

## REVIEWS

EDITED BY BRUCE M. BEEHLER

*The following reviews express the opinions of the individual reviewers regarding the strengths, weaknesses, and value of the books they review. As such, they are subjective evaluations and do not necessarily reflect the opinions of the editors or any official policy of the AOU.—Eds.*

*To present a wide spectrum of opinion, we have solicited three reviews of Sibley and Ahlquist's "Phylogeny and Classification of Birds: A Study in Molecular Evolution" for your consideration.—Eds.*

**Phylogeny and Classification of Birds: A Study in Molecular Evolution.**—Charles G. Sibley and Jon E. Ahlquist. 1990. New Haven and London, Yale University Press. xxiii + 976 pp., 385 text figures. ISBN 0-300-04085-7. \$100.00.—For the past dozen years Charles Sibley and Jon Ahlquist have intrigued ornithologists with their quest for a phylogeny and classification of the extant birds, using the technique of DNA-DNA hybridization. In many papers and lectures they promoted this approach and reported their results, stimulating both enthusiasm and skepticism. Their efforts have culminated in this massive work, which reviews and summarizes their findings. How close have they come to their goal? How will their work affect the future of avian systematics? I will examine these questions from the viewpoint of an evolutionary morphologist.

Several chapters provide a biochemical background for the use of DNA-DNA hybridization in estimating phylogeny. This is not my field, and I will let others discuss it. Suffice it to say that the technique measures how much the DNAs of different species have changed since they diverged from their last common ancestor. Because this genetic distance increases with time, the method provides a basis for inferring the phylogeny of a group from a matrix of the genetic distances separating pairs of species.

*Phylogeny.*—The heart of the book is a section of more than 400 pages with accounts of avian groups organized into subsections. Each begins with a new classification based on Sibley and Ahlquist's phylogeny, followed by a synopsis of morphological characters used in previous classifications. These are valuable summaries of scattered information, although it is unfortunate that the characters are not divided into those that are diagnostic of a group (synapomorphic) and those that are merely descriptive. Next follows a historical review of the classification of the group; these accounts make the book a major treatise on the history of avian classification. Finally, the authors present their DNA analysis augmented by figures of experimental results (DNA melting curves) and phylogenetic trees. The entire phylogeny is depicted in segments that extend for 31 pages, representing an analysis by the average linkage (UPGMA) statistical

method. Some 27 smaller phylogenies, based on other algorithms, are also illustrated.

Many of Sibley and Ahlquist's groups conform to earlier ideas. The monophyletic ratite assemblage is retained as the sister group of the tinamous. This corresponds to the old concept of "paleognathous" birds, but the counterpart "neognathous" assemblage is paraphyletic. On the other hand, the buttonquails (Turnicidae) have resisted analysis, and Sibley and Ahlquist do not solve the problem. Other groups, whose affinities were ambiguous or not agreed on, are supported by the DNA evidence, including the grouping of the owls with the nightjars, and the swifts with the hummingbirds.

Some familiar groups are fragmented, and each reader will probably find some arrangements to question. For example, Sibley and Ahlquist break up both the traditional Coraciiformes and the Piciformes, which work in my laboratory has supported as being monophyletic. In these situations one should keep an open mind and weigh the opposing information. On the one hand, the morphological data supporting monophyly of the traditional Piciformes are compelling, involving a large, integrated character set (Raikow and Cracraft 1983). On the other hand, coraciiform monophyly is supported by only a few nonexclusive morphological characters, and we concluded that new data might make it necessary to abandon the position that the Coraciiformes is monophyletic (Maurer and Raikow 1981).

Not all areas are discordant, however. There is a high level of congruence between my work on the basal phylogeny of the passerine birds (Raikow 1987) and that of Sibley and Ahlquist, except in one instance. The morphological analysis places *Acanthisitta* as the sister group of the oscines. The DNA studies place it either as the sister group of the other suboscines (KITCH and UPGMA analyses, Figs. 344, 369), or yield a trichotomy (FITCH, Fig. 343). On p. 582 Sibley and Ahlquist misinterpret this trichotomy to mean that *acanthisittids* are the sister group of the other passerines. Otherwise, the same branching history is revealed by both studies. Thus, the real test of phylogenetic proposals, congruence, is largely met in this instance, lending strong support to the idea that our current understanding of basal passerine phylogeny, so different from traditional concepts, is historically accurate (Raikow 1987, Bledsoe and Raikow 1990).

*Classification.*—The significance of Sibley and

Ahquist's work is clarified by placing it in historical perspective. The authors review the work of the major systematists of the past 250 years, reproduce many classifications, and give extensive quotations to help the reader understand the ideas of various workers. It is significant that this section is a review of classification and not of phylogeny. Until recently, evolution has been more implicit than explicit in the work of most systematists. Traditional studies were vague and informal, and few workers explained their methods in any detail. Systematic understanding was thought to be intuitive, and this strange idea, so at odds with the general philosophy of science, was widely accepted. Sibley and Ahlquist explore this idea convincingly. Perhaps the most significant aspect of the revolution in systematics has been the idea that systematics requires rigorous methods that are open to analysis, and whose results are subject to testing.

Sibley and Ahlquist's classification is based on the branching pattern of their phylogeny. Because genetic distances are related to the passage of time, they consider their classification to be cladistic rather than phenetic in nature. Rank is determined by the estimated time of origin of taxa, and sister taxa, being of equal age, have equivalent rank.

The classification employs 16 category levels. This provides an approach to categorical equivalence, so that in any part of the tree, for example, families lie within one age range, orders within a different range, and so forth. Because there are more levels of subordination in the phylogeny than in the classification, some imprecision occurs in categorization. Unfortunately, this sometimes results in interesting groups, like the suboscine "tracheophone" clade, remaining nameless.

The full classification appears on pp. 256–264. Some workers may resist certain changes, even though the classification was constructed in a logical and consistent fashion. It is important to study the classification in detail, because some taxa, though bearing familiar names, delimit unorthodox assemblages. For example, the Limpkin (*Aramus guarana*) is now in the Heliornithidae; the Shoebill (*Balaeniceps rex*) is in the Pelecanidae; and the Ciconiidae now includes not only the storks, but the New World vultures as well. Similar surprises occur at the ordinal level, e.g. the Ciconiiformes now incorporates the shorebirds, hawks and falcons, grebes, loons, penguins, and others. Such unconventional groupings follow the hierarchical structure of the phylogeny, which provides a much more comprehensive theory of relationships than did earlier classifications.

*Testing against morphology.*—Sibley and Ahlquist seek to accentuate the importance of their approach by contrasting it with morphological methods of estimating phylogeny. They usually consider that the latter are inaccurate because homologous similarities may be confused with analogous similarities. The former reveal historical relationships, and the latter do

not. These problems are understood by practicing morphologists today. Early workers used too few characters and overstated their individual importance; they defined typological character complexes instead of unit characters; they clustered by general rather than derived similarity; and they used characters at the wrong hierarchical levels. It must be objected, therefore, that much of Sibley and Ahlquist's critique is irrelevant when it compares obsolete morphological with modern molecular methods. Morphologists today have much better techniques than those used by Garrod and Gadow, and so Sibley and Ahlquist's critique must be assessed within its historical context. Indeed, it is to their advantage that modern morphological approaches be as effective as possible, because the ultimate test of biochemical phylogenetics is congruence with morphological phylogenetics. Sibley and Ahlquist accept this idea when the two methods yield similar results, and cite this congruence in support of their method. Where these approaches disagree, however, they assume that morphology is always in error because of convergence (p. 6), to which, they maintain, their method is immune. However, their method is also prone to error (see below), so they are not justified in assuming that their conclusions are always correct. Congruence between molecular and morphological results is a powerful test of historical accuracy, but when it is lacking the appropriate response is to examine both studies for shortcomings, and not to assume in advance that one or the other is correct (Bledsoe and Raikow 1990).

*Limitations.*—As in all research, this project has potential sources of inaccuracy besides the usual experimental error. One of these is in data analysis. Like other methods, DNA-DNA hybridization does not generate a phylogeny directly. Rather, it produces distance estimates that must be analyzed to produce a tree. Most of the work was done with a method (average linkage or UPGMA) that assumes constant evolutionary rates in different lineages. Yet the authors observe (p. 147) that this assumption is not entirely realistic. Some groups were analyzed using another method, FITCH, which does not make this assumption, and a variant of FITCH called KITCH, which does. Not surprisingly, there is variation in results based on different assumptions. For example, UPGMA shows the sister group of the rheas to be the Ostrich (Fig. 357), while FITCH and KITCH give the rheas' sister group as a clade containing kiwi, Emu, and cassowary (Figs. 325, 326). Similarly, FITCH (Fig. 328) and UPGMA (Fig. 357) disagree on the position of *Anseranas* near the base of the waterfowl radiation. In the passerines discussed above, FITCH, which does not assume constant evolutionary rates, fails to cluster *Acanthisitta* with the suboscines as UPGMA does. Readers interested in particular taxa should search the relevant figures for other examples. Such ambiguities document that the DNA hybridization ap-

proach can be imprecise. To an unknown extent, the conclusions resulting from some DNA-DNA hybridization data depend on the statistical analyses to which they are subjected.

There is also a problem with regard to the limits of resolution of DNA-DNA hybridization. Sibley and Ahlquist point out (p. 6) that the method becomes ineffective beyond about 100 million years. Presumably, this is because the taxa have diverged so far that they lack enough comparable DNA sequences to support hybridization. But what about the other extreme? Is there a point at which taxa are so *similar* in DNA sequences that the technique cannot distinguish them clearly? In the basal parts of the phylogeny the distances are relatively large, and confidence is inspired that the structure of history has been recovered. But in many cases the distances between smaller branches are very short, raising the question of whether they fall below the limits of resolution of the technique. This problem is discussed briefly on p. 164. The authors examine a cluster of families separated by very short genetic distances (Fig. 17, p. 163). They defend the significance of these measures with a statistical test, but add that "The statistics at each node may be criticized as inappropriate, but essentially the same tree is derived from the Fitch algorithm." Why is this point raised but not explained? Is the statistical method used appropriate or not? We are left with an uncertainty about the validity of such clusters. Sibley and Ahlquist state further, "We view this as a trivial matter because it would make no difference in the classification . . . if the series of closely stepped branches . . . were collapsed into a polychotomy. . . ." This ignores the fact that a phylogeny has important applications in addition to its use in classification. To an investigator who wants to use the phylogeny as the foundation for a study of evolutionary morphology, adaptive radiation, or historical biogeography, confidence in the accuracy of the phylogeny is a prerequisite.

Several papers critical of this project have appeared in recent years, and the authors themselves point out certain problems, but unfortunately they fail to discuss them at length. It would have been useful to have a chapter devoted to the limitations of the method and the validity of the criticisms raised against it.

*Conclusions.*—I posed two questions at the start of this review. How closely have Sibley and Ahlquist approached their stated goal of "the reconstruction of the phylogeny of the groups of living birds and the derivation of a new classification based on the phylogeny" (p. xvii)? They have produced the first comprehensive and coherent phylogeny of any major group of organisms down to the species level, and involving truly large numbers of species. Potentially their greatest achievement has been to propose a basal branching pattern for the avian tree, formulating a theory of relationships linking together traditional groups whose connections have remained indeter-

minable by earlier methods. Although some problematical taxa remain to be examined, all major groups are included, and their relationships are specified. This will surely become the standard model in the coming decade.

What does this work mean for the future of avian systematics? First, because more than 80% of avian species remain unstudied, there is an enormous amount of filling in, and perhaps rearrangement, still to be done. Second, their ideas will be tested both by attempts at independent replication and by congruence comparisons using other methods. Finally, if confidence in their approach is maintained in the long run, then many biologists will use their phylogeny as the basis for analyses of a variety of evolutionary problems.

This book belongs in all college, university, and museum libraries, and in the personal collections of avian systematists. Students would benefit by having their own copies to study and annotate, but the cost will preclude this for many.

The work summarized in this book has revolutionized systematic ornithology, and only time will tell how pervasive its effects will ultimately be. Sibley and Ahlquist have given us more to ponder and debate than anyone else in 20th-century avian systematics. They will keep us all busy for a long time to come.—ROBERT J. RAIKOW.

#### LITERATURE CITED

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**Phylogeny and Classification of Birds: A Study in Molecular Evolution.**—Charles G. Sibley and Jon E. Ahlquist. 1990. New Haven, Connecticut, Yale University Press. xxiii + 976 pp., 385 text figures. ISBN 0-300-04085-7. \$100.00.—Sibley and Ahlquist's DNA hybridization study of avian phylogeny is a monumental achievement. It represents a milestone not only for ornithology but for molecular systematics in that it is, to my knowledge, the only systematic mono-

graph of an animal class based solely on comprehensive molecular comparisons. For more than a decade Sibley and Ahlquist worked toward the goal realized in this volume (digressing only to explore a minor, genus-level problem in mammalogy). The magnitude of their accomplishment is most striking in some historical statistics: more than 300 coworkers involved, 1,700 bird species compared, and 26,000 DNA hybrids analyzed. Every researcher aware of the scarcity of funding resources, the challenges of collecting fresh tissue from species scattered around the world, and the daunting task of orchestrating laboratory work around a project of such magnitude must look on this book and the labor it represents with more than a little awe.

The book is in two parts: a 270-page Introduction and a sequential account of DNA hybridization results for the major bird groups. Several themes emerge early that serve to define the authors' perspective on phylogenetics—themes that will be familiar to those who have kept up on the steady stream of Sibley and Ahlquist publications since 1981. Chief among these is the view that phylogeny properly includes both the branching order of evolution *and* the age of divergence between lineages. While much of modern systematics is understandably preoccupied with the former, Sibley and Ahlquist press their data to yield answers to the latter as well. With what success, as they note, remains to be seen.

A second theme has to do with molecules and morphology. In explaining their motivations for undertaking DNA hybridization studies, Sibley and Ahlquist are careful to give morphological systematics its due, but they are equally quick to point out what they see as morphology's great shortcoming—convergence. Convergence is why morphological features become unreliable at higher taxonomic levels and explains why one needs to look at genetic data to sort out long-standing taxonomic problems. What makes this view distinctive is the now-familiar argument from Sibley and Ahlquist that DNA hybridization "solves the convergence problem" (p. 8). This is because, they say, the physico-chemical constraints on DNA base-pairing in solution make it highly improbable that nonhomologous sequences will form stable duplexes. If we are always comparing homologous genes, how can we go wrong?

Homology at the molecular level is a multifaceted concept. We may say correctly that genes in two species are homologous if the same gene was present in their common ancestor. But here we encounter the problem of duplicate genes, not all of which are highly repetitive or highly divergent, and not all of which are removed from "single copy" hybridization comparisons. The argument that stringency conditions eliminate paralogous pairings is overstated, though stringency *will* prevent hybridization between very divergent copies. On another level, however, the problem of convergence has certainly not been

solved—namely, the homology of individual sites within a DNA sequence. If DNA hybridization tells us that two genomes are 20% different on average, does this mean that the 80% of identical sites are homologous? Clearly not; parallelisms, reversals, and multiple substitutions are expected to occur. This kind of homoplasy is just as real in DNA hybridization as in other genetic distance (or, for that matter, discrete character) data. Moreover, the magnitude of the distortion increases with increasing divergence. While there are ways to address this problem (e.g. additivity transformation), Sibley and Ahlquist do not employ them.

Some of the material in the introductory chapters seems unnecessary (such as details of gene structure and regulation in Chaps. 3 and 4), but much of it is surprisingly helpful as a concise introduction to the molecular and biophysical chemistry of DNA hybridization. Topics such as DNA structure, reassociation kinetics, and frequency classes—all extremely germane to the interpretation of hybridization experiments—are described clearly and will be appreciated by nonmolecular readers. The information here may also help dispel the idea that this is a "black box" technique. It isn't.

Some of the literature review is dated (e.g. Chap. 6 on genome organization cites no references later than 1985), and some is overly optimistic. For example, Sibley and Ahlquist assure us that things such as intraspecific divergence, divergence beyond the range of  $\Delta T_{50}H$ , and variation in genome size, base composition, and sequence organization are not problematic for birds. While most of the available evidence does not contradict this view, there is very little information on these factors in avian groups. Other investigators would do well not to dismiss the issues out of hand.

One of the most disputed aspects of Sibley and Ahlquist's work over the years has been data analysis. It is therefore interesting to read and consider the authors' most recent views on some old problems. One of these is the choice of a distance. All the results reported here are based on the  $\Delta T_{50}H$  measure of melting point depression, and hence are linked to estimates of normalized percent hybridization (NPH). NPH is known to have a high variance due to experimental error, and so  $\Delta T_{50}H$  has been criticized for being imprecise. On the other hand, neither the mode nor  $T_m$  can effectively discriminate among taxa as divergent as most avian orders. Sibley and Ahlquist argue that  $T_{50}H$  is reliable out to  $\Delta 30$  (about 30% average sequence mismatch), even if measuring it relies on extrapolation beyond the end of the melting curve. I think most DNA hybridization practitioners would consider this to be "pushing it," and that results based on such large distances (e.g. relationships among many of the nonpasserine orders) will be among the most controversial in the book.

Another issue in data analysis is the choice of a

tree-building algorithm. While UPGMA is still their primary tool (in terms of numbers of species analyzed), Sibley and Ahlquist have also presented some analyses using the Fitch-Margoliash method. The chief advantage of the latter is its insensitivity to variable rates of evolution among lineages, and it is interesting to note how occasionally the phenetic and best-fit methods disagree in their assessment of topology. One example is found in the ratite results, where the FITCH tree has Ostrich and rhea as sequential branches rather than sister-groups as in the phenogram. In some such cases (like the ratites), Sibley and Ahlquist make a choice among alternative topologies rather than considering the situation unresolved. Readers should carefully consider the bases of these choices (e.g. positions of melting curves) when evaluating the results for particular groups.

The most contentious issue surrounding DNA hybridization has been "data correction," and the discussion of this in Chap. 11 focuses on the problem of variation between replicate comparisons that should produce identical results. The central problem is whether experimental results distorted by measurement error should be thrown out, analyzed as they are, or corrected. Noting the expense of repeating experiments, Sibley and Ahlquist argue in favor of the latter (interestingly, the second option is not discussed). Three kinds of corrections are described, two of which (temperature overshoot and linear scaling) seem relatively innocuous in that they involve obvious and simple sources of error. The third, "proportional correction," I find much more troubling. In some experiments, hybrid DNAs fail to reassociate completely, and so produce anomalously low NPH values and correspondingly distorted  $\Delta T_{50}H$ s. Using a regression line of  $\Delta T_{50}H$  on NPH for "good" data, Sibley and Ahlquist shift "bad" data points to where they "should" be and thereafter employ the corrected delta as an independently estimated distance. The statistical problem this creates should be apparent: If we need only a high regression coefficient to identify accurate distances, why replicate experiments at all once we have a single "good" data set?

My overall sense of the data-analysis procedures is favorable but slightly skeptical. Sibley and Ahlquist have applied some straightforward methods to build trees from their data, and these trees are more or less justified as point estimates of relationships. What is missing, however, is any attention to the reliability of the estimates. If for no other reason than random measurement error, DNA hybridization results can and should be assayed for statistical robustness. Despite the existence of many nodes separated by very short branch lengths, there is no jackknife, bootstrap, confidence interval, or other statistical treatment of the trees. If systematists have learned anything in the postcladistic era, it is that "the best" tree is never the end of the story.

Chapters 12 and 13 are on rates of genome evolu-

tion, and the conclusions here are appropriately cautious. During the early 1980s, Sibley and Ahlquist claimed that avian genomes evolved at a uniform average rate. But by the late 1980s, it was clear that rates among bird lineages are not the same. Reexamining their data in light of this finding led Sibley and Ahlquist to re-propose a correlation between generation time and average genome rate. Because generation time is a complicated demographic parameter, they employ age-at-first-breeding as a reasonable surrogate and find that birds with delayed maturity (e.g. many nonpasserines) have slower rates of genome change than those that breed at one year (e.g. most passerines). The arguments presented are plausible, but there is no quantitative analysis of the data. Relative rate tests, for example, are statistically complex, and one has to be careful when interpreting small differences as meaningless and big differences as important. Nevertheless, one strongly suspects that Sibley and Ahlquist are on to something here—an important molecular phenomenon with significance well beyond the realm of avian taxonomy.

Chapter 14 on the history of avian classification is superb and demonstrates the level of scholarship that Sibley and Ahlquist bring to their subject. Beginning with pre-Linneans, they trace major developments in bird taxonomy through 1982, providing always the right balance of anecdote and analysis, detail and generality, to make the story engrossing. Alternative classifications of most of the leading players are presented in indented format, facilitating (and, along with the text, positively inviting) detailed comparisons. In some cases, such as Hans Gadow's anatomical work, we are treated to summary descriptions of characters, their distribution among taxa, and their relative merits for taxonomy. This section, and the corresponding essay on passerines later in the book, will provide an excellent starting point for students of avian systematics for years to come.

And finally, what of the results? Each major group is described separately (including anatomical diagnoses, a history of classification, and the DNA findings), though the structure of the classificatory hierarchy is well preserved in the arrangement of text sections (i.e. one doesn't get "lost" in the classification). DNA results are described relatively briefly and illustrated by melting curves and trees, all of which are arranged sequentially at the end of the book. Given the amount of information here, one can forgive this awkward arrangement, but a couple of points are worth complaining about. One is that the distance matrices accompanying FITCH trees appear pretty much as PHYLIP spat them out; the lines are wrapped as they would appear on a computer monitor, making it extremely difficult to identify a cell of interest. Second, FITCH trees are accompanied by a table of branch lengths (also PHYLIP output) between numbered nodes or taxa. But the node numbers are not given on the trees, so it is impossible to identify which

lengths go with which branches! This is the only major editorial oversight I found in the book. Third, the UPGMA diagrams (reproduced from the famous "Tapestry") appear with no corresponding distance matrices. This is especially frustrating in that the text does not always cite original papers where the data may be found.

It would be pointless to go into the details of this or that group in a book so comprehensive. Indeed, such criticism, testing, and re-evaluation will be the work of generations to come (it has already begun). This is the lasting tribute that will surely come to Sibley and Ahlquist; their work will be cited by virtually every avian systematist for the foreseeable future. At a pizza parlor in New Haven in 1985, I asked Jon Ahlquist how he felt about this incredible accomplishment. He shrugged, smiled, and said, "Not bad for a couple of birdwatchers." Not bad indeed.—CAREY KRAJEWSKI.

**Phylogeny and Classification of Birds: A Study in Molecular Evolution.**—Charles G. Sibley and Jon E. Ahlquist. 1990 [1991]. New Haven, Connecticut, Yale University Press. xxiv + 976 pp., 385 text figures. ISBN 0-300-04085-7. \$100.00.—In different hands at different times, an individual book may serve a variety of purposes. A text used by one person for religious inspiration may be used by another as nothing more than an example of prose style. A reader today probably would not turn to Homer for information about Greek history, but it was a belief in the historical truth of the "Iliad" that led Schliemann to discover the city of Troy. Sometimes a book takes on a role so far removed from its intended one that it surprises us. I once saw a volume of Xenophon used, quite successfully, as a wedge to keep a ceiling light fixture from rattling.

The first purpose of a book of science is to provide a representation of the world that can be judged true or false. But science books can serve as many different purposes as works of history or literature, and this is worth remembering as we consider "Phylogeny and Classification of Birds" by Charles Sibley and Jon Ahlquist. It is worth remembering because it is in fulfilling its scientific purpose that this book is least successful, and professional systematists are likely to be disappointed by it. The value the book does have will be realized in unexpected contexts: among those who have up to now given little thought to phylogeny and its importance, and among the young.

"Phylogeny and Classification of Birds" is a compilation of Sibley and Ahlquist's DNA hybridization studies of avian systematics, studies that have been conducted over the last 20 years. The book is divided into two parts. The first part consists of 17 chapters that review the history of bird classification, the prin-

ciples of classification, and the methods of comparative molecular biology. The second part goes through the major groups of birds, reviews the history of the classification of each group, and then presents the authors' own phylogenetic conclusions. The second part concludes with a chapter on historical biogeography. Grouped at the end of the volume are more than 300 DNA melting profiles and about 30 evolutionary trees, the last of which is the famous "tapestry," a multipart diagram that is almost 5 m long when fully assembled.

Being largely a compilation and synthesis of Sibley and Ahlquist's earlier DNA hybridization work, this book is in the unenviable position of having had its methods and results widely criticized even before the volume appeared (Lanyon 1985; Templeton 1985; Ruvolo and Smith 1986; Cracraft 1987; Felsenstein 1987; Houde 1987; Sheldon 1987; Lewin 1988a, b; Bledsoe and Sheldon 1989; Marks et al. 1989; Sarich et al. 1989; Sheldon and Bledsoe 1989; Springer and Krajewski 1989; Bledsoe and Raikow 1990). The authors acknowledge some of this criticism, although they do not cite all of it (the papers of Templeton, Ruvolo and Smith, Cracraft, Houde, and Bledsoe and Raikow are not mentioned, nor is the news article by Lewin), and they do not respond very strongly to the criticism they do acknowledge. But the criticism has apparently been felt; anyone who was exposed to the authors' earlier claims for their method, and the uncritical praise of early reviewers (Diamond 1983, Gould 1985), will recognize in the Preface (p. xvii) a considerable admission: "Our data are not perfect and we did not subject them to every available statistical analysis; that we should have done many things better is undeniable, but hindsight is always crystal clear."

The DNA hybridization techniques the authors used will by now be familiar to many. If the double-stranded DNA of an organism is put into solution and warmed, the two strands will gradually come apart. If instead of starting with "homologous" double-stranded DNA, we join together single strands from two different species, and then melt this "hybrid" or "heterologous" DNA, we will find that it melts at a slightly lower temperature than does the homologous DNA of either of the component species. This is because the DNA strands of the two different species do not match one another perfectly, and so the hybrid helices can be more easily shaken apart. The difference in melting temperature between homologous and heterologous DNAs can be taken as a measure of the overall genetic "distance" between the two species being compared. The smaller the genetic distance, the more recently the species are assumed to have diverged from one another. From a table of such distances, calculated for a variety of taxa, it is possible to build up an evolutionary tree.

As simple as this procedure may sound, it is in fact fraught with practical and theoretical complexity.

Some of this complexity was uncovered by the authors themselves, and to the extent that they had not originally taken it into account, the discovery of this complexity has led them to undermine their own work. This is in a sense a mark of success, because it means that we now understand DNA structure and evolution better than we did before. While the range of the criticism leveled against Sibley and Ahlquist's procedures is such that it cannot be summarized in this short space, most of their critics have focused on two areas that can be mentioned: the choice and calculation of an appropriate distance statistic, and the techniques used to construct evolutionary trees from the calculated distances.

Double-stranded DNA does not melt at a particular temperature, but rather dissociates gradually over a temperature range. The difference in melting temperature between homologous and heterologous DNAs is therefore not a difference between two points, but between two curves, and this difference can be calculated in a variety of ways. The most common difference measures used are the  $\Delta T_{50}H$  statistic and the  $\Delta T_{mode}$  statistic. The trees published in "Phylogeny and Classification of Birds" are all based on  $\Delta T_{50}H$  values, but Sarich et al. (1989) have argued that this statistic can magnify small differences spuriously, and that its useful range is narrower than Sibley and Ahlquist claim (on this latter point see also Sheldon and Bledsoe 1989). Furthermore, Sibley and Ahlquist "corrected" some of the raw values obtained in their experiments before they calculated  $\Delta T_{50}H$  values (Lewin 1988a, b). They defend these corrections in this volume (pp. 150-164), but even if this practice is legitimate, the corrections introduce an additional measure of uncertainty into their calculations of genetic distance. Sibley and Ahlquist regularly resolve branches that are only a fraction of a degree apart, but the work of their critics suggests that such resolutions are unlikely to be reliable.

Once one has chosen a distance statistic and calculated a table of distance values, the next step is to construct an evolutionary tree from the calculated distances. In their earlier publications, Sibley and Ahlquist assumed that there was a uniform average rate of DNA evolution in all lineages. They assumed that they were gathering data from a molecular clock. Under such an assumption, a phenetic clustering algorithm such as UPGMA will produce a correct evolutionary tree, and that is in fact how the final tapestry (Figs. 357-385) was assembled. In this volume, however, the authors concede that their earlier assumption of a uniform average rate of DNA evolution was not correct. One very interesting factor that appears to influence the rate of DNA evolution is generation time: genetic distance "accumulates" more rapidly in taxa with short generation times than it does in taxa with long generation times. Sibley and Ahlquist believe this accounts for the anomaly of *Turnix*, a rapid

breeder, which is exceptionally distant in genetic terms from all other avian taxa.

We now know that the rate of DNA evolution is not uniform across lineages, so the structure of the tapestry (first presented publicly at the XIX International Ornithological Congress in 1986) must be regarded with considerable skepticism. The authors provide in this volume a collection of new trees constructed according to the Fitch-Margoliash algorithm, an algorithm that does not assume equal rates of change in all lineages, and many of these trees differ in branching structure from the tapestry (compare for example the position of *Colinus* in Figs. 334 and 360, or the position of *Anseranas* in Figs. 328 and 357). In many cases these new trees are based on pooled data from entire clades, a practice that might have been legitimate if the assumption of equal rates of evolution had been true, but that now seems inadvisable. An annoying editorial lapse must be noted here: the Fitch-Margoliash trees are accompanied by tables of branch lengths, but the internal nodes of these trees are not labeled. This means that although it is possible to determine from a table that the branch between node 2 and node 5 on a particular tree has a length of 2.24, it is difficult to determine from that tree which node is number 2 and which node is number 5.

The conclusion one is driven to is that the phylogenies presented here are uncertain to a degree that is itself uncertain. No one expects perfection, but in most phylogenetic studies today serious readers can get a feeling for how much confidence they should place in the result. Here that is not possible. We are given distance measures calculated from raw data (perhaps corrected, perhaps not; we don't know); these distance measures are pooled in many cases, thereby concealing their actual variation (which is of unknown extent); trees are calculated from these distance measures, but these trees are not compared with trees calculated from other distance statistics, nor are we shown a consensus of the trees that could be calculated if we allowed for an error of, say, 0.5° in the  $\Delta T_{50}H$  values. The phylogenies presented here will have value in suggesting appropriate outgroups for future phylogenetic studies, but no one should use them as a basis for studies of avian evolution without carefully taking into account their many weaknesses.

Turning from the DNA hybridization work, there is much in this book still to be examined. The early chapters review the general literature on molecular systematics, DNA structure, and genome organization. These chapters will be appreciated by all of us who have not kept up with the literature on molecular evolution as well as we should have. As extensive as these reviews are, however, they are short on critical analysis and synthesis, and are somewhat unsatisfying. We learn a great many details—Glaus et al. studied mtDNA in galliforms; Avise and many others studied mtDNAs in various vertebrates; Avise and

Nelson studied mtDNA in *Ammodrammus maritimus*; Ovenden et al. studied mtDNA in *Platycercus*; Ball et al. studied mtDNA in Red-winged Blackbirds; Anderson et al. studied mtDNA in humans (p. 102)—but if we seek an overall synthesis or general interpretation of these myriad studies we will not find it. I had the sense that I was reading a collection of note cards that had been strung together, one after another. The bibliographic value of these lists is undeniable, but there are better ways of organizing an annotated bibliography. Because authors' names generally are not listed in the Index, the reader who wishes to know, for example, whether Ovenden's work is commented on anywhere else in the volume will be out of luck.

Woven together with the biochemical reviews and the phylogenetic results in this book is another item of value: the most comprehensive review of the systematic literature on birds ever published. Detailed histories of passerine and nonpasserine classification are provided, and still more detailed discussions accompany the systematic treatments of each family or order. As with the biochemical reviews, the usefulness of these compilations is great, and I have already had occasion to consult them several times myself. Their style will be familiar to readers of Sibley and Ahlquist's earlier egg-white protein monographs (Sibley 1970, Sibley and Ahlquist 1972). But in point of fact, more than the style will be familiar, because the greater part of the text of the historical reviews in "Phylogeny and Classification of Birds" is copied directly from these earlier monographs. Sometimes this copying is word for word, and sometimes minor stylistic changes are made, as from "can be important in the phyletic understanding of such groups" (Sibley and Ahlquist 1972: 28) to "can be important in understanding the phylogeny of such groups" (p. 220). These reviews contain new information, but more often than not this new information is simply tacked onto the beginning or end of a copied passage, rather than worked into the text. The only acknowledgment that this great quantity of material has been copied from the authors' earlier work is a single sentence in the Preface (p. xvii) stating that "Most of these reviews [from their earlier egg-white protein monographs] are included in this book." While I suppose that strictly speaking there is nothing wrong with copying extensively from one's own work, it doesn't strike me as a particularly noble practice. Readers who are under the impression that "Phylogeny and Classification of Birds" is a new work are simply mistaken: half of it is 20 years old.

But what of the quality of these systematic reviews, independent of their age? As with the biochemical reviews, they are long on detail and short on interpretation. The authors may fairly claim that they are not historians, and that these reviews are not intended to be professional works in the history of science. But if this is so, then they should have been more

careful with the occasional commentary they do provide. For example, in speaking of the quinarian approach to systematics, common in the 1820s and 1830s, they declare that "this excursion into self-delusion was discredited long before Darwin provided a solid basis for systematics" (p. 185, copied from Sibley and Ahlquist 1972: 5). The quinarian approach was wrong, of course, and it was eventually rejected. But for a period of time it was seriously defended in the professional literature by able writers; no less a systematist than T. H. Huxley experimented with it (Winsor 1976); while it is true that Darwin never accepted the quinarian position, it was hardly rejected "long before" Darwin, inasmuch as Darwin discussed it extensively in his notebooks and was at pains to understand how evolution might produce the sorts of systematic patterns that the quinarians believed they saw (Ospovat 1981: 101-113). The knowledgeable reader can skip over remarks about "excursions into self-delusion," but the novice should be aware that comments such as these make professional historians wince.

There is one interpretive theme that does run through all of the historical reviews in this volume, and an examination of it will help us to understand why the authors went astray in a number of areas. That theme is the failure of morphology to solve systematic problems, and the inherent superiority of genetic information. In the last 30 years systematics has been through a good deal of turmoil, and a reader who has not followed these controversies closely might assume that "Phylogeny and Classification of Birds" is an outgrowth of that turmoil. But this is not the case. Technically, this book is a product of 1980s molecular biology, but conceptually it is a product of 1950s systematics, and the "failure of morphology" theme is one of the indelible stamps of its origin. The systematics of the 1950s was highly successful at the species level, but it was poorly developed in its understanding of phylogeny. The inane remarks of Stresemann (1959), quoted with approval by Sibley and Ahlquist (pp. 235-236), show this clearly. In the 1950s the important distinction between classification and phylogeny reconstruction was imperfectly made, and it was not understood that "homology" is composed of two distinct similarity relations, namely primitive or ancestral homology, and derived homology. Ignorance of these distinctions undergirds the "failure of morphology" theme, and allows the authors to claim that "only homologous similarities may be used to reconstruct phylogeny" (p. 4), when in fact homology (inherited similarity) tells us almost nothing about phylogeny; only derived homology is informative, even in DNA hybridization studies (Springer and Krajewski 1989). The "failure of morphology" theme assumes that theory enters into systematics hardly at all: all that matters is data, and everyone interprets data in the same way. We can see this assumption at work in the historical reviews, where the divergent



methods and goals of systematists over 150 years are almost completely ignored. All past authors are treated as though they were doing the same thing—"classifying birds"—when in fact some were classifying (according to a variety of principles), some were reconstructing phylogeny (also according to a variety of principles), some were doing both, and some didn't think long enough to know what they were doing (see O'Hara 1991 for an indication of the complexity of systematic history). That older systematics was weak in its methods rather than its data is clearly shown by the approximate congruence between Sibley and Ahlquist's DNA hybridization results and contemporary morphological cladistic studies (Raikow 1987, Bledsoe and Raikow 1990). Such congruence was acknowledged with approval by Sibley et al. (1988: 413-414), but its implications for the "failure of morphology" theme are nowhere explored. Systematists have generated quite a bit of hot air in the last 30 years, but they have also gained many important insights into their discipline. Unfortunately, none of those insights are reflected in this volume.

What role will this book play, now and in the future? In spite of its many weaknesses, can it be redeemed? It can be, I think, if we change our notion of its proper audience. Professional systematists will use it primarily as a bibliographic reference, and as a rough starting point for future phylogenetic analyses. For these reasons alone it should find a place on the shelves of every university, museum, and public library of any size, and in the personal collections of all who are interested in avian evolution. But if we consider "Phylogeny and Classification of Birds" to be a book only for professional systematists, we will unnecessarily restrict its usefulness. The greatest value of this book will come not from its systematic conclusions, but simply from its scope, and that value will be realized among readers—especially young readers—who have heretofore given little thought to the importance of evolutionary history. What this book does very successfully is present the *idea* of phylogeny, the *idea* of the history of life, in a way that it has rarely been presented before. Many of us will have had some particular book that inspired us when we were young, and that showed us the possibility of a scholarly career. For me, it was Mayr's "Principles of Systematic Zoology," which I had nearly memorized by the time I was 15; for a colleague of mine it was Romer's "Vertebrate Paleontology." These books were important to us not because of any particular facts they taught us; they were important because they mapped out whole new worlds of knowledge that we could expand into and endlessly rechart for ourselves. "Phylogeny and Classification of Birds" is just the sort of book that can serve that purpose for a whole generation of young scholars. Anyone who wants to do something positive for systematics should photocopy the long string of figures that make up Sibley and Ahlquist's tapestry, tape them together, and hang

the result along a wall in a high school science laboratory or a college corridor. (Keep in mind as you do this that for \$100 the publisher should have provided you with a fold-out chart.) That one diagram, however inaccurate it may be from the viewpoint of a professional systematist, will convey to the mind the idea of the tree of life more forcefully than any other diagram I know; an idea that no checklist or collection of smaller trees can convey. Colleagues who are not accustomed to "tree thinking" may come to see from that diagram how far more interesting all of the phenomena of biology are—whether of behavior, ecology, physiology, biochemistry, biogeography, or anatomy—when they are considered in the context of history. And some stray, odd student might even be sufficiently inspired by that image to make of systematics a career.

A hundred years ago, Richard Bowdler Sharpe published another "tapestry" of bird phylogeny, one that he had displayed at the II International Ornithological Congress in Budapest (Sharpe 1891; reproduced in O'Hara 1991). Sibley and Ahlquist's phylogeny is in many ways a direct descendant of that earlier tree. Sharpe's diagram had the misfortune of appearing toward the end of the early Darwinian period—toward the end of phylogeny's golden age—and after it appeared systematists began to turn away from the larger questions of evolutionary history, and toward the smaller and more tractable problems of species and geographical variation. "Phylogeny and Classification of Birds," in contrast, appears at the beginning of a new age of phylogeny, an age filled with excitement for all of us in systematics. To the extent that this book leads more people to understand and share in that excitement, it will be considered a success.—ROBERT J. O'HARA.

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- Seabirds of Hawaii: Natural History and Conservation.**—Craig S. Harrison. 1990. Ithaca, New York, Cornell University Press. x + 249 pp., 41 color plates, 16 text figures. ISBN 0-8014-2449-6. Paper, \$15.95; cloth, \$36.50.—This volume is a rather odd contribution, a hybrid between an academic work and a popular book, and both suffers and benefits from these attributes. The 18 chapters are divided into four parts that deal with the environment and humans (3 chapters and ca. 12% of the text), comparative biology of Hawaiian seabirds (5 chapters, 26%), treatments of Hawaiian seabird groups by family (7 chapters, 34%), and conservation (3 chapters, 16%). At the end of the book are an appendix of common and scientific names for plants, birds, mammals, fish, and a few invertebrates; a 6-page "selected" bibliography with pertinent references for each chapter; and an index.
- The book intersperses more or less academic material with chatty observations based on Harrison's extensive personal experience in the Northwestern Hawaiian Islands. The latter are highly evocative of field research in the islands and provide the closest approach to the book's stated objective of conveying the wonder of Hawaii's seabirds.
- Part I, "The environment and humans," introduces the area, with general descriptive accounts, maps of the main Hawaiian Islands, and a paragraph or two on each of the Northwestern Hawaiian Islands. Subsequent chapters deal with the environment at sea, including remarks on food chains and marine organisms important to seabirds and a short historic account of man in relation to the seabirds of Hawaii. This section is concisely and adequately presented.
- Part II, "Comparative biology of Hawaiian seabirds," falls farther from the mark, at least in the first chapter, "Origins and adaptations." This chapter mentions fossil history and summarizes characteristics of seabird orders, but includes a paragraph on penguins, which seems inappropriate for a book on tropical seabirds. The next chapter, "Populations," provides population figures (8 tables) for each of the atolls, main islands, and principal colonies offshore. Many of these data, except those for the Northwestern Hawaiian Islands, are previously unpublished and represent the principal original contribution of the book. A page or two are devoted to population regulation and variation, but this material is superficial and of limited value. The third chapter in this section, "Breeding ecology," deals with topics such as timing of breeding, nesting habitat, and other aspects of nesting. It also introduces material that is repeated again and again later in the book. The concluding chapter in this part, "Feeding ecology," is largely a condensation of Harrison's earlier monograph on the subject.
- The chapters in Part III treat families of Hawaiian seabirds. Each has a few introductory remarks, sections on distribution and abundance, and biology at sea and on land; and a concluding page or two on conservation of the included species. The accounts reflect the amounts of information available for each taxon. For example, the chapters on storm-petrels, frigatebirds, and tropicbirds lack sections on distri-

bution and abundance, while the chapter on albatrosses includes sections on arrival at the colony and on courtship and incubation.

Most of the book's outright errors, ambiguity, and inaccurate generalizations occur in Part III. For example, Harrison remarks that most Great Frigatebirds "are nonmigratory residents that do not wander far from their breeding islands." Unpublished recovery data from the Smithsonian Pacific Program suggest that both juveniles and adults of this species, like the Lesser Frigatebird, disperse widely across the Pacific. Indeed, published maxima and minima from the Northwestern Hawaiian Islands indicate winter populations no more than half the size of breeding ones. The "residency" of the birds is doubtless based in part on the presence of birds from other colonies and on the fact that adults and young do not migrate on an annual schedule.

To state that "Red-foot[ed Boobies] are the only member of the family that can perch" is wrong, as Brown Boobies readily do so, and I have often seen Masked Boobies perched on the low limbs of dead trees. And "In the Phoenix Islands [Red-tailed Tropicbirds] are still used as carrier pigeons, carrying messages attached to their legs," but as these islands are uninhabited by humans, I wonder by and for what or whom. Another particularly infelicitous statement is "Tern eggs are quite edible and sooties are probably the world's largest producers of wild eggs," which actually was meant to mean "for human consumption" and not that Sooty Terns are the most abundant of wild birds.

Other statements exaggerate original sources. Great Frigatebirds are said to have "suffered virtually a total nesting failure on Kure in 1966, when many adults were attacked by Polynesian Rats . . ." The original source (1972, *Atoll Res. Bull.* 164) indicates only that "at least six [adults] with typical rat wounds on the back were found" of at least 200 nesting pairs, perhaps 300 adults handled, and at best 2% of the adults. Hawaii is also said to have fewer than 3,000 adult Brown Boobies, "only 2,000 of which breed." I presume that Harrison meant that only 2,000 might breed in any given year, because it is unlikely that hundreds of adults would permanently forgo breeding.

Further, sources of original information are not given, which makes the book frustrating reading for an academic ornithologist. Some of the information I thought was new (e.g. an average 5-day incubation bout for the Christmas Shearwater) may be published somewhere, but I did not find it in the sources cited in the terminal bibliography. The Christmas Shearwater fledging period is said to be 100-115 days, but 6 on Johnston Atoll averaged 96 days with a maximum of 103 (1976, *Atoll Res. Bull.* 192). Similarly, the fledging period for Bulwer's Petrel is given as 63-70 days, but 8 on Johnston Atoll averaged 62 days with a range of 57-67. I suspect that the figures Harrison gives are from unpublished studies in the Northwestern Ha-

waiian Islands by U.S. Fish and Wildlife Service personnel, but I would be happier had such data been documented adequately.

The book has too much redundancy from chapter to chapter, particularly in the remarks on conservation. The same threats are mentioned in some of the introductory chapters, in chapter after chapter of Part III, and then again in the first chapter on conservation in Part IV.

The remainder of Part IV summarizes and analyzes federal and state legislation that directly or indirectly protects Hawaiian seabird colonies. This section is the most useful and effectively presented part of the book, and many statements are footnoted with sources. The first two chapters of Part IV treat legislation relating to land areas and the sea. The third chapter, "Conservation dilemmas," points out that the problems in conservation in Hawaii stem largely from "inadequate funding, poor implementation of policies, or weak enforcement of statutes." Harrison goes on to point out numerous deficiencies in conservation policy and practice in Hawaii, addressing pointed (and surely sometimes deserved) barbs at various state agencies and at his former employer, the U.S. Fish and Wildlife Service. I doubt that any long-term employee of any large bureaucracy will find his remarks especially surprising. Most of his criticisms, while often apt, probably apply equally well to other agencies that do not have environmental preservation as part of their mandate. Harrison's remarks about the private sector are more positive, although it is discouraging to realize that Harrison picks 1988 as a watershed year for private conservation. Only then did larger national private conservation groups such as the National Audubon Society establish offices in Hawaii.

The color plates are all from photographs, most evidently taken by the author. All but three scenic shots portray Hawaiian seabirds. Most are of high quality, and some are very fine indeed. I particularly liked those of a rain-drenched Laysan Albatross chick and one of a Wedge-tailed Shearwater at the mouth of its burrow. Two photographs, a head and shoulder shot of a Masked Booby and one of an adult Bonin Petrel, are blurred and partly out of focus and would better have not been included. The pictures are almost certainly a selection of the author's best rather than an attempt at complete representation of Hawaiian seabirds. Pictures of 6 of the 22 breeding species of seabirds, admittedly mostly difficult species to photograph, are omitted.

The book's flaws largely result from an unsuccessful integration of the subject matter. The material included would have received better treatment had it appeared in three separate publications. One would be an expanded version of Harrison's personal experiences and be a truly popular book that I think would be well received. The others would be a monograph bringing together the various technical data

mentioned or alluded to, and a treatise on Hawaiian seabird conservation. I have no doubts as to Harrison's ability to produce such varied fare, and am sorry that he was relatively unsuccessful in his attempt to integrate the technical and popular.

The book may be better received by the general public, who will find in it much of interest. Its lapses and lack of documentation are severe enough flaws that I would not recommend the book for an ornithologist's personal library unless it is needed for its scattered bits of original data.—ROGER B. CLAPP.

**Auks at Sea.**—Spencer G. Sealy (Ed.). 1990. Western Found. Vertebrate Zool., Stud. Avian Biol. No. 14. vi + 180 pp. ISBN 0-935868-49-6. Cloth. \$16.00. (Available through Cooper Ornithol. Soc.)—The Alcidae have long fascinated and inspired biologists who wish to probe behavioral, evolutionary, and ecological interactions within avian taxa. As virtually the only taxon of wing-propelled diving seabirds in the Northern Hemisphere, alcids "give us an opportunity to examine a group remarkably free of interactions with other groups, a condition seldom encountered in terrestrial situations" (Bédard 1969). "Auks at Sea" presents the proceedings of a symposium sponsored by the Pacific Seabird Group in December 1987 at Pacific Grove, California. Although alcids have been covered by symposia previously, this is the first to examine the biology of the group exclusively at sea. The scope and content of this volume not only constitute a milestone in alcid biology, the findings could have lasting and wide-ranging consequences for issues confronted elsewhere in ornithology.

The topical and taxonomic contents inside are predicted by the cover: a Thick-billed Murre (*Uria lomvia*) occupies center stage on the ocean surface, framed by a murre diving below and several murrelets in flight overhead. Two papers report on alcid flight at sea, five papers at least partially focus on the relationships of alcids with the subsurface environment, and the balance of the material represents some aspect of alcid biology at the surface of the ocean. Murres get the heaviest coverage (12 of the 17 symposium papers are based on one or both murre species), whereas 12 of the 22 extant alcids received little or no treatment. Geographically, papers originate from work conducted in the Bering Sea (3), western Atlantic Ocean (7), eastern Atlantic Ocean (1), and the Pacific coast of North America (6). Sealy provides an overview and introduction to the symposium, and sets the tone by linking the studies to the historical development of marine ornithology. Thereafter, the volume is organized into five subject areas.

The first and longest series of papers deals with "Patch use" by alcids. Hunt, Harrison, and Cooney present a wealth of insights into the environment, foraging, and diet of Least Auklets (*Aethia pusilla*) in the northern Bering Sea. Associating with stratified

water, especially where plankton biomass in the upper water column was highest, colony-based auklets occasionally ignored unstratified water containing suitable and abundant prey to forage in more distance habitats. New tows and acoustic surveys were combined with oceanographic measurements to assess interactions of habitat (i.e. thermocline) and prey availability. Either salinity or density gradients more accurately portray structural and process-oriented properties characteristic of water masses within the Bering Sea, so use of these descriptors in the study might have been preferable. Similarly, it is unclear why very small gradients in surface salinity (e.g. 0.4 ppt/10 km) qualified as an "ocean front," a feature at which Least Auklets aggregated. Aside from a somewhat arbitrary choice of habitat descriptors, this study is strengthened by extensive sampling in both time and space, and it is among the first to cast successful implications of patchiness and patch use by diving seabirds in both horizontal and vertical dimensions.

In a similar study by Schneider, Pierotti, and Threlfall, the distributions, flight orientations, and patch scales of Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*) are hypothesized to be related to bathymetric features that generate flow gradients (currents). The results are rendered less than convincing, however, because of a lack of supportive oceanographic measurements *in situ*. An equally plausible and more parsimonious explanation of why alcids associate with shallow bathymetric features (constricted water columns and reduced volumes in which to find and capture prey) was also not considered. Piatt compares the aggregative response of and segregation between Common Murres and Atlantic Puffins to their capelin (*Mallotus villosus*) prey in Witless Bay, Newfoundland. Murres occurred over larger, deeper schools, whereas puffins were concentrated over smaller, shallower schools. Diving abilities (arising from differences in body mass and buoyancy) of the two alcids parallel this pattern, so it may be unnecessary to invoke competitive mediation as the mechanism for segregation. Cairns and Schneider describe habitat affinities of Thick-billed Murres (steeper bathymetric gradients in waters 40–120 m deep) near the Nuvuk Islands in Hudson Bay, Canada. In what is probably the most detailed study of its type, Schneider, Harrison, and Hunt given an excellent account of murre diet in relation to the mechanics of a fine-scale tidal front (water mass boundary) near the Pribilof Islands, Alaska. Gaston and McLaren report that Black Guillemots (*Cepphus grylle*), wintering at high latitudes in Hudson Bay and Davis Strait, are pagophilic (=an affinity for ice) rather than truly pelagic in their choice of habitat. Black Guillemots were distributed mainly among mobile, first-year pack ice in water sufficiently deep to preclude foraging on the bottom. Changes in foraging behavior and diet arising from this flexible response to habitat choice are still unknown, but such a strategy provides a distinct

alternative to the long migrations undertaken by most arctic birds.

Three papers examine "Allocation of time and energy" by alcids. Burger and Piatt report on a four-year study of the relationships between parental behavior of Common Murres and the relative abundance of their principal prey, capelin, in Newfoundland. Results from this important study indicate that chick growth and survival are not always reliable indicators of food availability in marine environments. In another study, Cairns, Montevecchi, Birt-Friesen, and Macko found that energy expenditures (field metabolic rates) of Common Murres were 50% higher than predicted for seabirds. This is attributed either to the thermal costs of operating in a cold ocean environment, or to high locomotion costs associated with a wing structure that must function for the needs of both flying and diving. Carter and Sealy provide a descriptive model of flocking, distribution, flight behavior, and patch use of Marbled Murrelets (*Brachyramphus marmoratus*) in coastal and sill habitats in Barkley Sound, British Columbia. This study is probably unique in its use of an appropriate sampling strategy at sea for representing two-dimensional views of seabird patchiness *per se*.

"Chick rearing at sea" offers fresh insights into this little-known aspect of seabird biology, focusing on one precocial and one precocial/semiprecocial species. Scott provides behavioral, distributional, and dietary information on adult-chick interactions of Common Murres off coastal Oregon. Most murre chicks were attended by a single adult (almost always a male) and were most abundant at sea within 1.75 nautical miles (NM; 3.24 km) of shore, although family groups were observed occasionally out to distances of 15 NM (27.75 km). Duncan and Gaston radio-tagged and tracked Ancient Murrelets (*Synthliboramphus antiquus*) in Hecate Strait, British Columbia. Family groups of murrelets traveled rapidly (as much as 50 km the first day) away from the colony. The authors calculated that chicks catabolize 41% of their lipid reserves in the two days between hatching and colony departure, and that remaining reserves can sustain the chicks for less than two additional days.

Harrison presents the first of three papers that consider "Diets in relation to prey resources." Following diet comparisons among the three *Aethia* auklets in the northern Bering Sea, she hypothesizes that both the social behavior (dispersed and more solitary feeding) and morphology (bill structure) of the Parakeet Auklet (*A. psittacula*) reflect its specialization on gelatinous taxa of zooplankton. These plankters, which harbor associated crustaceans and larval fish with high nutritive value, are dispersed but also widely distributed. Elliot, Ryan, and Lidster report on the diets of Thick-billed Murres wintering off Newfoundland. Murres switched from feeding predominantly on fish to feeding on crustaceans throughout the course of winter as fish descended to great depths in search of

warmer layers and as euphausiids migrated into coastal areas in association with pack ice. Croll's study in Monterey Bay, California, also emphasized the opportunistic feeding strategies of alcids. Common Murre diet, distribution, and abundance within the bay was influenced by the seasonal timing and location of upwelling.

"Auks in peril" focuses on issues related to alcid conservation, and illustrates the interactive and regionally localized nature of factors that affect seabird populations. Page, Carter, and Ford develop a model that estimates carcass deposition on beaches as well as carcass loss at sea to determine numbers of Common Murres, Rhinoceros Auklets (*Cerorhinca monocerata*), and Cassin's Auklets (*Ptychoramphus aleuticus*) killed by the February 1986 'Apex Houston' oil spill on the central California coast. Their model shows that beached carcass counts and aerial surveys of birds at sea are best combined if total mortality is to be fully incorporated into oil-spill contingency plans. Takekawa, Carter, and Harvey attribute declines of Common Murres along the coast of central California to a combination of high mortality from a near-shore gill-net fishery, oil spills, and the 1982-1983 El Niño-Southern Oscillation (ENSO) event. Vader, Barrett, Erikstad, and Strann describe a historical decline of murre populations in Norway as the result of two confounding factors: incidental take in fishing nets and an acute collapse of capelin stocks in the Barents Sea. The former acted chronically on populations of both murre species, but because pelagic capelin form a larger part of Common Murre diets, that species suffered disproportionately from reduction of these prey stocks. Their study also complements earlier work that has revealed the differential ability of Thick-billed Murres to exploit benthic, demersal, or invertebrate prey in the absence of pelagic food sources.

The remarkable implications of some symposium findings could allude to a modification, perhaps even a dramatic shift, in paradigms governing seabird research. In this context, the study of flexible time budgets used by murres as behavioral buffers against variable food resources stands out. Burger and Piatt found that in spite of 10-fold changes in capelin abundance across years and seasons, adult murres managed to provision their chicks at constant rates. Murres did so either by taking alternative prey or by spending more time at sea (see also Cairns et al. 1987). Although life-history traits of seabirds, especially their breeding adaptations, have long been attributed to environmental variability and severe constraints on seabirds' abilities to exploit patchy marine resources, there is a sense that the earlier theories of Lack, Ashmole, and others "can no longer bear the weight of new observations and experimental studies" (Ricklefs 1990). The notion that regulation of seabird populations is strictly density dependent, with population size and other attributes all fine-tuned to resource availability, is difficult to reconcile in circumstances where com-

unities are dramatically affected by ENSO episodes, for example (see Ainley and Boekelheide 1990). Because some of the few significant associations reported between seabirds and their prey at sea have been improperly-demonstrated by haphazard methodology (see below), the tendency for seabirds to track prey poorly at fine spatial scales is a logical expectation if behavioral buffering is extended into the spatial dimension. We cannot say if food supplies in marine environments actually are so limited that seabirds must always find and exploit the optimal patch (largest, densest, most accessible).

The section on "Patch use" could have provided a more rigorous test and development of these ideas. Unfortunately, many of its strained conclusions seem insufficiently robust. Patch use by seabirds must be among the most provocative and difficult subjects faced by marine ornithology. In spite of recognition that a problem exists (e.g. Hunt and Schneider 1987), the pitfalls and challenges of scale are generally not handled well across all conceptual levels: scale of the patch itself (including differentiating gradients from discrete units in the fluid mosaics of the ocean), scale of behavioral and social interactions that facilitate patch exploitation, and the scale at which sampling, observation, or analysis is conducted. Massaging the latter has become almost universally accepted as a means to ascertain either or both of the former. This practice led to tautological excess in more than one paper in the "Patch use" section. The inconveniences of sampling at sea are partially to blame; the lack of synoptic perspectives and inability to collect environmental data in real time (or with adequate resolution) probably make assumptions in methodology unavoidable. Even so, the convoluted and contrived approaches to data handling are tough going here. Readers will at times have to navigate a veritable maze of jargon regarding Type I and Type II error rates, bin and frame sizes, length scales, aggregation intensities, and Monte Carlo simulations. Shortcomings run a spectrum from the relatively minor but still statistically flawed practice of iterative testing (i.e. failure to control for experiment-wise error rates) up to and past conceptual assumptions for which no justifications are given. By way of illustration, the authors of one paper acknowledge the inevitable problems that result when the same arbitrary sampling interval is used to construct both independent (environmental) and dependent (alcids) variables, yet this precaution is ignored in at least half of the papers treating patch use. Stronger correlations, achieved by increasing the size of the observational or sampling window, cannot be used as a reliable indication of a scale relationship. Consequently, alcid locations were not always referenced efficiently to detected patches (e.g. prey location) within the study areas, and the mistaken notion that scales of alcid aggregations must track the scale of patches for a linkage to occur was propagated. In his overview of the symposium, Sealy wisely cau-

tions against this overreliance on correlative comparisons. The real culprit, however, has been an abiding fascination with "bin" manipulations in marine ornithology, regardless of the statistical techniques employed. More appropriate methods for treating observational data are available, and it would not require great effort to apply them to marine studies (e.g. "blocking" [see James and McCulloch 1985] and "analytical sampling" [see Eberhardt and Thomas 1991: 64]). Otherwise, detection of linkages between seabirds and patches will be compromised, and eventually the utility of matrixing patterns and processes at sea via scale will become trivialized.

Attention to detail by both the symposium (S. G. Sealy) and *Studies in Avian Biology* (J. R. Jehl) editors, along with high quality in the production by Allen Press, resulted in very few errors in the technical presentation. On p. 158 some words were apparently not typeset ("... murrees often aggregate on the outer [?] also frequent nearshore . . ."), and on p. 75 an error in printing partially obscures some of the text. This volume is attractively prepared, and the copious tables and figures complement the text.

The real strength of "Auks at Sea" lies in the range of concepts investigated. Such diversity can be a drawback to multi-authored symposia, but decades of summarized research, restriction to a single taxon, and organization of the papers into common themes by the editor all prevented excessive scatter. "Auks at Sea" is a magnified window through which one is offered tantalizing glimpses of marine ornithology as it is practiced today. The bridges that were constructed between biology at sea and biology at colonies contribute greatly to its successes. Readers expecting a mere recitation of alcid biology could be surprised, but it was not intended to be an authoritative compendium of that subject. Indeed, Sealy points to many topics that would provide intriguing research opportunities well into the future. To his suggestions, several more could be emphasized, such as figuring the confounding influences of the subsurface medium (water column) on patch exploitation by this taxon of diving seabirds, and the social mechanisms whereby alcids commute to, encounter, and exploit patches. The technical analyses might temper acquisition of this volume for every community or personal library. But "Auks at Sea" will be indispensable to alcidophiles of every description, to all seabird biologists, and to any ornithologist who wishes to become familiar with ecological topics as envisioned and investigated within the marine realm.—J. CHRISTOPHER HANEY.

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**Fundamentals of Molecular Evolution.**—Wen-Hsiung Li and Dan Graur. 1990. Sunderland, Massachusetts, Sinauer Associates. xv + 284 pp. ISBN 0-87893-452-9. Paper. \$22.95.—Studies of molecular evolution have come of age; the growing and widening field is now so extensive that it requires a book-length introduction. Courses in the subject are being taught, and the birth of academic departments cannot be far behind. Wen-Hsiung Li is one of the bright young theoreticians in this would-be discipline; together with Dan Graur, he has produced the requisite textbook.

In their preface Li and Graur write that the book is an introduction to the “hard science” of molecular evolution. It is intended for beginners interested both in the processes of evolutionary change at the molecular level and in the methods of comparative and phylogenetic analysis of molecular data.

The volume is organized as follows: Chapter 1 contains a discussion of the structural organization of DNA—introns, exons, control of expression, etc. The second chapter treats elementary population genetics and the rudiments of neutral theory—sampling and drift, substitution, and fixation probabilities. Chapter 3 deals with modeling nucleotide substitution, the problem of sequence alignment, and DNA restriction and hybridization. Rates of substitution are discussed in the next chapter; this includes treatments of protein function, synonymous codons, the molecular clock, and relative-rate tests. Chapter 5 introduces the topic of phylogenetic tree construction; rooted and unrooted networks, cladistics vs. phenetics, and estimating branch lengths are considered. The evolution of proteins is the subject of Chapter 6. Gene duplication, gene families, and concerted evolution

are all discussed briefly. Some of the stranger discoveries of the last 15 years are treated in the seventh chapter; these include transposable elements, retrosequences, hybrid dysgenesis, and horizontal gene transfer. The last chapter is a discussion of gene organization—C value, GC content, repetitive structure, and junk DNA.

This comprises somewhat esoteric material for the average ornithologist, but the treatment is not overly difficult and there are many examples, in keeping with the introductory nature of the book and its intended audience and purpose. All of the equations in the material involve elementary algebra. For the interested but uninitiated researcher, I suspect this will be difficult, but useful, reading. As a textbook for an introductory class in molecular evolution, this volume, along with additional, more advanced texts (perhaps Hillis and Moritz 1990, *Molecular Systematics*, Sinauer Assoc.), would be satisfactory. But the major question in this regard is whether such a course ought to exist.

Two related research programs are both referred to as “molecular evolution.” First is the use of biochemical characters in the inference of phylogenetic relationships among organisms; this will be familiar and of concern to most ornithologists. A second program is the study of the evolutionary history of molecules, especially DNA. For example, the genome is actually rather mobile in nature and pieces of DNA change position over evolutionary time, new sequences are added, others are deleted, genes are duplicated and acquire new functions, etc. Thus, the physical structure of DNA in a lineage has its own evolutionary history, which can be deciphered. This book ostensibly covers both of these research programs, but the problem of phylogenetic inference is treated only in one brief chapter, whereas the problem of DNA structural evolution is dealt with in seven. Clearly, neither of these research areas arose *de novo*. Their origins trace to still-extant disciplines.

In most cases the theory and practice of phylogenetic inference will be taught in a systematics course; DNA structure is the subject of molecular genetics and biochemistry departments. Consequently, this volume is an introduction to a chimera, and I cannot wish it well in its struggle toward Bethlehem. As an introduction to the history, literature, and algorithms of modern phylogenetics, it is inadequate. It is better as a prelude to the fundamentals of structural, but not functional, molecular genetics. It is probably desirable for college and university libraries; most individuals will not need a copy.—GEORGE F. BARROWCLOUGH.

**The Known Birds of North and Middle America: Distribution and Variation, Migrations, Changes, Hybrids, etc. Part I, Hirundinidae to Mimidae, Certhiidae.**—Allan R. Phillips. 1986. lxi + 259 pp. Den-

ver, Colorado, published by the author. Available (check payable to author) from Known Birds, 3540 S. Hillcrest Dr., A 5, Denver, CO 80237 USA. ISBN 0-9617402-0-5. \$60.00.—

“Devoted to no school of natural science, and carried away by the dictates of no authority however high, no reputation however imposing, I have come to the investigation of my subject . . . unsecluded by the fascinations of theory, and unfettered by the trammels of system.” (Vigors)

“Known Birds” is the culmination of Allan Phillips’ long and productive career in elucidating the taxonomy and relationships of North American, particularly Mexican, birds. It reflects many years of largely independent work in the field, museum, and library. Although Part I includes contributions by Robert W. Dickerman, Amadeo M. Rea, and J. Dan Webster, the series (Part II will be available by the time this long-overdue review of Part I appears) reflects Phillips’ views of avian systematics and his idiosyncratic scientific philosophy.

The first 61 Roman-numbered pages tell why and how Phillips wrote the book and indicate the essence of that philosophy. This includes an explanation of the “strange, if not ridiculous” title, an “Apologia” for ornithology today, discussions of problems in the use of museum specimens, the biological species, and the tasks ahead, as well as a section on methods. The next 202 pages contain species accounts. This is the meat, the technical portion, of the book, in which Phillips’ taxonomic conclusions are set forth—the Phillips Check-list. The volume concludes with 4 appendices, an addendum, a list of new names proposed, and 5 indices.

The introductory sections should be required reading for every beginning ornithological student, every nontaxonomic ornithologist, and every birder—but not without a word of warning from one who knows, or knows about, the author. Be prepared to roar with laughter and burn with rage—sometimes simultaneously—at the way Phillips expresses his disdain, disrespect, distrust, disgust, and dismay of other taxonomists, earlier or contemporary, who have reached conclusions with which he differs, and of agencies and organizations that constitute the “officialdom” of ornithology or of science in general—particularly the AOU Check-list Committee, the International Commission on Zoological Nomenclature and its Code, and the National Science Foundation. Phillips is not one to let the chips fall where they may; he places each one carefully. Expect to experience sympathy and outrage, directed both toward the author and his targets. Be prepared to read truth, half-truth, and mistruth, and not necessarily know which is which. Above all, be prepared to think and to agree with much that is said despite the way it is said.

The title “Known Birds . . .” is meant to counter the oft-repeated statements “of how wonderfully

completely we know birds,” without acknowledging that such statements are generally made relative to our knowledge of other animal classes. Phillips points out that several North American species have been split, and that others have been lumped out of existence, in the past 50 or so years, as evidence that our knowledge has been and is less than perfect, and that “the true Recent avifauna is different indeed from the lists of the omniscient!,” i.e. from all earlier published lists. Phillips notes that he has seen at least three “obviously undescribed” species of which he has been unable to obtain useful specimens. The latter admission, plus the facts that some of his examples have since been shown to be wrong and that additional splits and lumpings have been proposed, indicates that the true avifauna consists of both known and unknown species and that our knowledge will never be static or complete.

Another reason for writing about Known Birds is that Phillips considers much of the present “knowledge,” particularly of distribution, to be incorrect because it is based on misidentifications that are a premium in the game of listing or ticking and on records that lack adequate (if any) documentation. Indeed, he includes a long section on why we cannot trust our eyes, listing examples of misidentifications by himself and others of birds seen in the field (and then collected) or even examined in the hand. Sight records, of course, cannot be verified or corrected by later examination, and Phillips is inclined to disbelieve them all—except those he uses to make a point. Phillips is particularly contemptuous of those who object to collecting birds even when the specimens might serve to verify or correct identifications based on sightings, particularly of “accidental” or out-of-range birds.

The “Apologia” for modern ornithology reveals that Phillips has a very narrow view of the field, limited to specimen-based information and excluding anything with a theoretical or statistical basis. The section devolves, however, into a diatribe against those who oppose collecting, and therefore science, and particularly against the permit granting (or denying) Division of Law Enforcement of the U.S. Fish and Wildlife Service and its state counterparts. His biting criticism is well placed, as anyone who depends on permits to work in ornithology can attest, but on the extreme side. Unfortunately, criticizing Law Enforcement for its permit policies in this book will be about as effective as criticizing the Pope for his stance on birth control in *Good Housekeeping*.

Even though I agree with much of what Phillips writes, including some of his criticisms of the AOU Check-list Committee on which I serve, I am troubled by the self-righteous and vindictive way his thoughts are expressed. The introductory portion of the book, and much in scattered comments throughout, is written as though by a political or religious prisoner who has suddenly been released and given leave to criti-



cize the establishment that imprisoned him, to vent his pent-up rage. If Phillips has been imprisoned, or otherwise exiled from the scientific community, it has been self-imposed by his narrow thinking over the years and his failure to realize that reasonable, intelligent, professional colleagues can disagree. For Phillips, hypercritical seems like a mild descriptor. Phillips has "an attitude" that has been a trademark for years. Probably each of us has, but most of us try to leave it behind in scientific writing. Unfortunately, the expression of this attitude tends to obscure the underlying basis for his science and makes it hard to take him seriously even when—as is often—he is right.

Phillips has favorite targets for his scorn, as indicated by the number of entries by names (other than his contributors) in the Subject and Author Index. These are the AOU (especially the Check-list Committee), L. Griscom, E. Mayr, A. H. Miller, and B. L. Monroe Jr. (It is telling that the index has an entry for "lumping" but not one for splitting.) In a mild moment, Phillips admits that "no one is immune from error" (p. xxx). But in the previous sentence he states that the AOU Check-list Committee "evidently knows little or nothing of ecology" because it repeated a distributional record that may have been based on a misidentification. Phillips consistently, and apparently deliberately, miscites Part II of the Mexican Check-list (1957, Pacific Coast Avif. No. 33), as Miller and Griscom 1957 (p. xxxviii) and merely as Miller 1957 repeatedly—wherever the reference has a negative implication. Presumably this is to relieve the other editors of that work, H. Friedmann and R. T. Moore, of the disrespect showered on Alden Miller, one of his favorite targets. Phillips goes out of his way to knock the AOU Check-list Committee, as on p. xxxviii for "completely ignoring the Song Sparrow's . . . spectacular geographic variation," knowing full well that the 1983 edition of the Check-list did not treat subspecies for reasons other than ignoring geographic variation (AOU Check-list, 6th ed., 1983: xiii).

Elsewhere, Phillips seems to imply an evil intent to those who have made what he considers to be errors—which often are merely differences of opinion—as though they are deliberately attempting to obscure knowledge. He goes out of his way to point out errors that have been made by others, as in commenting on possibly erroneous statements about migrating geese and hummingbirds in a discussion of martins, or on egrets and hawks in a discussion of the Bushtit. Errors are more frequently noted than corrected. Many species accounts have sections headed "Erroneously reported . . ." but the basis for the error generally is not given. Often, close reading reveals that the "error" is a difference in identification to subspecies based on recognition or nonrecognition of a particular taxon.

Phillips writes so concisely that in many places his

style is more nearly cryptic than telegraphic. Some paragraphs can be read repeatedly before a glimmer of understanding appears. In many instances one must know as much about the background of a particular matter as Phillips does to be able to understand his discussion of it. Perhaps nowhere is this abbreviated style better expressed than in the long list of references preceding each family grouping of species accounts and the citations to them. One expects citations in the species accounts to be found in that list of references, but often that is not the case. In the account of *Tachycineta bicolor* (p. 17: line 5), Phillips cites Monroe 1968 and Delacour 1938, neither of which is listed among the references to the Hirundinidae. Other examples of "hanging" references abound. Phillips is so intimately familiar with the literature, as well as with the birds, that he seems to assume everyone shares his knowledge. This shows up occasionally also in the "Remarks" sections of species accounts, as in that under *Calocitta formosa* (p. 57).

An important feature of "Known Birds" is the inclusion of keys to members of select families or genera. Often the characters of taxa that Phillips raises to the species level (e.g. *Stelgidopteryx ridgwayi*, *Microcerculus philomela* and *lusciniia*) are noted only in the keys, not in the text. Additional keys would have been helpful.

Species accounts are straightforward, giving citations to the original description with type locality; English, Spanish, and French names; and AOU number. This is followed by statements of breeding, resident, and winter ranges; timing of Middle American migrations; casual, accidental, dubious, or erroneous records; and remarks. The section headed "geographic variation" (where appropriate) introduces a listing of recognized subspecies, with synonyms. The frequent use of question marks by these names, indicating uncertainty, as explained in the Methods (p. lxi), somewhat belies the title of the book. Characters and details of ranges are given for each subspecies, as are often remarks on nomenclature or doubtful earlier records.

Phillips and his contributors name 31 new subspecies in this volume and provide new names for 3 other races. The 15 of these new forms that occur north of the Mexican border have been evaluated by Browning (1990, Proc. Biol. Soc. Washington 103: 432), who accepted 10 of them as valid. The other 16, Mexican and Central American, new subspecies merit further review. My impression is that Browning was generous in accepting the validity of as many of the new forms as he did, and I suspect that many of the more southerly races will end up in synonymies when reviewed by systematists interested in the particular groups. Phillips has an almost uncanny ability to see minor color differences, and his disdain for statistical analysis erodes the value of the often minimal mensural data. In previewing the manuscript for Browning's (1990) analysis, I noted that Phillips tends to name

new taxa from the edges of the range of the species (in contrast to Oberholser, for example, who tended to name geographically intermediate populations), which often represent populations at the ends of clines.

One problem with Phillips' descriptions of new taxa is his failure to designate type specimens. He had type specimens, or type series, in mind and at hand, and gave accurate type localities and the month and day (but not year) of collection. His refusal to give institutional names and catalog numbers, and full date of collection, for types and for critical specimens mentioned in other accounts is discussed in the introductory material. He does not want "to aid and comfort the enemies of science in their hounding of those who contribute to human knowledge for posterity. . . ." These enemies are agents of wildlife law enforcement agencies, who would presumably track back on the catalog information to determine if specimens were taken or imported without appropriate permits—permits they themselves might have refused to issue. Although I agree with Phillips that many of those empowered to give permits do not understand or necessarily wish to advance science, I frankly cannot believe that any enforcement officer would read enough of this book to pick up on the clues of any illegal specimens mentioned. I believe this degree of paranoia is unwarranted, and we all would be better served if Phillips had followed Recommendation 72F of the International Code of Zoological Nomenclature and published full data for his designated types to facilitate future recognition. I wish he had also followed Recommendations 73A and 73C and designated a holotype rather than basing his taxa on a type series. This is another way he expresses his disdain for the Code, but it translates into disrespect for his colleagues. Fortunately, Phillips did annotate specimen labels in museum drawers, and most of his types will be recognized fairly easily and set aside in type collections by future investigators.

Phillips differs in many instances from the subspecific treatment of both the 1957 AOU Check-list (5th ed.) and the Mexican Check-list of that year. He recognizes races not listed in those works (some named in the interval) and synonymizes many that those works recognized. He also refines, or redefines, the ranges of many taxa, at both the specific and subspecific levels. Future students of these groups will have to sort out which treatment is closer to the "truth." He also points out several instances in which putative races are waiting to be named, for which he did not have adequate material.

Most readers will be more interested in nomenclatural differences at the specific and generic levels. There are some differences from AOU 1983 in English names, about which I will not comment. For the sake of continuity, I suggest that English names from the AOU Check-list should be used, even if one thinks that better names exist. The more important changes in scientific names and taxonomic treatment are cat-

aloged below. These differences from the AOU treatment are not as easily rejected as the differences in English names. Each of them establishes a problem that some future taxonomist will have to work out. Students, take note.

In the swallows, Phillips merges the genus *Phaeo-progne* into *Progne*, of which he recognizes 5 species in contrast to the total of 7 species in the two genera listed by the 1983 AOU Check-list; the AOU "species" *cryptoleuca* and *sinaloae* are treated as subspecies of *dominicensis*. Phillips places the species *cyanoleuca* and *pileata* in the genus *Atticora* rather than in *Pygochelidon* and *Notiochelidon*, respectively, as used by the AOU. Phillips separates *Stelgidopteryx ridgwayi* from the Northern Rough-winged Swallow, *Stelgidopteryx serripennis*. He uses the specific name *albifrons* rather than *pyrrhonota* for the Cliff Swallow.

In the Corvidae, Phillips treats the Scrub Jay, *Apelocoma coerulescens*, as three species: Florida Scrub Jay, *A. floridana*; Western Scrub Jay, *A. californica*; and Santa Cruz Jay, *A. insularis*. The name *coerulescens*, applicable to the Florida form, is replaced by *floridana*, a Bartam name that is unavailable under a ruling of the International Commission of Zoological Nomenclature. He treats the Brown Jay in the genus *Psilorhinus* rather than *Cyanocorax*, and merges *Collocitta collei* into *C. formosa*. He also merges the Yellow-billed Magpie with the Black-billed, as *Pica pica nuttalli*. He doubtfully treats *Corvus sinaloae* as a species distinct from *C. imparatus*.

The Bushtit is placed in the genus *Aegithalos* rather than *Psaltriparus*.

Phillips' taxonomy in parts of the Troglodytidae is perhaps the most confusingly different from that of the AOU. He recognizes two species of Nightingale Wrens, *Microcerculus philomela* and *M. luscini*, both distinct from the South American *M. marginatus* with which these both were lumped by the AOU. He treats the Timberline Wren as a member of *Troglodytes* rather than in a separate genus *Thryorchilus*. He also merges the genus *Thryomanes* into *Troglodytes* and replaces the specific name *sissoni* of the Socorro Wren with *insularis*, on the basis that the former was not properly published. This generic merger also necessitates a new name for the San Clemente Island subspecies of Bewick's Wren, for which Rea provides *anthonyi*. Phillips uses the Wilson name *domesticus* rather than Vieillot's familiar *aedon* for the House Wren, from which he separates the Cozumel Island *beani*. Also in this genus, he merges the species *ochraceus* into the South American *solstitialis*, which name has priority. He removes the disjunct *albinucha* from the species *ludovicianus* as a distinct species in the genus *Thryothorus*, although he includes *albinucha* in his key to the genus *Troglodytes*, where he suspects it belongs.

In the Mimidae, Phillips raises the Saint Andrews Island population of mockingbird to species status as *Mimus magnirostris*, separating it from *M. gilvus*; the rest of *gilvus* is incorporated into *M. polyglottos* without

comment. Phillips uses the generic name *Lucar* instead of *Dumetella* for the Gray Catbird. The only other difference in the mimids is the use of the specific name *crissale* for the Crissal Thrasher instead of *dorsale*, as in the 1983 AOU Check-list and most earlier works. Phillips overlooks (or merely does not mention) the fact that the AOU (1984, Auk 101: 348) published the change to *crissale* less than a year after the Check-list was issued, as soon as a ruling from the International Commission became available. However, had he admitted that he would have lost his opportunity to refer to the Check-list Committee as "The Archbishops of Baal," perhaps his choicest slam.

The resolution of any or all of these taxonomic/systematic differences from the AOU treatment is not of issue here. Undoubtedly, Phillips is correct in some instances, and he is almost definitely wrong in others. To an extent, the differences reflect taxonomic viewpoint and the 3-year gap between the publications, but the primary factor may be that of individual vs. conservative committee thinking. One might note, as Phillips did not, that most of the differences in taxonomic treatment were suggested as options in the 1983 AOU Check-list, whose committee members wanted more convincing evidence than was then available to them.

"Known Birds" is an important book, one that deserves consideration by ornithologists of every ilk. The main thrust is taxonomic, and parts will be of most interest to the next taxonomists who study members of the included families, but it is an important reference book in other ways. In one respect it should remind every ecologist, ethologist, and birder that a bird name associated with a locality and date constitutes a distribution record. Much of ornithology involves working with distribution records, and many aspects depend on what the taxonomist can make of your records. "Known Birds" demonstrates the frustration of working with bad records, and how to improve them. "Known Birds" should be on your bookshelf and in your institutional library—but keep it separated from your AOU Check-list to avoid spontaneous combustion.—RICHARD C. BANKS.

**The Petrels: Their Ecology and Breeding Systems.**—John Warham. 1990. London, Academic Press. viii + 440 pp., 149 text figures. ISBN 0-12-735420-4. \$59.95 and £28.50.—Although John Warham has worked for at least 40 years on procellariids, this book is much more than just a summary of a distinguished research career. It is a useful synthesis of the vast and often obscure literature on the more than 100 species of shearwaters, petrels, albatrosses, and fulmars that comprise the avian order with the widest range of body mass (19.5 g to 8.7 kg) and widest distribution, throughout the world's oceans, from the tropics to open leads in polar ice packs. The order's literary

credentials are also impressive, with contributions from Dionysus (200 AD), St. Augustine, and Coleridge (not cited). Warham has also unearthed useful references from journals not examined by many ornithologists, such as *Bocagiana*, *Il-Merill*, and the *Journal of the Manx Museum*. He also appears to have done a good job of covering the Japanese-language literature.

The book opens with nine chapters on the major procellariid taxonomic subdivisions. Each chapter covers morphology, molt, taxonomy, paleontology, distribution, feeding, breeding, population biology, and conservation. The last five chapters cover various stages of breeding biology. There is extensive information on the techniques used to study procellariids, particularly burrowing species. The field worker will appreciate the advice of Figure 11.2 on how to avoid the projectile-vomiting defensive behavior of giant petrel chicks when banding them, although this seems to be a necessary baptism for those working on the seabirds of the Southern Ocean.

"The Petrels" is well written and readable, but probably only a petrel fanatic will read it cover to cover, as the pages are "data-rich" and it is difficult to keep more than 100 species straight for more than short sections. I found it most interesting to browse different topics such as paleontology or life styles for each of the taxonomic groups, or to read one chapter at a sitting.

The potential reader should be warned that Warham uses Harper's pioneering work (1978, New Zealand J. Zool. 5: 509) on the biochemical genetics of the procellariids. During the 1970s electrophoretic gels were compared qualitatively, rather than quantitatively as at present, by examining gene frequency and heterozygosity. Further work may reveal a different story from that presented.

The discussion is limited to two pages, a review of the contrasting views of Ricklefs and Lack on whether food limits chick growth in seabirds. This is a bit disappointing. I would have preferred a chapter with more of Warham's opinions concerning what the procellariids are all about and what general themes of importance these species hold for the rest of ornithology and biology. Warham sprinkles such interpretations through the text, but in general this is not a book that dwells on theory, models, and interpretation, although it is likely to prove a rich source of data for such efforts.

This is an essential book for seabird biologists, both to read and for future reference, and it would be a very useful addition to any academic library that supports ornithology.—DAVID CAMERON DUFFY.

**Birds of Malheur National Wildlife Refuge, Oregon.**—Carroll D. Littlefield; illustrated by Susan Lindstedt. 1990. Corvallis, Oregon State University

Press. vi + 294 pp., 8 maps, 15 black-and-white line drawings. Paper: ISBN 0-87071-361-2, \$15.95; cloth: ISBN 0-87071-360-4, \$25.95.—This is the first book specifically on birds of a U.S. national wildlife refuge. The author provides information on 312 species of birds from Malheur National Wildlife Refuge, an area representing one of the largest freshwater wetland complexes in the western United States. The species accounts are based on sight records and banding, and specimen data from 1874 to 1988. Littlefield provides information on geography and climate, 12 plant communities that range from submergent to dune communities, and bird finding. There are three pages of literature cited, and an appendix of the common and scientific names of plants, mammals, fish, and reptiles mentioned in the text. The index to birds unfortunately does not list the scientific names, nor does it include all names used in the text.

The species accounts occupy 236 pages. There are separate accounts for two subspecies of the Sandhill Crane (*Grus canadensis*), Littlefield's research specialty. Some of the headings of other accounts use trinomials. The status of each form is given with a general statement followed by detailed information on specific dates and localities. The author summarizes published and previously unreported data on distribution and frequency, dates for arrival and departure, peak migration, breeding, and winter occurrence. The author sometimes explains population changes with information on water levels or other changes in habitat. Many accounts also include original information on nesting habitat and breeding biology.

I am troubled by the author's reliance on sight records to document certain species, particularly at the subspecific level. Subspecific identifications are mentioned several times but almost always without evidence that the author or anyone else examined specimens. I especially question Littlefield's references to subspecies of Savannah (*Passerculus sandwichensis*), Fox (*Passerella iliaca*), and Song (*Melospiza melodia*) sparrows. Littlefield also mentions some sight records of subspecies based on geographic probability. Identifying subspecies without specimens is unacceptable.

Other problems in the species accounts are few. The trinomial *gambelli* for the "Tule Goose" (p. 64) should have been *elgasi*. English name of subspecies should have been omitted. The author implies but does not state that the Gray Partridge (*Perdix perdix*) is an introduced species (early introductions in eastern Oregon were probably at the turn of the century; the species was reintroduced in 1951). I am also bothered by Littlefield's statements that "probably a few" Short-tailed Dowitchers (*Limnodromus griseus*) are among larger flocks of Long-billed Dowitchers (*L. scolopaceus*), and that "it is only a matter of time before Western (*Larus occidentalis*) and Mew (*L. canus*) gulls make their appearance" at the refuge. Such statements may have been made to alert readers to look for certain species. However, the publication of names

of birds that might eventually occur, combined with the overzealous use of "how-to" field guides on identifying subspecies and similar species, may lead to misidentifications.

These few problems are much outweighed by the many good qualities of this informative book. I found no typographical errors or misspellings. The line drawings are pleasing, and the maps appear to be accurate and useful. The paperback edition is sturdily bound, but field users probably will prefer the cloth-covered edition. I highly recommend this book to anyone planning to visit the refuge and to anyone interested in western ornithology. It should be a welcome addition to personal as well as institutional libraries.—M. RALPH BROWNING.

**Four Neotropical Rainforests.**—Alwyn H. Gentry (Ed.). 1990. New Haven, Connecticut, Yale University Press. xiii + 627 pp., 96 figures, 112 tables. ISBN 0-300-04722-3. \$57.50.—In the last five years "biodiversity" and "rain-forest conservation" have become hip catchwords for biologist and politician alike. This multiauthored book is the product of a symposium sponsored by the Association for Tropical Biology. Edited by one of the foremost students of the rain forest, it provides a much-needed window on the world of tropical forest research and the progress we are making in cataloging the richness of this realm that is so far removed from most of our daily lives. If nothing else, the "biodiversity boom" has shown thinking naturalists how very little we know about the composition and dynamics of the world's rain forests. This book, first of all, documents this sobering fact, but also casts considerable light where darkness recently dominated, at least for the humid Neotropics.

This volume compares four forest field sites where long-term studies have been carried out by teams of tropical ecologists, mostly botanists, ornithologists, mammalogists, and herpetologists: Barro Colorado Island, Panama (70 years of team research); La Selva, Costa Rica (21 years); Cocha Cashu Station, Manu National Park, Peru (20 years); and the Minimum Critical Size of Ecosystems (MCSE) Reserves, near Manaus, Brazil (11 years).

The 37 contributors have produced 30 chapters that are organized by topic or taxon rather than by site. The book comprises six parts: The Sites (4 chapters), Floristics (5), Birds (5), Mammals (5), Reptiles and Amphibians (5), and Forest Dynamics (6).

The initial section provides a series of useful, succinct introductions to the four field stations. This gives the reader a good idea of the major differences and similarities between the study sites and their histories. The floristics section focuses on familial and generic composition of the forest floras at each site. Species, in general, are not treated because of the difficulty of making between-site comparisons of

poorly known taxa. The chapters on mammals and the herpetofaunas focus on species enumeration, community composition, and relative biomass per unit area.

From a reading of this book, it is safe to say that the bird faunas are the best known of any of the biotic components of the four ecosystems. The remainder of my review will focus on the five bird chapters.

The birds of La Selva are discussed by J. G. Blake, F. G. Stiles, and B. A. Loiselle. They focus on three topics: habitat selection, trophic composition, and the importance of migrants to the bird community. The resident breeding birds are primarily forest-dwelling (70%), whereas the geographic migrants use both forest and nonforest habitats. Mist-netting data (based on 100-capture samples) show no difference in bird species richness between old forest and two ages of secondary regrowth. Is this the product of mist-netting bias? Most interestingly, the authors found abundant evidence of altitudinal (or elevational) migration with the seasons, a phenomenon that requires further study and that also has important implications for the design of protected areas in tropical forests.

The avifauna of Barro Colorado Island (BCI) and the adjacent Pipeline Road forest (PR) is treated by J. R. Karr, based on long-term mist-netting studies. It is remarkable that, in spite of their proximity to each other, 51 bird species have been recorded from BCI and not PR, and 69 from PR but not BCI—more than a quarter of the avifauna as a whole is not shared by the two sites. Mist-netting data, primarily from the Pipeline site, are presented as a species accumulation curve, and the comparison to like data from La Selva shows a remarkable similarity, with 1,000 captures producing ca. 80 species. These figures are comparable to those expected for southeast Asia and New Guinea.

S. K. Robinson and J. W. Terborgh examine the exceedingly rich bird communities of the Cocha Cashu forest site of Amazonian Peru. Using mist-netting and vocal census methods, the two authors have brought together information on the ecology of most of the 435 species of resident land birds that inhabit the forests within 15 km of the field station. Focusing on a specific succession of habitats, from river-edge to mature old forest, their research shows that bird species richness increases monotonically with successional stage. The oldest and grandest forests have the most species. This supports the findings of earlier workers and contradicts the habitat-based mist-netting data for the La Selva chapter. Robinson and Terborgh present their netting data to show that these data, too, are strongly biased, and are not useful for habitat comparisons unless combined with other census methods. Finally, it is interesting to note that some 80 Cocha Cashu species are restricted to early successional habitats—a large number for the interior of one of the earth's great forest wildernesses. Here it becomes clear that the oft-cited distinction between

“man-disturbed” and “undisturbed” forest is often misleading, because natural disturbance—by river meandering and an array of other natural events—is as much a part of tropical forest as it is of other habitats.

R. O. Bierregaard focuses on the understory birds of the MCSE site, on the nutrient-poor soils far to the east of the Cocha Cashu. The 352 species of birds recorded at the scattering of MCSE plots comprise about 200 fewer than at Cocha Cashu, and are comparable to the La Selva and Barro Colorado lists. The mist-netting effort reported for MCSE must dwarf all other tropical efforts: Bierregaard reports ca. 25,000 captures over 136,000 net-hours of effort. This prodigious data set supports the trend found so commonly in long-term netting studies: the gradual decrease in trapping rate. With time, birds become net-shy and capture rate declines. Netting at MCSE also showed that the small frugivorous and nectarivorous passerines so common in the netting samples at the three other sites are much less common on the MCSE plots. This is argued to be a product of the lower productivity of this section of Brazil. In addition, migrants from North America are found to be quite rare here, again in contrast to the other sites.

In the last bird chapter, Karr, Robinson, Blake, and Bierregaard compare and contrast the birds of the four sites. The data show that the Peruvian site is far and away the richest in bird species, and that the three other sites support comparable, poorer communities. Once again, an analysis of the mist-netting data on a per-100-capture basis gives what appear to be very misleading results, with Peru having the lowest numbers of trapped species.

These bird chapters exhibit the diversity of field method and approach employed during the last two decades. The lack of methodological equivalence prevents a true site-by-site comparison. This methodological problem appears also in the other sections, and points out how far we have to go in establishing a workable agenda for the worldwide study of rain-forest biodiversity. My criticism of methods is not a criticism of the book, because this compendium was put together after the fact, and the editor and authors have made the most of what they had to work with. For this they should be congratulated. Here is a very important contribution to the study of Neotropical humid forests. All fieldworkers who focus on rain-forest biotas should have the book, as should all university libraries. I hope the authors see fit to give us an update of these continuing efforts in the year 2000.—BRUCE M. BEEHLER.

#### OTHER ITEMS OF INTEREST

**Survey Designs and Statistical Methods for the Estimation of Avian Population Trends.**—John R.

Sauer and Sam Droege (Eds.). 1990. U.S. Department of Interior, Fish and Wildlife Service Biological Report 90(1). v + 166 pp. ISBN 0895-1926. Available at no cost from Publications Unit, USFWS, 1849 C St., NW, MS 130-ARLSQ, Washington, DC 20240 USA.—This publication is the result of a workshop held in April 1988 to assess various broad-scale surveys of bird populations. The first part of the publication describes the North American Breeding Bird Survey, checklists, Audubon Christmas Counts, Colonial Bird Register, banding at migration stations (such as bird observatories), migrant hawk counts, and British Common Birds Census. These generally descriptive papers do not evaluate the strengths and weaknesses of the various techniques. Some potentially valuable methods are left out, such as the mist-netting Constant Effort Sites Scheme of the British Trust for Ornithology and methods for censusing certain breeding birds such as owls and shorebirds.

The strength of the publication is in its detailed treatment of the Breeding Bird Survey (BBS) method. The BBS is a useful technique, and the Fish and Wildlife Service has invested a great deal of effort in it. The method involves volunteers stopping along roads at 50 stations, one-half mile (800 m) apart, and recording all birds seen or heard for 3 min at each station. This is a "point count" technique, widely used by many investigators, usually involving fewer stations and longer (5, 8, and 10 min) counts. I would have been happier if the title had reflected the editors' concentration on BBS, and it would have been useful if they had discussed in some detail how the method could be modified to avoid some of its biases, for instance those associated with surveys along roads.

The second section, "Methods of trend analysis," is primarily a discussion of "route-regression analysis" of the data taken by the BBS. The advantages of this method are many, not only for the BBS data but for any data that attempt to monitor between-year changes in populations. Some analyses of the other survey methods are also given, but in less detail. The last section involves a trend analysis of the BBS data on the Scissor-tailed Flycatcher.

While the publication does not evaluate in any detail the usefulness of most of the other methods, it does offer some gems. Temple and Cary present data on the method of using checklist records to monitor changes in Wisconsin. Over 5 years 430 observers submitted checklists of the species seen on 30,000 field trips. While these data lack any assessment of population size, recording just presence or absence, they are popular, easy to do, very inexpensive, and year-round. The authors found good agreement of their data with BBS data, Christmas Bird Counts, and some raptor migration watches. I would have been more convinced if some measure of person-days per data point were included. I would expect a checklist to be sensitive to an increase in a species, but perhaps less sensitive to decreases. Birders will go to great

lengths to see a given bird species as it becomes scarce, possibly imparting a lag function to this data set's ability to detect a decline.

Data taken at migration stations for raptors seem to be useful, according to a paper by Titus, Fuller, and Jacobs. The authors found that their study suffered somewhat because few stations take such data. As with all migration data, the source of the migrants usually is not known, and a good year in part of a range can offset a bad year in another, making such data less useful for knowing the circumstances of a population.

Overall, the publication will be helpful to those who wish to use data derived from the BBS or a point count survey and should be in their personal libraries. It will be less useful to anyone who wishes to make an overall evaluation of this or other methods.—  
JOHN RALPH.

**Monitoring Bird Populations in Varying Environments.**—Yrjo Haila, Olli Järvinen, and Pertti Koskimies (Eds.). 1989. *Ann. Zool. Fennici* 26: 149–330. Available for U.S. \$30.00 from Finnish Ornithol. Soc., P. Rautatiekatu 13, SF-00100 Helsinki, Finland.—This volume of 23 contributions is the proceedings of the "10th International Conference on Bird Census Work and Atlas Studies" held in Helsinki in August 1987. As with many symposia, it suffers from uneven treatment of some topics, but the editors have done an adequate job of bringing together current topics of interest in bird censusing.

The Methods section includes several critical evaluations of line transect and point counts, and problems of observer bias. This section is extremely well done and should be read by anyone who works on surveys. The paper by Verner and Milne on observer variability is a cautionary tale. They show how the lack of ability of a single observer among 7 could alter results markedly. Perhaps more rigorous training and screening would have helped. The excellent paper by Koskimies and Poysa describes a valuable method for censusing waterfowl from shore. Massa and Fedrigo describe how to use point counts to compile a winter bird atlas. This is an interesting approach and demonstrates that point counts can be used to good advantage outside of their usual breeding-season applications. Flousek documents the devastating effect of industrial emissions on birds in the spruce forests in Czechoslovakia. This study is especially noteworthy because these kinds of data have long been suppressed by the authorities in Eastern Europe.

The next sections describe some case studies. The most interesting is P. C. Lack's analysis of British warbler populations over 25 years using the territory-mapping Common Birds Census technique. He tabulated data on 7 species of warbler in the genera *Acrocephalus*, *Sylvia*, and *Phylloscopus*, and found that populations of those species wintering in the Sahara

area declined with the onset of drought there. Other papers in these later sections are less cosmic. As the editors point out in their preface, "too much of the effort is wasted in censusing birds without a definite problem in focus." They lament that "knowing exactly the numbers of birds in a haphazardly selected small study area does not usually contribute anything to any field of science." For instance, the paper by Fuller, Stuttgart, and Ray, while interesting, is on only a single 30-ha area. However, the first few papers, and several of the later ones, make this publication worth reading. Although in North America we have made excellent progress in organizing programs such as the Breeding Bird Survey, in other methods we are finally getting ourselves to a level the Europeans attained over the past 10 years. This book will help those planning our effort and evaluating other methods. This publication series should be in university libraries.—C. JOHN RALPH.

**Monitoring Bird Populations.**—Pertti Koskimies and Risto A. Vaisanen (Eds.). 1991. Helsinki, Finland, Zoological Museum, University of Helsinki. 144 pp. ISBN 951-45-5413-2. Available from Natural History Book Service, 2 Wills Rd., Totnes, Devon TQ9 5XN, United Kingdom, at £50.00 surface and £18.00 air (ACCESS, VISA, Diners, and checks drawn on U.S. banks at current exchange rate are accepted).—The Finns have been among the most active in monitoring bird populations, and their preemptive strike in translating their successful 1988 manual into English will establish them as the pace-setters in this increasingly important field. This manual is basically a detailed how-to-do-it treatise on 13 (!) techniques. The contributors, including Olavi Hilden, the late Olli Järvinen, and the editors, are leading Finnish investigators.

The techniques range from the very popular "Point Counts of Breeding Land Birds" and "Mapping Census of Breeding Land Birds" to the more obscure "Register of Faunistically Valuable Records." Each method is discussed following a common outline. First, the "Background and Aims" clearly puts forward the uses and advantages of each method. Then the methods are explicitly detailed in sections entitled (e.g. in point counts): Equipment and time needed; Choosing of a counting route and points; Census period; Time of day; Weather; Field work (how to walk through the plot and record the data); Interpreting observations (how you decide to count an observation as a pair or a single); Filling in the forms (excellent sample forms are provided); and Repeating the count. I found very interesting their methods of counting waterfowl, which could easily be applied in near-shore ocean waters to great advantage, and their Archipelago Birds Census, which is a model for counting breeding water birds on smaller islands. The Night-singing Birds

Census, Raptor Grid Scheme, and Winter Bird Census are also useful.

The volume should be in the library of any biologist who is involved with bird census work in any way. The various authors, translators, and editors are to be congratulated for an excellent job.—C. JOHN RALPH.

**The Ruff.**—Johan G. van Rhijn. 1991. San Diego, California, Academic Press Inc. xii + 209 pp., 14 black-and-white plates, 41 text figures, 24 tables. ISBN 0-85661-062-3. \$39.95.—The study of sexual selection and lek mating behavior has received a great deal of attention in the scientific literature. To integrate for one species the frequently disparate realms of empirical natural history and evolutionary theory of social behaviors, Johan van Rhijn compiled this book about Ruffs (*Philomachus pugnax*). His goal was to combine information from diverse sources in hopes of offering new insights into the evolution of the social system of the Ruff. The book is written for amateur as well as professional bird enthusiasts. Van Rhijn has undertaken the difficult but welcome task of attempting to accomplish all of this with one volume.

Approximately half of the book is devoted to discussions of male behavior and interactions. Most of the information comes from studies of a handful of male display arenas in Roderwolde, near Groningen in the northern part of The Netherlands. Although this detailed discussion may be fatiguing for the novice, those devoted to studying leks will find much of it interesting; it appears to be a thorough treatment. Information on females is sparse, however, but this is true in general for lek breeding species. Only 10 pages are devoted to "the vigilant mother," and these also contain information on nesting and fledging of young.

The fourth of the book's five chapters discusses routes and timing of migration, physiological energetics of movement patterns, sex ratio over time and geographical region, site fidelity, diet, foraging behaviors, molt, and paleontological data. Van Rhijn compiled diverse details, some difficult to find, of lek mating systems to realize his goals. He has assembled an extensive collection of pieces to the puzzle of lek mating behavior.

In the final chapter, van Rhijn attempts to synthesize the data into a scenario of Ruff evolution that includes a phylogeny of calidridine sandpipers. In many ways it is a collection of adaptive stories: why the Ruff is sexually dimorphic, the purpose of territory display, and how parental care evolves, to name just a few. Along with his discussion of each topic, he introduces some of the important scientific questions pertaining to Ruff evolution and uses comparative data from other species to illustrate similarities and differences. While it is not meant to be the final word on Ruff evolution, the book offers new ideas

for study and suggests the importance of considering information that is seldom examined when discussing social evolution.

Van Rhijn's conclusions are not always apparent from the information he provides. The figures and graphs sometimes are misleading. For example, he presents no statistical analyses, and no graphs or figures contain error bars or confidence intervals. While it is understood that technical details are omitted to avoid overwhelming a partially nontechnical audience, he often deals with small sample sizes and it is unclear whether the trends suggested by his figures have any significance. Another example is the phylogenetic tree presented with putative dates of branchings, followed by statements such as "dating on a geological time scale, however, is only a guess" and "the considerable disagreement among taxonomists about the classification of Charadriiformes suggests that phylogenetic relationships are only poorly revealed." It leaves one wondering if any of the information in the figure (and thus the phylogeny from which other conclusions are drawn) should be believed.

Van Rhijn has tried to accomplish so much in this volume that the book is not perfectly suited to any single level of reader. However, most readers will appreciate van Rhijn's description of his enchantment by the Ruffs as a young student and acknowledge the fascinating array of evolutionary questions raised by the Ruffs. Students may find his presentation of ideas a good starting point, and his bibliography will lead them to additional sources. Most advanced readers will appreciate his compilation of diverse facts and may be interested in his interpretation of these facts.—JOHN P. DUMBACHER.

**Birds of the Lower Colorado River Valley.**—K. V. Rosenberg, R. D. Ohmart, W. C. Hunter, and B. W. Anderson. 1991. Tucson, University of Arizona Press. xv + 416 pp. ISBN 0-8165-1174-8. \$40.00.—Most of the "Birds of . . ." books received are defined by some political unit. The best known are state "bird" books. We also have birds of the Grand Canyon, Canadian Rockies, etc. State bird books tend to be annotated checklists, but may include an amazing variety of other topics depending to some degree on the proclivities of the authors and publishers. Some tend a bit more toward being field guides, especially if they relate to a park or some natural area.

This volume deals with a 320-km portion of a single river. Granted, it is perhaps the major river of the

American southwest and so laden with economic and political implications that it is more than simply a geological feature. The bulk of this book is given to species accounts. They provide a valuable summary of the status and habitat of about 400 species. Much of the data were gathered in association with a survey organized by Bob Ohmart. The information in the book both pre- and postdates that effort, which adds even greater perspective to the work. Compared with other "Birds of . . ." books, this one's tone is different.

The Colorado, because of the value of its water resources to humans, has been changed dramatically in the past 70 years. As a consequence, the lands that surround it—both nearby and to some great distances—have also been changed. The Colorado, as most readers know, no longer flows to the sea. All its waters are taken for human use. We have dammed, drained, channeled, and modified it almost beyond recognition. Rosenberg et al. discuss these processes and events with an evenhandedness and patience that could lead to sainthood. They are to be commended.

The vegetation along the river course has changed dramatically. The populations of birds have changed accordingly. Both are chronicled in a chapter on the recent history of the last 320 km of the river. The changes are man-made and have their origin in changes in flow quantities and patterns due directly to attempts at water management. While we think immediately of irrigation projects or water for consumption in southern California, it was interesting to read that steamboat traffic in 1860–1890 affected the cottonwood and willow trees that were used for fuel.

The most sensational aspect of the volume is the review of the research that generated this book. A main concern was to document and ultimately understand the forces that influenced the seasonal habitat use of each species. They did this with some success, but plead for more work. In addition to some meaningful theoretical progress, they used predictions derived from this work in the development of programs in management and habitat manipulation. The results of the efforts in conservation are described and discussed.

Besides its role in the production of valuable data on the birds of the lower Colorado River valley, the book is a font of information on the native and introduced plants, and points to specific solutions that can succeed with proper management. It should be available in most libraries and, while it is not "Men to Match My Mountains," provides interesting reading.—A.H.B.