

BOOK REVIEWS

RAYMOND PIEROTTI, EDITOR

Phylogeny and Classification of Birds. A Study in Molecular Evolution—Charles G. Sibley and Jon E. Ahlquist. 1990. Yale University Press, New Haven, CT. xxiv + 976 p. ISBN 0-300-04085-7. \$100.

Many of the questions in evolutionary biology that are of interest to ornithologists can only be addressed by the comparative method. A frequent limitation of this approach is that, in order to differentiate between historical (phylogenetic) and other effects, one must have a reliable phylogeny for the taxa under study. Sibley and Ahlquist present what appears to be the largest and most massively detailed phylogeny for birds ever attempted, based on extensive DNA hybridization comparisons. Not surprisingly, it has been received enthusiastically by many ornithologists longing for a phylogenetic framework for their studies (Diamond, *Nature* 350:537–538; Harvey and Cotgreave, *Trends in Ecol. and Evol.* 6:268–269), and has already been incorporated into computerized databases at several institutions as an aid to comparative studies of avian evolution.

The enthusiasm with which this phylogeny has been accepted by non-systematists does not necessarily mean that Sibley and Ahlquist have gotten it right. In fact, many systematists have already criticized this work on a variety of philosophical and methodological grounds. To non-systematists who have grown tired of the decades-long acrimonious debates over systematic philosophies and methodologies, the temptation may be strong to ignore criticisms emanating from a camp that is never quiet. My conclusion, however, is that the phylogeny of Sibley and Ahlquist is not what it appears and should *not* be used as the foundation of comparative studies for the reasons that follow.

In this review, I suggest that an evaluation of the scientific merit of the Sibley and Ahlquist phylogeny can be made without making value judgements about alternative systematic philosophies, computer algorithms, distance measures, etc. Even if one accepts this work on its own premises (e.g., to have no qualms about the validity of distance data, or of the undocumented data massage [Gill and Sheldon, *Science* 252: 1003–1005]), the phylogeny presented by Sibley and Ahlquist *cannot be reproduced from their own data using the methods they describe*.

The “Tapestry,” a tree containing 1,118 taxa and spanning 29 pages, is the focal point of my review because the authors identify it, and the classification based upon it, as the goal of their research (p. 8). Furthermore, it is specifically the Tapestry that has generated so much enthusiasm among non-systematists.

The authors tell us that the Tapestry was produced using the UPGMA algorithm. This algorithm constructs a branching structure, often interpreted as an evolutionary tree, from a distance matrix containing a distance value between each pair of taxa. In DNA hybridization studies, these distance values are obtained experimentally by determining the degree of similarity between radioactively labeled DNA from one taxon

(the tracer DNA) and the unlabeled (driver) DNA from another taxon. For the Tapestry with its 1,118 taxa, a minimum of 624,403 hybridizations are required.

Clearly, there is a discrepancy between what was required to produce a UPGMA-derived Tapestry and the work actually conducted (26,554 hybridizations or 4% of the total required). One reason for this discrepancy is the fact that only 307 of the 1,118 included taxa were used as tracers (indicated by an * in the Tapestry). Because DNA hybridization data are comparative in nature, it is impossible to obtain a distance between two taxa for which DNA was not labeled (i.e., between two driver taxa). Consequently, distances between pairs of the 811 unlabeled (driver) taxa used in this study *could not have been obtained*, leaving 577,432 (92%) of the necessary distance values unknown. The UPGMA algorithm cannot produce a tree from a distance matrix with an empty cell, much less when over 90% of the values are undefined.

Therefore, the authors’ claims notwithstanding (see legend for Fig. 353), the Tapestry cannot be a UPGMA-generated tree. In the text (p. 150) the authors state that the UPGMA was modified, although they do not indicate exactly how: “Figures 353–385 were derived from average linkage clustering done by hand, thus empty cells could be ignored and varying numbers of taxa and branches within principal groups could be used. The figures derived from UPGMA also contain many branches for which few measurements were made; thus complete matrices are not available, even among the species used as tracers.”

The authors imply that implementation of the UPGMA algorithm by hand enabled them to avoid the requirement of a complete data matrix. Implementing an algorithm by hand rather than on a computer in no way alters the requirements of that algorithm. When an impossible task is required, we may choose to modify the algorithm with additional assumptions to permit continued analysis while a computer would halt processing and issue an error message. Of course, for the product to be interpretable it is necessary to explicitly document any modifications.

Although the authors only describe UPGMA, Sibley et al. (*Evolutionary Biology* 21:97–125) indicate a means by which the Tapestry could have been formed by rigorous, repeatable means. First, the authors could have performed a UPGMA analysis on a complete matrix for tracer species. Then, assuming a perfectly functioning molecular clock they could have added the driver taxa. The rules the authors seem to have applied are that (1) each driver taxon was first associated with a single tracer taxon to which it was found to be most similar, and (2) then for each tracer species, all drivers that had Delta $T_{50}H$ values differing by less than 0.2 were placed together at a polychotomous node.

For example, Sibley and Ahlquist (p. 396–428, *in* Buckley et al. [eds.], *Neotropical ornithology. Ornithological Monographs* 36. American Ornithologists’ Union, Washington, DC) hybridized the tracer *Say-*

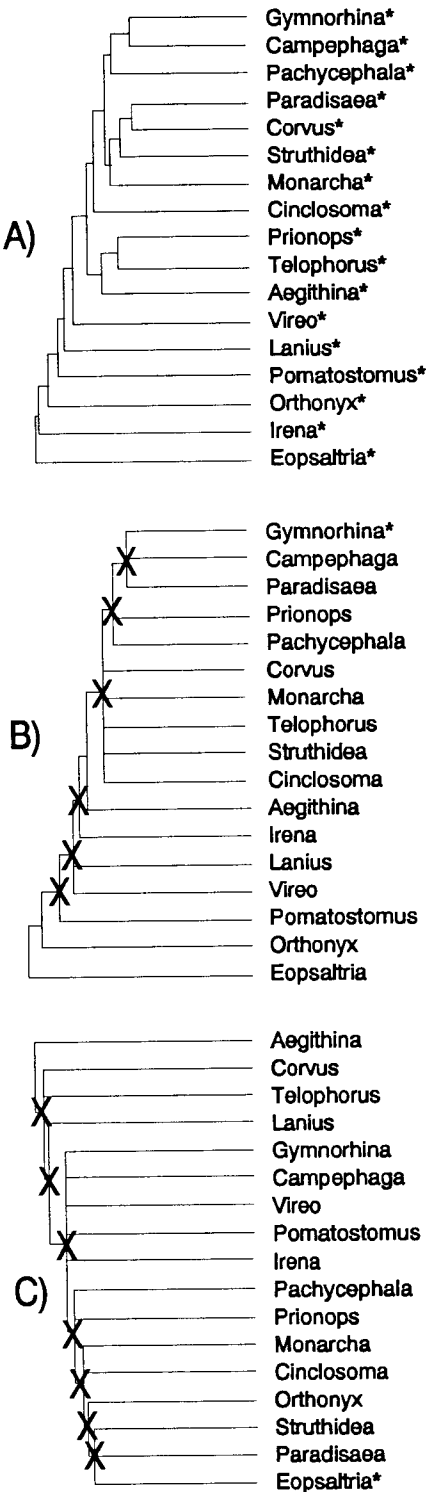


FIGURE 1. Illustration of the reliability of using distances from a single tracer taxon to a set of driver taxa

ornis phoebe with three drivers, *Muscigralla*, *Pyrocephalus*, and *Sublegatus*, and obtained Delta T₅₀H values of 4.4 for all three comparisons. In Figure 373, these drivers are placed equidistant not only from the tracer but also from each other. Experienced users of phylogenetic trees should recognize that this polychotomous node represents uncertainty about the phylogenetic affinities of the contributing lineages. However, most readers will also interpret this node as indicating that *Muscigralla*, *Pyrocephalus*, and *Sublegatus* are separated from each other by approximately 4.4 degrees (1.8 million years). In fact, given the assumption of a molecular clock, the DNA data indicate that 4.4 degrees is the **maximum** distance between these taxa. It is conceivable that any pair, or perhaps even all three, of these taxa are genetically identical. Inclusion of *Muscigralla*, *Pyrocephalus*, and *Sublegatus* in the tree implies information about their relationships that simply is not present in the data collected by Sibley and Ahlquist. For over 30% of the driver taxa included in the Tapestry, relationships among these taxa are explicitly hypothesized in exactly this same manner *when no supporting data exist*.

However, this particular problem arises only when multiple driver taxa are equidistant from a tracer taxon. When driver taxa are found to be at variable distances from a tracer taxon they could conceivably be added to a UPGMA tree by assuming a molecular clock. For example, in Figure 373 the driver *Myiozetetes* is placed 0.2 degrees closer to the tracer *Myiarchus tyrannulus* than is the driver *Attila*. This arrangement follows from the fact that *Myiozetetes* and *Attila* have Delta T₅₀H values of 2.9 and 3.1 respectively when compared to the tracer (p. 411 in Ornithological Monograph 36). Fortunately, the authors provide a means of determining whether their method for including driver taxa in the Tapestry is internally consistent.

A complete data matrix containing seventeen composite passerine taxa (Fig. 347) was analyzed by the authors using the KITSCH algorithm, which assumes constant rates of molecular evolution, and the resultant tree is presented here in Figure 1A. We can examine whether inclusion of driver taxa using the method outlined above is internally consistent by comparing their KITSCH tree with a structure generated from just one row of the data matrix (equivalent to having a single tracer taxon). For example, the structure obtained from an examination of distance measures from *Gymnorhina* to the 12 remaining taxa in the matrix (Fig. 1B) contains six nodes (indicated by X's) that conflict with the KITSCH tree obtained from the complete matrix.

←

to construct a partial branching structure. (A) KITSCH tree for members of the Corvoidea (Sibley and Ahlquist 1990; Fig. 348) derived from a complete data matrix. (B) Branching diagram obtained from Delta T₅₀H values between the tracer *Gymnorhina* and each of the remaining sixteen taxa. (C) Branching diagram obtained from Delta T₅₀H values between tracer *Eopsaltria* and each of the remaining sixteen taxa. Tracer taxa are identified by an *. Nodes found in diagrams (B) or (C) and not found in the KITSCH tree derived from a complete matrix are identified by X.

Similarly, 55% of the nodes constructed from Figures 325–352 using this same method, conflict with the relationships depicted in the Tapestry. Note that the situation is much worse if by chance the tracer taxon is in fact the oldest lineage. For example, if in the former example, *Eopsaltria* rather than *Gymnorhina* had been the only tracer taxon from this assemblage, the resulting branching sequence (Fig. 1C) contains seven nodes, all of which conflict with the KITSCH tree. When the oldest lineage as indicated by the Tapestry is chosen as the tracer for each of the complete data matrices (Figs. 325–352) all resultant nodes conflict with the relationships shown in the Tapestry. Therefore, the data presented by the authors indicate that attempts to place driver taxa in the manner discussed would result in from 50% to 100% erroneous placement. This high rate of failure raises doubts about the authors' ability to include any driver taxa.

In light of the fact that the data matrix (1) lacks distance values between pairs of unlabeled taxa that would permit them to be included in a UPGMA analysis, and (2) attempts to place driver taxa in a tree by assuming a perfectly functioning molecular clock conflict with trees developed from complete matrices, it is essential that all driver taxa included in the Tapestry be ignored. Of the 876 nodes contained in the Tapestry, fully 65% have no empirical support because taxa contributing to those nodes were not radioactively labeled. Although many of the 818 driver taxa included in the Tapestry represent additional members of an assemblage for which other taxa were included as tracers, some represent key "lineages." Thirty-three taxa at the Tribe level or above in the Sibley and Ahlquist classification were not included as tracers (excluding the six listed by the authors as *incertae sedis*) and, therefore, are without support from the DNA hybridization study (e.g., Dendrocygnidae, Oxyurinae, Cygninae, Anserini, Turnicae, Lybioidea, etc. . .).

Unfortunately, even removal of all driver taxa from the Tapestry doesn't produce an interpretable branching structure. There are 46,971 pairwise comparisons for the 307 tracer taxa. This figure is still well in excess of the total number of distance values generated in this study, many of which were between tracer taxa and the 811 driver taxa. Although the authors have not indicated how they modified the UPGMA, it is possible that the authors constructed the Tapestry of tracer taxa using sequential UPGMA analyses. That is, a number of small but complete data matrices may have been constructed (requiring a number of assumptions of monophyly that would have had to have been stated explicitly) and a UPGMA tree generated for each. Subsequently, the authors may have constructed additional small but complete data matrices using representatives from each of these initial data sets and used a UPGMA analysis to link each of these smaller initial trees together. However, if this were true, a complete distance matrix should be evident at the higher taxonomic levels. Sibley and Ahlquist identify 23 avian orders as the result of their work. Construction of a UPGMA tree for these taxa requires a much more manageable 253 distance values. However, Figures 18–352 indicate that the authors had data for only 123 of these comparisons (48.6%). Clearly, the authors have additional data they chose not to publish, but it is unlikely that inclusion of these data would result in a complete matrix. On

page 267, in a discussion of the melting curves, the authors state that "the sets in the figures cover as much of the domain of avian relationships as our data permitted and space allowed. Any gaps are due to lack of DNAs or to lack of useful data. Perfection remains elusive."

Two conclusions can be drawn from the above points. First, it remains unclear whether any portion of the Tapestry resulted from a true UPGMA analysis. Second, it is obvious that even after removal of driver taxa, a large number of taxa and nodes remain that have been included in a manner that remains unknown. Without the entire set of pairwise values obtained by the authors, it is impossible to determine which nodes in the Tapestry are the result of a true UPGMA analysis and which were placed by hand on the basis of incomplete information and unstated assumptions.

Despite the foregoing discussion, some readers might still be inclined to use the Tapestry as the foundation for their comparative studies. Even with all of its faults, it could be argued that the Tapestry is still the best available phylogeny for birds of the world. However, as demonstrated in this review, from a philosophical perspective the Tapestry is no better, and no worse, than previous classifications and phylogenies of birds of the world; all are non-rigorous. I hasten to add that my emphasis on scientific rigor should by no means be interpreted as an assumption that rigorously generated phylogenies are always correct. However, without rigor, the scientific community has no means of assessing whether the results of a study follow from reasonable assumptions and interpretations.

The concerns outlined above represent logical flaws in the construction of the Tapestry. It is important to note that I have reached this conclusion without questioning the authors' systematic philosophy, choice of distance algorithm, distance measure, or correction factors, although all of these have been criticized by others. Based solely upon consideration of the information given by the authors (the number of experiments conducted, the taxa that were used as tracers, and the tree-building algorithm used), the Tapestry cannot have been constructed as claimed. If it is impossible to determine how the Tapestry was constructed, it is equally impossible to extract information from it. Consequently, the information implied by the Tapestry cannot, and should not, be used in a scientific context.

This conclusion does not mean that the research of Sibley and Ahlquist presented in this book is without value. On the contrary, there remains much of great interest. However, scientists must focus their attention not on the Tapestry, which has great allure due to the large number of included taxa, but rather on the topologies and data in Figures 325–352. These figures contain the valuable product of the extensive research conducted by Sibley and Ahlquist: complete data matrices. Accompanying these matrices are branching structures derived using the FITCH or KITSCH algorithms. Subsequent workers may elect to use the topologies presented or to reanalyze the matrices using alternative algorithms. Perhaps, in the future, the authors will consider publishing the entire set of distance values obtained during their study. Their work will be of limited value until they do so.—SCOTT M. LAN-

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Seabirds of the Farallon Islands—David G. Ainley and Robert J. Boekelheide. 1990. Stanford University Press, Stanford, CA. 450 p. \$60.00 (hardback).

When I was a boy I often had the opportunity to glimpse the Farallon Islands as I trudged the few blocks home from school in San Francisco's Sunset District. Often veiled in fog, these small offshore islands, only 25 miles from San Francisco, were a mystery to me and everyone I knew. We had no idea that these islands constituted one of America's major seabird colonies. Ainley and Boekelheide's book provides the first extensive, detailed information about the islands and their avifauna.

Little was written about these islands between early accounts of visits late last century and the mid-1970s. In 1971 the Point Reyes Bird Observatory began a comprehensive study of the numbers, breeding biology and foraging ecology of the 11 species of seabirds breeding on the Farallons (the foraging ecology of the Sooty Shearwater, an abundant summer visitor, was also studied). Studies continued through 1983 and, for some variables and some species, beyond. It appears that Ainley and Boekelheide's book was originally intended to summarize only those data collected through 1983. Apparently, work on the book progressed as some aspects of the fieldwork continued. Data for later years were added to some portions of the book but not others. For example, most Appendices summarize only those data that were collected through 1983, but associated portions of the text generally present information collected through the mid-1980s. It is unfortunate that the book does not provide both a consistent compilation and discussion of data, and, given its publication in late 1990, a treatment of data collected in the late 1980s.

The stated aim of the book is to explain the structure and dynamics of the seabird community. The study does represent a major effort in documenting seasonal and annual variation in reproductive success of virtually all the breeding species over a 13-year (in some instances longer) span, providing excellent information for species comparisons. Regional climate and physical and biological oceanography are also well documented. However, the study, like virtually all others of this sort, falters in the attempt to fully integrate information about marine conditions and foraging ecology of the avifauna due to relatively imprecise information about patterns and variability in abundance and availability of zooplankton and forage fish.

There are 12 chapters; Ainley is the lead author or sole author of five of them; Boekelheide is the lead author on three and a coauthor on five others. This pattern results in very comparable, well-organized presentations throughout the book, an excellent feature not often found in edited volumes with numerous contributions.

The first chapter sets the stage, posing questions about the role of interspecific competition for food and nest sites to which Ainley returns in the final chapter. The introductory chapter also provides a brief overview of the methods and rationale of data collection and anal-

ysis; it ends with a brief history of the population histories of Farallon seabirds.

Chapter 2 summarizes seasonal and annual variability in climate and oceanography in the region, emphasizing seasonal development of coastal upwelling. Advection of nutrients from the north also appears to be important. Although the importance of annual variation in upwelling is emphasized throughout the remainder of the book, no index of upwelling is developed and used extensively in later chapters to adequately account for annual variability in population status and breeding success of the seabirds. This is unfortunate because it is unclear whether upwelling or advection of nutrients from the north is the primary factor influencing the foraging and breeding ecology of the seabirds (no mention is made of terrestrial inputs through the Golden Gate, even though it is later mentioned that seabirds concentrate at the front caused by the seaward movement of this plume [p. 58]). Zooplankton abundance is presented only as a series of monthly means for the period 1949–1979 in waters near the Farallon Islands. It is unclear from the text why annual variability in zooplankton abundance was not summarized in one way or another to examine relationships between numbers and reproductive success of the seabirds and zooplankton abundance in later chapters.

Chapter 2 closes with information on availability of prey. Unfortunately, abundance of juvenile rockfish (*Sebastes* spp.), the primary prey of all offshore piscivores in years of good reproduction, was assessed only qualitatively during the study period, precluding quantitative analysis of the relationship between prey abundance and reproductive success. I had always thought that the Northern Anchovy (*Engraulis mordax*) would be the key prey, but its importance during the period of this study apparently was minor relative to rockfish. Throughout the book, little mention of the Sardine, *Sardinops caerulea*, is made. This species seems to respond favorably to warm conditions, but it virtually disappeared in the 1940s and 1950s, perhaps because of heavy fishing. In pristine conditions this species could have been an important prey during warm-water years. The authors could have developed indices of abundance of those age classes of various prey species that may be important to seabirds and used them in later chapters to examine relationships between prey abundance and the biology of the seabirds.

Chapter 3 presents an extensive treatment of feeding ecology. Data were collected in numerous ways (at-sea transects throughout the region in April and June, 1985 and 1986); 1–3 censuses monthly in 1972–1980 from a supply vessel making a transect from the Golden Gate to the Farallons, "semicasual" or comprehensive counts of foraging "flocks" within 3 km of a vantage point on Southeast Farallon Island in 1972–1983, dive times at a site near the island in 20-m-deep water, and nest relief schedules for cormorants (*Phalacrocorax* spp.) and Common Murres (*Uria aalge*) for several years. It is difficult to wade through the diverse approaches to foraging ecology and develop a perspective on the underlying patterns.

To portray foraging areas of each species during four surveys, the authors assigned a density estimate for each block in a grid system. Uncensused blocks were assigned average densities of surrounding blocks. I do not understand how density estimates were made for

blocks on the perimeter even when no transects passed through them; this procedure seems to artificially inflate the data base. Figures show that transect patterns and coverage differed for each survey, making among-survey comparisons difficult. The figures for each of the four survey periods do show general patterns well, but the calculations of association to compare distributions at sea were limited to the June 1985 and June 1986 surveys and were based on all blocks, rather than only on those blocks actually surveyed both times. Data on food habits are voluminous and result primarily from observations of birds carrying prey and regurgitations. Apparently, some adults were collected at sea, but no details are provided. Sample sizes are expressed only in terms of numbers of prey items; I found myself looking for numbers of samples (by sample type), but this information is not presented.

Tables 3.3–3.5 present interannual comparisons in formats found throughout the remainder of the book. Favorable and unfavorable years (cold-water and warm-water, respectively) are shown respectively in italics and bold type in these tables, and even a quick glance shows that typically there are not clear groupings by this criterion. In general, there is only a loose correspondence between the tables and the text wherever such tables are presented. The text commonly overstates the degree of clumping of unfavorable years.

Chapters 4–11 present data on the breeding biology of each species or species group. Each chapter starts with an informal but informative introduction followed by a section on methods. The status of the Farallon population is then reviewed with a table showing numbers in California and elsewhere. There are some confusing disparities between these tables and associated text. For example, Table 8.1 provides murre numbers in western North America from 1977–1979, citing a figure of 46,000 for the Farallons. The text states that the Farallons represent the largest concentrations of murres outside Alaska and that two colonies within California exceeded 100,000 birds during a 1979–1980 count period. It would be far less confusing if tables and text were based on the same data.

Even with a small army of observers, simultaneous documentation of reproductive performance of 11 species is a daunting task. Readers expecting extensive replication of study plots will be disappointed. The bulk of the information for all species is based on one to several plots. For example, murres were studied on one plot of about 25 m² from 1972 to 1976; thereafter, because densities had increased, murres were studied on a subsection of that plot (15 m²).

Generalizations about annual reproduction on the Farallons are certainly limited (or precluded) when studies have been limited to a few (or one) study plots, but the authors of the various chapters and the editors apparently felt that annual differences were so pronounced that they would mask spatial variability within years. While I sympathize with the logistical difficulties of daily (or near daily) watches of one to several study plots lasting several hours on 11 species, it must be recognized that results based on one plot or results pooled among a few plots are not necessarily representative of the regional system.

Breeding chronology is presented in figures, with asterisks denoting significant skewness; skewness is used

as an index of synchrony. Kurtosis is also used as a measure of synchrony. To me, use of both skewness and kurtosis to examine synchrony is questionable. If distributions of laying dates are positively skewed, then not only are more pairs breeding somewhat earlier, but also others are breeding much later than would be expected if the data were normally distributed. Similarly, leptokurtotic distributions have relatively more observations at the extremes, as well as at the mean, than normal distributions with the same mean and variance. Skewness in laying dates is plotted against the decrease in sea-surface temperature in late spring (the “spring transition”) for several species, and the results vary strikingly among species (e.g., positive for the Common Murre, negative for the Pigeon Guillemot, *Cephus columba*, and obviously quadratic for the Cassin’s Auklet, *Ptychoramphus aleuticus*). Given my conceptual difficulty in interpreting skewness, I would have welcomed analyses and graphs of median laying date (and productivity) vs. the spring transition rather than, or in addition to, the graphs of skewness vs. the spring transition.

Statistical approaches are outlined only briefly, but they often appear inadequate or inappropriate, as shown in the following examples. Annual differences in mean laying dates are evaluated using the Student-Newman-Kuels pairwise comparison procedure on raw values. It would be more appropriate to first log transform the data to minimize skewness or do an analysis of variance (ANOVA) and pairwise comparisons (e.g., Tukey’s) on the ranked values (Kruskal-Wallis test). Paradoxically, the parametric approach is justified in the introduction with the statement that the normality assumption was usually satisfied (p. 16). Violations of normality assumptions are certainly extreme for chick production of all species because success is a discrete variable with only two values for species laying one egg and at most 3–4 for species laying larger clutches. Use of ANOVA and the Student-Newman-Kuels procedure is not appropriate in this context (see p. 233 in Conover, W. J. 1980. Practical nonparametric statistics for a powerful alternative).

It is unclear to me how annual variability in variables such as hatching success and fledging success was actually analyzed. For the Common Murre, for example, the authors state that they conducted *t*-tests after arcsine transformations. However, murres lay only one egg, and data were collected only on one plot in each year. Therefore, the data are counts of successful and failed attempts for each year. Therefore, there is only one value, not a sample of values, for each year. In addition, it is clearly inappropriate to use a *t*-test to compare more than two years.

Analyses of eggs and chicks for species laying more than one egg apparently did not treat eggs and chicks from the same nests as related samples. For example, annual variation in growth parameters of older and younger Pigeon Guillemot chicks in the same broods was examined using ANOVA but the design (which should have specified year as a fixed grouping factor and chick category as a repeated measure within broods) is not clearly stated.

In some instances data were pooled for one criterion when examining variability with respect to another and then the procedure was reversed. There are more ef-

fective analytical approaches to portray relationships. For asymptotic weights of Cassin's Auklets, for example, there were both significant seasonal and annual effects. An analysis of covariance, grouping the data by year and specifying date as a covariate could show whether year itself is important or effects of hatching date are expressed similarly in all years. Similarly, differences between study plots and among years in dates of clutch initiation of Western Gulls (*Larus occidentalis*) were examined separately, pooling data for one factor when examining the effect of the other. The appropriate analysis would be a two-factor ANOVA on the raw values or ranks, grouping the data by plot and year. Based on these examples and numerous others, readers should not be expecting rigorous statistical treatment of the data.

Chapters 4–11 provide excellent information on within- and among-year variability in breeding success of each species. The associated Appendices provide detailed summaries of the breeding data for each species and are invaluable to researchers looking for comparative data. While reading each of these chapters, however, I hoped to see a detailed examination of reproductive success relative to indices of upwelling conditions, zooplankton abundance, and abundance of potential prey. Such examinations were either missing or cursory.

The final chapter examines the evidence for competition for nest sites and food. Ainley argues persuasively that nest site competition is occurring and probably limits breeding numbers of certain species at present. Interestingly, such competition would have been much more intense when various populations were markedly higher (mid-1800s). The data on food habits and foraging distributions show that overlap is high in good reproductive years and low in poor years. Ainley concludes that ecological specialization "is more a function of surviving difficult times than of maximizing production of offspring" (p. 373).

High overlap occurs in years when food is "superabundant," i.e., in years of strong upwelling. Although I like this conclusion because I think the roles of density dependence and interspecific competition are generally overstated by seabird biologists, I do not think that Ainley has demonstrated "superabundance." As noted earlier in the chapter, despite major differences in potential fecundity among species in this community, realized fecundity during the years of this study varied much less among species than might be expected. This suggests to me either that food may only rarely be superabundant (when all species would have reproductive success that is near their maximum potential) or that food generally is not the key factor limiting reproductive success in "good" years.

Long-term changes in the prey base due to human fishing activities and environmental change deserve more attention in the final chapter. The demise of the sardine and major changes in anchovy stocks in the past century require a multispecies perspective on the dynamics of foods available to the seabirds. I would also like to see more discussion of the upwelling system from a regional perspective, e.g., are the post-breeding northward movements seen in several of the species related to later development of upwelling and availability of key prey to the north?

I found few grammatical errors or misspellings. Generally, the tables present the data well. The figures that are presented in histogram form generally portray the points made in the text convincingly. However, the use of a single topographic map of the islands to repeatedly present maps of nesting distribution is not very effective. Various strip charts (e.g., Fig. 2.4) distill the raw data so little that patterns stated in the text are not clearly evident.

Two fundamental questions are: Should you buy the book and should you read the book? For me, the book will be a valuable reference on breeding biology of several species for the foreseeable future, and I am glad to have a copy on my bookshelf. If you are a seabird biologist, you will certainly want to read the book; probably you should buy it. Certainly, you will want a nearby library to purchase the book if you do not do so yourself. The book is not just for seabird biologists, although I did find the comparisons to terrestrial songbirds too abbreviated to be very instructive. The book provides detailed accounts of the breeding biology of long-lived species with low potential fecundity; these species show surprisingly varied responses to highly variable environmental conditions. Consequently, the book will be useful not only to seabird biologists, but also to any professionals studying population and community ecology. The book will also provide nonprofessionals with an exceptionally rich account of the natural history of seabirds breeding remarkably close to one of the most urbanized regions in America.—EDWARD C. MURPHY, Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775-0180.

Food Hoarding in Animals—Stephen B. Vander Wall. 1990. University of Chicago Press, Chicago, IL. 445 p.

Consider this sample of the remarkable variety of food-storing phenomena. An Australian dung beetle (*Onthophagus parvus*) piggybacks on a wallabee rump, falls to the ground with a fecal pellet, and buries the pellet as a brood mass. A red fox (*Vulpes vulpes*) buries Black-headed Gull (*Larus ridibundus*) eggs in the sand dunes of Scotland, returning to retrieve them a month or two later. A Northern Shrike (*Lanius excubitor*) in Algeria skewers dates on the spines of palm fronds during the spring to supplement its summer diet. A honey ant (*Myrmecocystus mexicanus*) carries nectar and honeydew to the nest where it is transferred to the gasters of specialized conspecifics that cling to the ceiling and act as living honey pots. A male MacGregor's Bowerbird (*Amblyornis macgregoriae*) wedges a ripe fruit in the fork of a branch near his bower, where it will be available as a snack while he waits to court visiting females.

Perhaps the most striking aspect of the food-hoarding literature is the disparity between how much we already know about ecological and behavioral aspects of hoarding in a some species (mostly arthropods) and how little we know about the rest. Vander Wall's book, *Food hoarding in animals*, is an exhaustive (and occasionally exhausting) account of how and why animals alter the spatial and temporal distribution of their food. Confronted with a catalog of the widespread nature of food

caching and its importance to the success of so many species, it becomes immediately obvious that we have only just begun to understand the basic phenomena and to pose the most interesting questions. Vander Wall integrates information on 286 species of birds and mammals and 22 families of arthropods. While such a comprehensive treatment cannot avoid being overwhelming in places, the organization of the book, however, mitigates the problem of the density of information. The first half consists of discussions of the ecological, evolutionary, and behavioral issues concerning food hoarding (e.g., cache-loss and protecting behavior, food-hoarding animals as dispersers of plants). The second half is organized taxonomically. There is therefore some inevitable repetition of information in each half. The advantage of this organization outweighs the added length, however, in that it reflects the primary reason for writing (and reading) review volumes: we can view the same data from various points of view simultaneously, in this case, taxonomically and functionally. Vander Wall's book reads as though he is able to keep many questions in the air at once.

The best chapters were those in which Vander Wall collects well-dispersed observations and ideas and bundles them together into a cohesive package. For example, the chapter on the evolution of food hoarding contains a section on the proximal conditions that led to the development of hoarding in its various forms. For many species of birds it seems that food caching may have evolved from leaving food at a feeding site and that food concealment may have initially been a consequence of food-handling behaviors (e.g., hammering large food items into cracks where they could be broken). For small mammals, by contrast, food storage was probably occasioned by the advantage of transport of food to a safe refuge. And prey storage in large carnivores may have evolved from concealment of food from competitors. Nearly all the hypotheses about initial steps in the evolution of hoarding involve peculiar food preparation; Vander Wall suggests that lack of a precursor behavior might account for the absence of hoarding in species that could conceivably benefit from it, e.g., seed-eating sparrows. He then shows, via a complex but decipherable flow diagram, how a relatively non-specialized hoarding species could be transformed by ecological circumstances into a specialized hoarder. Some generality in the adaptive strategies exhibited by food-storing species is thus distilled from their variation. Vander Wall also understands animal-plant relationships very thoroughly; the chapter on food-hoarding animals as dispersers of plants is particularly rich and informative. I learned, for instance, how corvids have been responsible for the migrations of certain conifers during the Holocene, and that seed dispersal by caching birds is critical to establishing and maintaining populations of trees across fragmented landscapes.

There are two small weak areas in the book. First, the section on motivational aspects of hoarding is confused and of questionable relevance. As Vander Wall admits, most of the data are from studies with captive Norway rats, which are not known to hoard in the wild. The data are contradictory and the theory is mostly 50 years out-of-date. The discussion of the relation be-

tween hunger and hoarding in wild animals is also somewhat flawed. I found unconvincing the data presented in support of the notion that hoarding and eating are independently motivated. Vander Wall's presentation of diurnal patterns of caching in passerines was much more interesting than any of the rather arbitrary studies with lab rats. McNamara et al. (1990) have recently developed two models to account for daily routines of storage and retrieval in parids.

Second, there is virtually no consideration of the adaptive specialization of the mechanisms underlying the recovery of stored food. In both the chapter on evolution of hoarding and that on cache-recovery behavior, the psychological issues are not fully addressed. The experiments supporting the role of memory in cache recovery by birds are, for the most part, adequately described, but the larger theoretical issues of how memory structure may relate to ecological and evolutionary variables are not elaborated. Sherry (1988) argues convincingly that the cache-recovery phenomenon is prime for the study of the adaptive specialization of learning mechanisms. The nature of the memory that makes cache recovery possible is as central to the understanding of food hoarding as is, for instance, the nature of the food transport structures. Nevertheless, the treatment of cache-recovery research does indicate that the phenomena of food hoarding provide an arena where ecological, behavioral, and cognitive questions intersect.

Knowing very little about arthropod food storage, I appreciated the presentation of wasp, bee, and beetle data alongside the more familiar bird and mammal data. Perhaps in the distant future, we will know as much about vertebrate food storage and use as we do about, say, that of cell-provisioning arthropods. Indeed, as Vander Wall indicates, it is sobering to comprehend how little we understand about the use of stored food by vertebrate foragers and its implications for nutrition, life-history tactics, and community structure.

The quality and variety of the information on food caching in birds renders this book extremely useful for any ornithologist with an interest in food relations. This is a well-written, carefully organized, attractive book. In the taxonomic section, for example, are tables summarizing the food-storing behavior (dispersion of seeds, food type, substrate, storage duration and use) of related species or groups. The index is thorough and I particularly liked the simple, confident drawings by Marilyn Hoff Stewart depicting various caching scenes. Store it for future use.—SONJA I. YOERG, Department of Psychology, California State University, Hayward, CA 94542.

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