellent book is packed with information on all aspects of the ornithology of St. Helena, a very isolated island in the Southern Atlantic Ocean. St. Helena was spared from human presence until AD 1502, when the native flora and fauna began a rapid decline. The authors document in carefully referenced detail the past five centuries of St. Helena's changing avifauna, now dominated by introduced species.

The excellent introductory chapters review topics such as geography, geology, climate, the history of ornithology, zoogeography, and conservation. The species accounts ("Systematic list") cover all native or exotic species of bird recorded on or within 200 nautical miles (370 km) of St. Helena. The 11 appendices consist of 55 fact-filled pages on topics ranging from extinct species to vagrant landbirds to a chronological list of 142 ornithologically significant visitors to St. Helena. The 50 color photos do a good job of depicting the island and some of its birds.

Our understanding of the tragic loss of birdlife on St. Helena is bolstered immeasurably by the paleontological studies of Storrs L. Olson. The pre-human avifauna of St. Helena featured eight extinct, presumably endemic species (two petrels, a shearwater, two rails, a pigeon, cuckoo, and hoopoe) and four other breeding species of seabirds that still exist elsewhere but are no longer found on the island. Most of these fascinating species probably were lost during the first decades of human influence, including the flightless rails *Atlantisia podarces* and *Porzana astrictocarpus*, the enigmatic cuckoo *Nannococcyx psix*, and the weak-flying hoopoe *Upupa antaios*.

What a wonderful place St. Helena must have been before mice, rats, cats, dogs, rabbits, pigs, sheep, goats, cattle, and donkeys took over. The only indigenous resident landbird that survives today is an endemic plover known as the Wirebird (*Charadrius sanctaehelenae*), with a total population of ca. 500. Most breeding species of seabirds are confined to small offshore rocks. Nearly the entire landscape is anthropogenic. Today's conservation efforts, while important and admirable, have come 500 years too late to save much of the indigenous flora and fauna.

As far as I can determine, The Birds of St. Helena

is remarkably free of errors. The authors are to be congratulated for producing a book that will be important to anyone interested in island birds. I only wish that similarly thorough compilations were available for

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most other oceanic islands.—DAVID W. STEADMAN, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, e-mail: steadman@flmnh.ufl.edu