ECOLOGY

Voices from Bird Bones

Jared Diamond

Paleontologists studying animal bones excavated from early archaeological sites on Pacific islands have identified many previously unknown bird species that evidently became extinct soon after human arrival. Those extinctions have implications for human history in the Pacific, biogeography, and evolutionary biology. Two recent books, which complement each other geographically and by chance appeared simultaneously, summarize current knowledge of extinct birds on all Pacific island groups except Hawaii.

Extinct Birds of New Zealand

by Alan Tennyson and Paul Martinson

Te Papa Press, Wellington, New Zealand, 2006. 190 pp. NZ$65. ISBN 9780909010218.

Extinction and Biogeography of Tropical Pacific Birds

by David W. Steadman

University of Chicago Press, Chicago, 2006. 608 pp. $110, £69.50. ISBN 9780226771410. Paper, $45, £28.50. ISBN 9780226771427.

Alan Tennyson and Paul Martinson's *Extinct Birds of New Zealand* adds to Trevor Worthy and Richard Holdaway's earlier book (*1*) by illustrating New Zealand's 58 extinct bird species. Although the most famous of these are the giant flightless moas, nearly as remarkable were the world's largest eagle (up to 16 kg) and its smallest flightless bird (22 g). Martinson's gorgeously detailed paintings bring home the tragic loss of formerly breathing real animals in a way that descriptions of bones cannot achieve.

The New Zealand fossil avifauna is by far the most completely sampled in the world: most of the extinct species are known from bones of hundreds or thousands of individuals, and almost all modern species have been recovered as fossils. Among the points made in Tennyson's text and by Worthy and Holdaway (*1*) is that the New Zealand extinctions were followed by the founding of New Zealand populations of at least 16 Australian species in response to human-induced habitat changes and to disappearances of related former resident species. Small Australian swamphens, coots, and harriers replaced extinct giant congeneric species; a coastal vegetarian shelduck spread inland after the extinction of the vegetarian Finsch's duck; and Australian pied stilts prospered as populations of New Zealand black stilts crashed.

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In *Extinction and Biogeography of Tropical Pacific Birds*, David Steadman summarizes fossil avifaunas of Pacific islands other than New Zealand and Hawaii. His account is based in large part on his own discoveries over the past 22 years. He personally excavated dozens of sites, retrieved hundreds of thousands of bones, measured the bones of over 25,000 individual birds, and prepared uncounted skeletons of modern species for comparison. This monumental research program was accomplished mostly single-handedly, against obstacles in obtaining permits, finding sites, enlisting cooperation of local people, and obtaining funding from grant agencies that admire studies of molecules and scorn descriptions of species.

Done in by rats and cats. The smallest flightless bird, Lyall's wren (*Traversia lyalli*), depicted here in a colony of fairy prions (*Pachyptila turtur*), survived on Stephens Island until 1895.

CREDIT: PAUL MARTINSON/FROM *EXTINCT BIRDS OF NEW ZEALAND*

The resulting discoveries include over 20 previously unknown extinct species now named and described, dozens of others recognized but not yet named or described, and some large geographic range extensions. Bird species diversity and endemism prove to have been higher, sympatric congeneric species more frequent, and flightless species far more numerous than previously realized. Contrary to the former view of pre-industrial humans as treading lightly on their environments, human colonization of every well-studied Pacific island group was followed by a wave of vertebrate extinctions.

All these discoveries represent new data against which to test previous conclusions about biogeography, extinction, and community ecology. Throughout the book, Steadman criticizes conclusions reached by previous authors (especially Ernst Mayr, Robert H. MacArthur, and Edward O. Wilson) who worked before the impact of human-caused extinction in Oceania was recognized. Steadman concludes that impact "revolutionizes avian biogeography on Pacific islands." One might therefore expect the book to be full of analyses of the new data, demonstrating how earlier interpretations are thereby altered. Sadly, such analyses are not offered for most of the obvious questions, and only crude analyses are offered for others—although the book often provides enough data to let others do the missing calculations.

For instance, two of Mayr's conclusions about Pacific island avian biogeography were that an Australian biogeographic component in the islands' mainly New Guinea–derived avifaunas is strongest on New Caledonia, decreasing to the east and north (*2*), and that island endemism increases with island area and isolation (*3*). Other researchers have concluded that the body masses of an island's top herbivore and carnivore increase with island area and possibly with island age and productivity (*4*, *5*). Steadman discusses none of these points. (My preliminary impression is that his data confirm rather than overturn these conclu-

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sions.) Ian Atkinson (*6*) and others have suggested that susceptibility of island birds to extermination by introduced mammalian predators depends on prior evolutionary exposure to native mammalian predators and also to nonmammalian predators such as land crabs and land crocodiles. Steadman provides much data suitable for quantitative evaluation of the idea, but he does not pursue the analysis beyond an anecdotal example (New Ireland) and some qualitative discussion. Another much-discussed topic of avian biogeography that Steadman does not explore is the trade-offs between costs and benefits that lead to the evolution of flightlessness in island birds. With the author's discoveries, the prehistoric avifaunas of the tropical Pacific now encompass the largest number of flightless birds in the world, and Steadman lists the 25 bird families that contain flightless species. Yet he does not discuss why flightlessness never appeared in so many other bird families, or why it evolved in several Pacific pigeons and megapodes, only three Pacific songbirds, and many ground-dwelling rails but no ground-dwelling quail.

The book's most glaring omissions are statistical analyses of island species numbers *S* and their control by area *A*, distance *D*, and elevation *L*—despite long discussions of those subjects. For all Pacific islands other than New Zealand, small sample sizes mean that their fossil avifaunas are incompletely known and that their actual *S* values must be estimated by statistical sampling models. In paleontology, such statistical calculations—e.g., ones that incorporate specimen numbers and relative species abundances recovered to date and known sampling biases (*7*)—are now routine and mandatory. Unfortunately, none appear in the book. Island biogeographers routinely tease apart effects of *A*, *D*, and *L* on *S* by multiple regression analyses and other statistical methods, but the book offers no such analyses of the prehistoric avifauna. There are no graphs of prehistoric *S* plotted against either *D* or *L*. Despite a whole chapter on species-area relations and their slope (termed *z*), the book presents only a single graph (fig. 19-14) of new fossil data adequate for calculating *z*; that plot for prehistoric land birds among seven islands in Tonga yields a *z* of 0.07, virtually unchanged from the modern z of 0.06. Several graphs in the species-area chapter combine fossil and modern species on the assumption that all existed simultaneously. But Tennyson and Martinson's accounts of the far-better-known New Zealand avifauna warn us that many modern species arrived only as or after the original species declined. It's as if one combined the 1940 and 1980 Manhattan telephone directories and assumed that all people in one directory shared their island with all people in the other.

Despite this lack of supporting analyses, Steadman offers specific but implausible conclusions: e.g., that *L* has little or no effect on *S* of Pacific islands other than low atolls; that "inter-island distances less than ca. 100 km have had a minimal effect on species richness"; and that *S* is virtually independent of island *A* for any island exceeding some threshold *A* (ranging from 1 to 5 km^2 in East Polynesia to 50 to 100 km^2 further west). Where do these detailed conclusions come from?

Steadman's method throughout the book is to replace quantitative analyses with anecdotal examples that he then overgeneralizes, state the overgeneralizations as beliefs, and finally relabel the beliefs as conclusions. For instance, he often remarks that a certain species confined today to some particular large island has been found as a fossil on one or more smaller islands of the same archipelago, then concludes that this suggests that most or nearly all species were formerly present on most or nearly all islands of the archipelago. The verbs believe, expect, predict, speculate, and suspect and the adverbs possibly, presumably, probably, and undoubtedly are used throughout the book—e.g., on the average more than twice per page in the chapter on species-area relations—to precede statements that scientists normally draw as conclusions from analyses. In the final chapter, words like "I believe" and "probably" become scarce, and the former beliefs become stated as facts.

Why would someone spend 22 years excavating, cleaning, and microscopically scrutinizing 25,000 bird bones and then neglect modern analyses? The answer emerges on the first page of the Preface and appears repeatedly thereafter: Steadman states his disdain for many things, including computers, data transformations, dynamics, elegance, equations, generalizations, macroecology, overall frameworks, rules, statistics, and theory. He also repeatedly criticizes conclusions by biogeographers who used these approaches or concepts—not only MacArthur, Wilson, and Mayr but also James Brown, Stephen Hubbell, Mark Lomolino, Stuart Pimm, Robert Ricklefs, Dolph Schluter, Thomas Schoener, and (full disclosure) me. With these self-imposed blinders, it becomes tragically clear why Steadman did not undertake quantitative analyses of his own data, nor collaborate with others who could have complemented his expertise.

The data in *Extinction and Biogeography of Tropical Birds* are now available for others to analyze. But we shall have to look past Steadman's dismissals of surviving modern avifaunas as unnatural and resistant to interpretation at face value. Yes, answering some questions requires a historical perspective. However, biotas are buffeted today, and have been buffeted for hundreds of millions of years, by impacts other than those of humans. Living birds still eat, prey, compete, breed, disperse—and challenge our understanding. They remain the only birds in which we can study basic ecological processes directly.

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PHYSICS

Astronomers' Relativity

Peter Galison

Einstein's special and general theories of relativity began enraging people a century ago. Although the list of charges against them has fluctuated from year to year, many return to the same themes. Relativity is wrong, some insist. It is unintuitive, too geometrical, say others. The list goes on: General relativity uses unreasonably complicated mathematics. It violates Kantian philosophy. One or both theories of relativity are correct but were anticipated by the French mathematician-physicist Henri Poincaré, the German mathematician David Hilbert, or the Dutch theorist Hendrik Lorentz. Relativity's premature demise has been announced time and again. Its effects don't exist, or they do exist but have other explanations. The sun is oblate, thus causing the precession of the perihelion of Mercury. Or the ether can be detected by a souped-up Michelson-Morley experiment. Starlight isn't bent as Einstein predicted—or

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