

- nization, 1984], pp. 221–234.
128. C. V. Kidd and D. Pimentel, Eds., *Integrated Resource Management: Agroforestry for Development* (Academic Press, San Diego, 1992).
 129. U.S. Bureau of the Census, *Statistical Abstract of the United States 1990* (Government Printing Office, Washington, DC, 1992).
 130. L. Lave and E. Seskin, *Air Pollution and Human Health* (Johns Hopkins Press, Baltimore, MD, 1977).
 131. F. D. Whitaker and H. G. Heinemann, *J. Soil Water Conserv.* **28**, 174 (1973).
 132. W. C. Moldenhauer and M. Amemiya, *Iowa Farm Sci.* **21**, 3 (1967).
 133. P. Faeth, R. Repetto, K. Kroll, Q. Dai, G. Helmers, *Paying the Farm Bill: U.S. Agricultural Policy and the Transition to Sustainable Agriculture* (World Resources Institute, Washington, DC, 1991).
 134. K. C. McGregor and C. K. Mutchler, *Trans. ASAE* **35**, 1841 (1992).
 135. ———, R. F. Cullum, *ibid.*, p. 1521.
 136. C. K. Mutchler, L. L. McDowell, J. D. Greer, *ibid.* **28**, 160 (1985).
 137. L. C. Johnson and R. I. Papendick, *Northwest Sci.* **42**, 53 (1968).
 138. K. C. McGregor, C. K. Mutchler, M. J. M. Romkens, *Trans. ASAE* **33**, 1551 (1990).
 139. F. H. Bormann, G. E. Likens, T. C. Siccama, R. S. Pierce, J. S. Eaton, *Ecol. Monogr.* **44**, 255 (1974).
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Prehistoric Extinctions of Pacific Island Birds: Biodiversity Meets Zooarchaeology

David W. Steadman

On tropical Pacific islands, a human-caused “biodiversity crisis” began thousands of years ago and has nearly run its course. Bones identified from archaeological sites show that most species of land birds and populations of seabirds on those islands were exterminated by prehistoric human activities. The loss of birdlife in the tropical Pacific may exceed 2000 species (a majority of which were species of flightless rails) and thus represents a 20 percent worldwide reduction in the number of species of birds. The current global extinction crisis therefore has historic precedent.

Human activities are causing major changes in the Earth’s biota (1). Extinction, the ultimate change, is occurring today across a broad range of terrestrial and aquatic habitats (2). Although much of this “biodiversity crisis” is due to human impact during recent centuries or decades, few plant and animal communities were unaffected in pre-industrial times (3). Nowhere is this seen more dramatically than on islands in the Pacific Ocean.

Nearly all islands in Melanesia, Micronesia, and Polynesia (Fig. 1) were inhabited by prehistoric peoples. Melanesia was occupied as far east as the Solomon Islands by 30,000 years before the present (B.P.) or earlier (4). Much later, about 3500 years B.P., humans arrived in West Polynesia and Micronesia, reaching virtually all of Oceania by 1000 years B.P. (5). Native birds vanished as colonists cleared forests, cultivated crops, and raised domesticated animals (6). Having evolved in the absence of mammalian predators, the birds undoubtedly were tame and easy for people to hunt (7).

The loss of birds on oceanic islands may entail extinction (global loss of a

species), extirpation (loss of a species from an island or region, with one or more populations surviving elsewhere), or reduced population. Extinction and extirpation are long-term losses (8), not short-term departures of populations soon to be reestablished from elsewhere (9). All families of Pacific island birds have been affected. Land birds have suffered high levels of both extinction and extirpation, especially among species of rails, pigeons, doves, parrots, and passerines. Although seabird colonies (especially of shearwaters and petrels) have vanished from numerous islands, species of seabirds have undergone little extinction.

Island birds have been lost mainly to predation by humans and nonnative mammals (rats, dogs, and pigs) and because of the removal or alteration of indigenous forests through cutting, burning, and introduction of nonnative plants. The soil erosion caused by deforestation has eliminated nest sites for burrowing seabirds. Although the rate of extinction varied with ruggedness of terrain and size or permanence of the prehistoric human population, we have no evidence that the processes responsible for prehistoric extinctions (10) differed fundamentally from those that continue to deplete surviving

species today (11). The differences are mainly technological (snares versus guns and stone adzes and fire versus chain saws and fire, for example).

On average, fewer species and numbers of seabirds now nest on tropical or subtropical (0 to 35°S latitude) than on temperate or subantarctic (above 35°S latitude) Pacific islands, with lower marine productivity in the tropics generally cited as the reason for the difference (12). Without prehistoric human impact there would be less difference. For example, the number of nesting species of seabirds has declined on Ua Huka (Marquesas) from more than 22 to 4 (13) and on Huahine (Society Islands) from more than 15 to 4 (14). Today’s global patterns of seabird distribution are not natural.

Remote Outposts: Hawai’i, New Zealand, and Easter Island

The highly endemic land bird faunas of the Hawaiian Islands and New Zealand evolved independently from those in the Polynesian heartland—the island groups from Tonga and Samoa to the Marquesas Islands that are the primary focus of this article. The prehistoric record of birds is extensive and well studied in the Hawaiian Islands (15, 16) and New Zealand (17). As elsewhere in Polynesia, both seabirds and land birds were lost, with the land birds sustaining much more species-level extinction.

The Hawaiian Islands are renowned for radiations of endemic drepanidine finches and flightless ducks, geese, and ibises. Since human arrival at about 1500 to 2000 years B.P. (18), 60 endemic species (representing at least 90 populations) of land birds known only from bones have become extinct (Table 1). Another 20 to 25 species have been lost in the past two centuries. The large island of Hawai’i has the archipelago’s richest modern avifauna, although more species are known from O’ahu and Maui because of their richer fossil records.

Temperate New Zealand once featured endemic radiations of moas, kiwis, water-

The author is at the New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, USA.

fowl, and xenicids. With prehistoric human settlement, at least 44 endemic species of land birds became extinct in the past millennium. In the well-studied Punakaiki karst area on the South Island (19), bones reveal the loss of 20 species of land birds (8 moas, 3 waterfowl, 2 rails, 1 shorebird, 1 parrot, 1 owl, 1 owl-nightjar, and 3 passerines). Today, 23 native nonmarine species occupy the region, with another 7 species known historically but no longer extant. Thus, of the 50 species of land birds that once inhabited Punakaiki, 27 are gone.

On isolated Easter Island (162 km², elevation 507 m), bones from the Ahu Naunau archaeological site date from 900 to 650 years B.P. (20). The Ahu Naunau fauna differs from late prehistoric (less than 500 years B.P.) assemblages from Easter Island (21) in that bones of marine mammals and native birds are much more common, whereas those of fish, humans, and chickens are relatively rare. Although bones of extinct or extirpated seabirds and land birds occur throughout the Ahu Naunau deposit, they are more common in the deepest strata, a pattern seen at other East Polynesian sites (22). The indigenous avifauna of sub-tropical Easter Island once included at least 25 species of seabirds, of which 8 to 10 no longer breed on Easter Island and 13 to 16 others no longer breed even on any of its offshore islets (Table 2). The entire prehistoric seabird fauna of Easter Island probably exceeded 30 breeding species, more than are known from any other single Polynesian island. Of these, only *Phaethon rubricauda* still nests on Easter Island itself.

Ahu Naunau also provides the first evidence that indigenous land birds once lived

on Easter Island. Except for a rail (*Porzana* sp. nov.), the land bird bones found thus far are too fragmentary to identify as to genus but do represent at least six species in four families.

Evidently Easter Island lost more of its indigenous terrestrial biota than did any other island of its size in Oceania. Before human colonization at about 1500 years B.P., most of Easter Island was forested with a palm (*Jubaea disperta*) and the trees *Sophora toromiro* and *Triumfetta* sp. (23). Although depauperate by Polynesian standards, the terrestrial vegetation sustained indigenous insects, land snails, and land birds. Deforestation of Easter Island was virtually complete by about 550 years B.P. (24).

The Polynesian Heartland

Outside of the Hawaiian Islands, New Zealand, and Easter Island, the prehistoric record of Polynesian birds is based on bones from Henderson Island (25), the Marquesas Islands (6, 13, 26, 27), the Society Islands (6, 14), the Cook Islands (6, 28, 29), Samoa (30), Tonga (8, 31), and Polynesian outliers in Melanesia (32). In West Polynesia, closer to the richer vertebrate faunas of Melanesia, the prehistoric extinctions involved lizards and bats (33) as well as birds.

New biogeographic concepts about Polynesian land birds derived from prehistoric bone samples include the following (8): (i) The ranges of most living species are much smaller today than they were at the time of first human contact (Fig. 2). (ii) Few volant species are naturally endemic to only one or two islands. (iii) Most species have become extinct in the past 3000 years.

(iv) Most or all islands supported one to four endemic species of flightless rails, virtually all now extinct. (v) In many cases, individual islands supported two or three species within a genus, unlike the situation today. (vi) At least four formerly widespread genera (*Gallirallus*, *Porphyrio*, *Macropygia*, and *Myiagra*) now are gone from East Polynesia. (vii) Although modern distributions of Polynesian land birds continue to be analyzed as if they were natural (see 34), they do not furnish unbiased data for proposing or testing ecological models (6). (viii) Although some of the range losses of extant species could be restored with conservation efforts (35), we are centuries too late to preserve any true likeness to the original Polynesian avifauna.

The Hane archaeological site on Ua Huka (78 km², elevation 855 m), Marquesas, has yielded the largest bird bone assemblage from tropical Polynesia (6). Most of the approximately 11,000 bones represent seven species of shearwaters and petrels, none of which still nests on Ua Huka. Land birds have declined on Ua Huka from more than 18 to 5 species, the losses including 2 endemic rails, 5 pigeons and doves, and 3 parrots. The early part of the Hane site may date to about 2000 years B.P. (36) and represent the first human settlement of Ua Huka. Native birds provided more than half of all vertebrate food in the early Marquesan diet, a contribution that declined to insignificance late in prehistory (22). From nearby Tahuata, bones with much better chronostratigraphic control represent at least 15 species of seabirds and land birds that did not survive beyond 700 years B.P. (27).

The Fa'ahia archaeological site on Huahine (77 km², elevation 669 m), Society Islands, dates to about 1100 to 800 years B.P. (14). Fa'ahia shares 12 of its 15 species of seabirds with the Hane site but only 5 of its 15 species of land birds. As at Hane, the most common land birds are rails, pigeons, doves, and parrots. Further sampling surely would increase the number of species prehistorically attributed to Huahine, where only seven species (five of seabirds and two of land birds) nest today. Thanks to the Fa'ahia site, more resident species of birds are known from Huahine than from the much larger (1042 km²) nearby island of Tahiti, where no prehistoric bird bones have been reported.

The exploitation of birds can be seen clearly at the Tangatatau Rockshelter (site MAN-44), Mangaia (52 km², elevation 169 m) (29), Cook Islands. The MAN-44 site ranges in age from 1400 to 1000 years B.P. (culturally cryptic zones 1A to 1B) to 200 years B.P. (protohistoric zone 17). Bones of domesticated animals (pigs, dogs, and chickens) are relatively rare in the lowest strata, increase as the number of native land

Table 1. Number of endemic species of land birds recorded on the five largest Hawaiian islands. F, fossil record (Holocene only; includes archaeological sites); M, modern record (19th or 20th century). F and M may represent the same species on any island, which is why the combined total is less than total F plus total M. Modified from (16).

Bird species and island characteristics	Kaua'i		O'ahu		Moloka'i		Maui		Hawai'i	
	M	F	M	F	M	F	M	F	M	F
Birds										
Ibises (3 spp.)	—	—	—	—	1	—	2	—	—	—
Ducks and geese (10 spp.)	4	1	4	1	3	1	4	1	3	1
Rails (12 spp.)	2	1	3	1	1	1	3	1	3	2
Stilts (1 sp.)	—	1	1	1	—	1	—	1	—	1
Hawks (3 spp.)	—	—	3	—	2	—	1	—	—	1
Owls (4 sp.)	1	—	1	—	1	—	1	—	—	—
Crows (3 spp.)	—	—	2	—	1	—	1	—	1	1
Monarchs (1 sp.)	1	1	1	1	—	—	—	—	1	1
Thrushes (4 sp.)	2	2	1	1	1	1	1	—	1	1
Honeyeaters (7 sp.)	1	1	2	1	1	1	3	—	2	2
Finches (51 spp.)	12	9	18	8	11	8	21	10	4	16
Total	23	16	36	14	22	13	37	13	16	26
Combined total		29		38		31		43		32
Island area (km ²)	1433		1574		676		1887		10,458	
Elevation (m)	1598		1232		1515		3056		4206	
Isolation (km to nearest island larger than 300 km ²)	112		40		13		13		46	

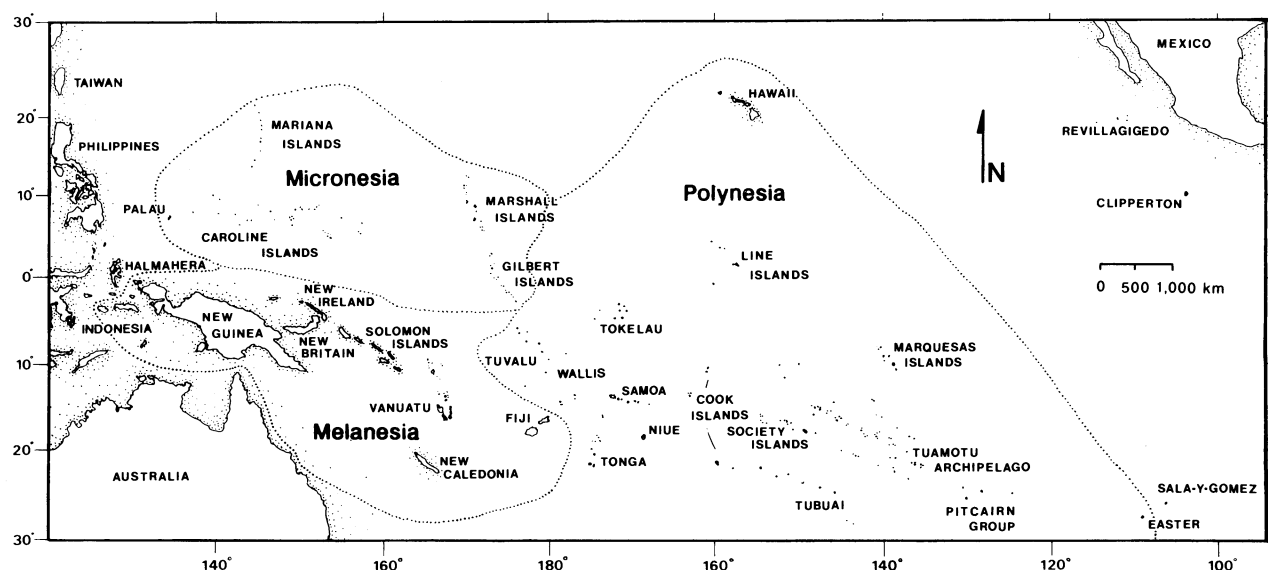


Fig. 1. The tropical Pacific Ocean, showing major island groups.

bird bones decreases in higher strata, then decrease again late in prehistory (zone 15), perhaps because of overconsumption by a large human population.

The number of bones from native birds is high in zones 1 to 4 of MAN-44, relatively low in the middle zones, and high again in zones 15 and 17 (Tables 3 and 4). Bones of extinct or extirpated land birds dominate zones 1 to 4, whereas seabirds account for the later increase in the number of bird bones. The longer survival of certain species of seabirds on Mangaia may be due to its precipitous, creviced limestone cliffs, which provided relatively rat-free nesting habitat. In spite of this, only two (the Brown Noddy and the Common Fairy Tern) of Mangaia's eight surviving species of seabirds have current populations of more than 100 pairs.

Bones of extinct or extirpated land birds from MAN-44 are most numerous in zones 1 to 4 (1400 to 700 years B.P.), declining sharply in zone 5 (Tables 3 and 4). Of 17 species of indigenous land birds, 10 are recorded in zones 5 to 7 (700 to 600 years B.P.) or higher, even if in reduced numbers. The most common flightless rail, *Porzana rua*, last occurs in zone 8 (600 to 500 years B.P.). The only extinct or extirpated land birds above zone 8 are two species of doves. Each of the four surviving species of land birds from MAN-44 tolerates some forest clearance.

Unlike other East Polynesian sites of similar age, zones 1 to 4 of MAN-44 have not yielded a single shearwater or petrel bone. Other evidence suggests that zones 1 to 4 of MAN-44 postdate the earliest human arrival on Mangaia. A major change in pollen and spore influx from more than 20 sediment cores from swamps and lakes shows that, beginning about 2500 years B.P., forest tree pollen gave way to fern spores and herb pollen that are indicative of

human disturbance accompanying settlement. The first appearance of charcoal and increased clay influx, with intensification of these signals at about 1600 years B.P. (37), accompanied the change in pollen and spores. Evidently human disturbance of the native biota began 1000 years before the earliest known cultural deposits at MAN-44 or other sites on Mangaia. Although extinction of rails, pigeons, doves, parrots, and a sandpiper is evident at MAN-44 (Table 3),

other birds may have been lost during the first millennium of human influence. I would speculate that they included several species of shearwaters and petrels. Mangaia is not unique in disclosing the earliest evidence of human occupation by changes in land use revealed in sediment cores rather than by the presence of habitation sites. Similar records exist for Easter Island (24), Mo'orea (38), and non-Polynesian islands such as Madagascar and Puerto Rico (39).

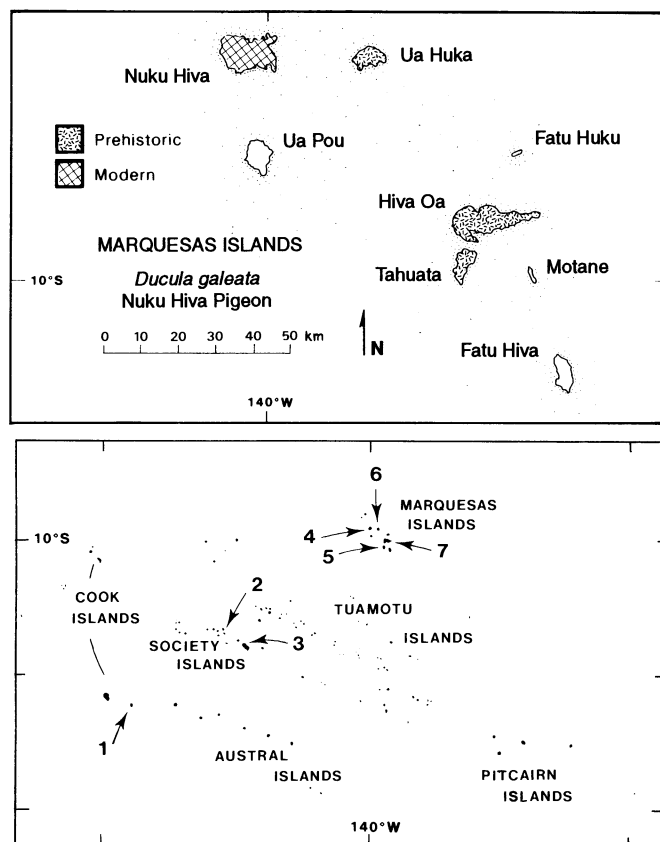


Fig. 2. The past and present distribution of the Nuku Hiva Pigeon, *Ducula galeata*. Regarded as endemic to Nuku Hiva (4), Marquesas, this species now has prehistoric or historic records from at least three other Marquesan islands (5 through 7), as well as Mangaia (1), Huahine (2), and Tahiti (3). Before human impact, it probably was found through most of East Polynesia.

Caves on 'Eua (85 km², elevation 300 m), Tonga, (Fig. 3), differ from other Polynesian heartland sites in yielding bone deposits that predate human arrival by tens of thousands of years (8). The data reveal little prehuman turnover in land birds on 'Eua until the arrival of humans at about 3000 years B.P. Climatic and sea-level changes at the end of the last glacial period may have had virtually no effect on the 'Euan land bird fauna. At least 27 species of

land birds lived on 'Eua in prehuman times (Table 5). Only six of these have survived into the past two centuries. Of the 13 indigenous species of land birds recorded on 'Eua during the past two centuries, 6 are known from prehuman strata, 3 probably occurred in prehuman times but have not been sampled, and 4 probably colonized 'Eua after the arrival of humans.

The unusual tooth-billed pigeon (*Didunculus*), regarded since its European discov-

ery 150 years ago as endemic to Samoa, once lived on 'Eua, as did the megapode *Megapodius pritchardii*, believed to be endemic to Niuafo'ou. 'Eua's 23 species of extinct or extirpated land birds represent 14 genera unknown in East Polynesia but living today in Melanesia or elsewhere in West Polynesia or in both locations. The nearest recorded conspecifics or closely related congeners are from the Solomon Islands (one species), New Caledonia (two species), Fiji or Samoa or both (nine species), elsewhere in Tonga (eight species), or unknown locations (three species). By eliminating taxa such as *Nycticorax* sp. nov., *Eclectus* sp. nov., *Eopsaltria* sp., and *Cettia* sp., the anthropogenic extinction of birds on 'Eua has artificially magnified the biogeographic distinction between Polynesian and Melanesian birds (8).

The impoverishment of 'Eua's land bird community has obvious ecological implications. Of more than 23 extinct or extirpated species, 3 are larger than, and 5 smaller than, any surviving species. The prehuman land bird fauna had more than 27 forest species and lacked nonforest species, as compared with 9 forest and 4 nonforest species today. All feeding guilds have been depleted (Fig. 4). When analyzed by foraging height, the losses were acute for ground-dwelling species (7 to 0), reflecting predation from humans, rats, dogs, and pigs. The natural means of pollination or seed dispersal for certain Polynesian forest trees probably has suffered through the loss of so many frugivorous and nectarivorous birds (35) and pteropodid bats (40). As in the Neotropics (41), the future of Polynesian forests is threatened because of vertebrate extinctions.

Micronesia and Melanesia

To date, each sample of bird bones from Micronesian or Melanesian islands is small (less than 1000 and often less than 100 specimens). Nevertheless, in Micronesia, cave deposits on Rota (Mariana Islands) have yielded bones of 22 resident species of birds, of which 13 are no longer on the island (1 shearwater, 1 tern, 1 duck, 1 megapode, 3 rails, 2 pigeons, 1 parrot, 1 swift, 1 monarch flycatcher, and 1 parrot finch) (42). Currently under study are bones, mainly of flightless rails, from sites I excavated on Tinian and Aguiguan (Mariana Islands) in June and July 1994. An archaeological site on Fais (Yap, Caroline Islands) has yielded 18 resident species of birds, of which 2 petrels, 2 boobies, 5 terns, 1 rail, and 2 pigeons are extirpated, whereas small bone samples from Pohnpei record the loss of 4 species (1 shearwater, 2 petrels, and 1 megapode (43). When it has been more fully studied, I expect that apart from details of taxonomy and chronology, the record of

Table 2. Resident native birds from Easter Island (27°S). Prehistoric record categories: x, present; dashes, no record. Modern status categories: B, breeds today on Easter Island; b, breeds today on an offshore islet or islets but not on Easter Island itself; E, extinct species; and e, extant species that is extirpated on Easter Island and all offshore islets.

Birds	Prehistoric record	Modern status	Modern latitudinal breeding range (°S)
<i>Seabirds</i>			
Albatrosses			
<i>Diomedea</i> sp.	x	e	01 to 51
Petrels, shearwaters			
<i>Fulmarus glacialis</i>	x	e	53 to 68
<i>Pachyptila vittata</i>	x	e	36 to 65
<i>Pterodroma macroptera</i> or <i>P. lessoni</i>	x	e	34 to 50
<i>Pterodroma ultima</i>	x	e	15 to 27
<i>Pterodroma externa</i>	x	e	24 to 33
<i>Pterodroma heraldica</i>	—	b	08 to 27
<i>Pterodroma neglecta</i>	—	b	20 to 33
<i>Procellaria</i> sp.	x	e	36 to 50
<i>Puffinus carneipes</i>	x	e	31 to 42
<i>Puffinus nativitatis</i>	x	b	00 to 27
<i>Puffinus griseus</i>	x	e	32 to 50
<i>Procellariidae</i> sp. nov.	x	E	?
Storm petrels			
<i>Nesofregatta fuliginosa</i>	x	e	00 to 27
Tropic birds			
<i>Phaethon rubricauda</i>	x	B	00 to 27
<i>Phaethon lepturus</i>	x	e	00 to 24
Frigate birds			
<i>Fregata minor</i>	x	b/e	00 to 27
Boobies			
<i>Sula dactylatra</i>	x	b	00 to 27
Terns			
<i>Sterna fuscata</i>	x	b	00 to 27
<i>Sterna paradisaea</i>	x	e?	—
<i>Sterna lunata</i>	—	b/e	00 to 27
<i>Procelsterna cerulea</i>	x	b	00 to 33
<i>Anous stolidus</i>	x	b	00 to 33
<i>Gygis candida</i>	x	b	00 to 27
<i>Gygis microrhyncha</i>	x	e	08 to 10
Total species	22	B = 1, b = 8 to 10, E = 1, e = 12 to 15	
Combined total species	25		
<i>Land birds</i>			
Herons			
cf. <i>Ardeidae</i> sp. nov.	x	E	
Rails			
<i>Porzana</i> sp. nov.	x	E	
cf. <i>Rallidae</i> sp. nov.	x	E	
Parrots			
cf. <i>Psittacidae</i> sp. nov. 1	x	E	
cf. <i>Psittacidae</i> sp. nov. 2	x	E	
Owls			
cf. <i>Tytonidae</i> sp. nov.	x	E	
Total species	6	E = 6	

avian extinctions in Micronesia will resemble that of Polynesia.

On average, the islands of Melanesia are larger and sustain richer biotas than those of Polynesia or Micronesia. Species of land mammals were lost (some translocated) in prehistoric Melanesia (44). Although studies of prehistoric birds are few, the fossils disclose the loss of land birds. New Caledonia (16,750 km², elevation 1639 m) features 36 species of nonpasserine land birds, many endemic. It is the only Melanesian island with more than 1000 identified fossil bird bones (45). Of 16 extinct or extirpated species of nonpasserine land birds from New Caledonia, 11 are known only from bones. In the case of New Ireland (9974 km², elevation 2399 m), which is close to New Guinea, well forested, and has about 108 species of resident land birds today, my preliminary data from 200 bones indicate the loss of at least 25% of its species since human arrival, including two or more species of flightless rails.

Extent of Extinction

Combining seabirds and land birds, I estimate conservatively that an average of 10 species or populations have been lost on each of Oceania's approximately 800 major islands (46), yielding a total loss of 8000 species or populations. The seven islands in the Polynesian heartland (Henderson, Ua Huka, Tahuata, Hiva Oa, Huahine, Mangaia, and 'Eua) with more than 300 identified bones all approach or exceed 20 exterminated species or populations, and none of these records is complete. 'Eua, for example, has lost at least 23 species of land birds and 10 of seabirds. Although many of the 800 major islands in Oceania are lower, smaller, and slightly more isolated than 'Eua, these islands also have fewer surviving species, typically fewer than five of seabirds and fewer than five of land birds.

Rails have lost the most species to human impact. Most extinct species of rails were flightless forest dwellers, endemic to a single island, rather than volant wetland or grassland species. Each of the 19 tropical Pacific islands with 50 or more land bird bones that are 500 or more years old has yielded one to four endemic species of flightless rails. Ua Huka, Mangaia, and 'Eua, with relatively thorough fossil records, each have two to four endemic species. Two to three extinct, endemic flightless species of rails are known as well from four Hawaiian islands (16). The mere seven land bird bones from Easter Island include those of two endemic species of rails (Table 2). Endemic species of rails evolved even on small, low, flat islands like Wake (*Gallirallus wakensis*) and Laysan (*Porzana palmeri*) and survived there in the absence of prehistoric colonizers. At one to

four endemic species per island, flightless rails alone may account for 2000 species of birds that would be alive today had people not colonized Oceania. Except for three barely surviving species of *Gallirallus* (from Okinawa, Guam, and the Solomon Islands) (47) and one living species of *Porzana* (on Henderson Island), only the bones remain as evidence of one of the most spectacular examples of avian speciation.

Knowledge of the prehistory of Polynesian birds vastly improves our understanding of a group of organisms that had been

considered, prematurely, to be well known. With data only from living birds (48), one might not predict that three species of *Vini* parrots once inhabited individual islands in the Marquesas, that five species of rails (including three species in the genus *Porzana*) coexisted on Mangaia, or that six species of pigeons and doves occupied a typical East Polynesian island, where only zero to three (usually 0 to 2) species per island are known in recent centuries. In biogeographical analyses of Polynesian birds, as in other natu-

Table 3. Bones of birds from the main excavation block, Tangataua Rockshelter (MAN-44), Mangaia, Cook Islands, expressed in NISP (number of identified specimens). Data are based on 1989 and 1991 excavations. Daggers indicate extinct species, asterisks indicate extant species extirpated on Mangaia, and dashes indicate no bones.

Birds	Zone									Total
	1A	1B	2 to 3	4	5 to 7	8	9 to 14	15	17	
Seabirds										
Shearwaters, petrels										
<i>Puffinus lherminieri</i>	—	—	—	—	—	2	2	10	3	17
<i>*Pterodroma nigripennis</i>	—	—	—	—	—	19	23	47	11	100
Storm petrels										
<i>*Nesofregetta fuliginosa</i>	—	1	—	2	3	—	1	1	—	8
Tropic birds										
<i>Phaethon lepturus</i>	4	2	19	12	2	—	1	1	—	41
<i>Phaethon rubricauda</i>	—	1	—	—	—	—	—	—	—	1
Frigate birds										
<i>Fregata ariel</i>	—	—	—	—	—	5	—	2	—	7
<i>Fregata minor</i>	—	—	1	—	—	4	—	—	—	5
Boobies										
<i>*Sula sula</i>	—	—	—	1	—	—	—	—	—	1
Terns										
<i>Anous stolidus</i>	1	1	—	—	1	5	3	3	1	15
<i>Procelsterna cerulea</i>	—	—	—	1	—	—	—	—	—	1
<i>Gygis candida</i>	2	1	6	2	1	—	—	—	—	12
<i>*Gygis microrhyncha</i>	—	4	7	1	—	—	—	—	—	12
Introduced birds										
Chickens										
<i>Gallus gallus</i>	—	—	22	20	27	16	12	1	2	100
Native land birds										
Ducks										
<i>Anas superciliosa</i>	—	—	3	1	2	2	8	11	3	30
Rails										
† <i>Gallirallus riplei</i>	10	5	12	16	1	—	—	—	—	44
<i>Porzana tabuensis</i>	—	—	2	1	—	1	—	1	1	6
† <i>Porzana rua</i>	11	44	41	21	2	1	—	—	—	120
† <i>Porzana</i> sp. nov.	—	2	1	1	—	—	—	—	—	4
† <i>Porphyrio</i> ? sp. nov.	—	1	—	—	—	—	—	—	—	1
Sandpipers										
† <i>Prosobonia</i> sp. nov.	1	1	1	1	—	—	—	—	—	4
Pigeons, doves										
<i>*Gallicolumba erythroptera</i>	3	5	3	5	—	—	—	—	—	16
† <i>Gallicolumba</i> sp. nov.	—	—	—	—	—	—	7	1	3	11
† <i>Gallicolumba nui</i>	3	3	—	3	—	—	—	—	—	9
<i>*Ptilinopus rarotongensis</i>	1	4	4	2	—	—	—	1	—	12
<i>*Ducula aurorae</i>	1	2	1	1	—	—	—	—	—	5
<i>*Ducula galeata</i>	3	1	5	2	—	1	—	—	—	12
Parrots										
<i>*Vini kuhlii</i>	14	41	15	23	1	—	—	—	—	94
† <i>Vini vidivici</i>	42	14	3	14	2	—	—	—	—	75
*† <i>Vini kuhlii</i> or <i>V. vidivici</i>	2	2	—	5	—	—	—	—	—	9
Kingfishers										
<i>Halcyon mangaia</i>	1	2	2	2	—	—	—	—	1	8
Warblers										
<i>Acrocephalus kerearako</i>	6	6	1	2	—	—	—	—	—	15

ral sciences (49), models have overshadowed data and thereby undermined their potential to be meaningful.

Much remains unknown about the biogeography of South Pacific birds. For example, DNA might be extracted from well-preserved bones to complement anatomically based taxonomies. We need more prehistoric bone assemblages from across Oceania, especially Micronesia and Melanesia. Sites that represent the first few centuries of human occupation are crucial for documentation of pristine avifaunas. None of the bone records now in hand is complete; with each return to Mangaia, 'Eua, or any other island with suitable deposits, I find bones of species previously unknown from the island, species that lived there before human intervention. The record of natural (background) extinction deserves greater effort. Was climate change of little or no consequence in driving species turnover?

Another challenge is to obtain more data from atolls and low-raised limestone islands. The largest bone samples in hand are from high-raised limestone islands (Mangaia, Henderson, and 'Eua) or volcanic islands (Easter Island, Huahine, and various Marquesan and Hawaiian islands). I recently received about 400 bird bones from three archaeological sites (50) on Lifuka and Foa islands (maximum elevation less than 20 m; most land less than 10 m in elevation) in Tonga (Fig. 3). The samples include 12 to 15 extirpated species of shearwaters, petrels, megapodes, rails, and pigeons. Thus, even low sandy islands, which today support a largely anthropogenic vegetation and an impoverished avifauna, once sustained a diverse fauna of seabirds and land birds.

Chronology and Cause of Prehistoric Extinction

The prehistoric extinction of vertebrates on oceanic islands can be calibrated by the rich Holocene fossil record of the Galápagos Islands (51). Unlike any entire island group in Polynesia, the Galápagos Islands were not inhabited by humans before their discovery by Europeans in 1535 A.D. Human impact, confined to the past 460 years, was relatively minor until about 1800 A.D.

About 500,000 Holocene bones of reptiles, birds, and mammals, more than 90% of which predate human arrival, have been collected from lava tubes on five islands in the Galápagos. They disclose a loss of only 0 to 3 vertebrate populations in the 4000 to 8000 years preceding human arrival, whereas 21 to 24 populations have been lost on the same five islands in the few centuries since the arrival of people (51). Thus, the rate of background (prehuman) extinction in the Galápagos was roughly two orders of magnitude less than the rate of human-

Table 4. Summary of bird bones from the main excavation block, Tangatautu Rockshelter (MAN-44), Mangaia, Cook Islands. NISP, number of identified specimens. This table is based on data shown in Table 3.

Bones and species	Zone									Total
	1A	1B	2 to 3	4	5 to 7	8	9 to 14	15	17	
Total NISP										
All species	105	143	149	139	42	56	57	79	25	795
All native species	105	143	127	119	15	40	45	78	23	695
Seabirds	7	10	33	19	7	35	30	64	15	220
Native land birds	98	133	94	100	8	5	15	14	8	475
Extinct and extirpated native land birds	91	125	86	94	6	2	7	2	3	416
Percent of NISP of extinct and extirpated native land birds										
Of all birds and mammals	72	57	5	21	4	0.4	2	0.5	2	11
Of all birds	87	87	58	68	14	4	12	2	12	53
Of all native land birds	93	94	92	94	75	40	47	14	38	88
Total species										
All	15	20	19	22	10	10	8	11	8	30
All native	15	20	18	21	9	9	7	10	7	29
Seabirds	3	6	4	6	4	5	5	6	3	12
Native land birds	12	14	14	15	5	4	2	4	4	17
Extinct and extirpated native land birds	10	12	10	11	4	2	1	2	1	13

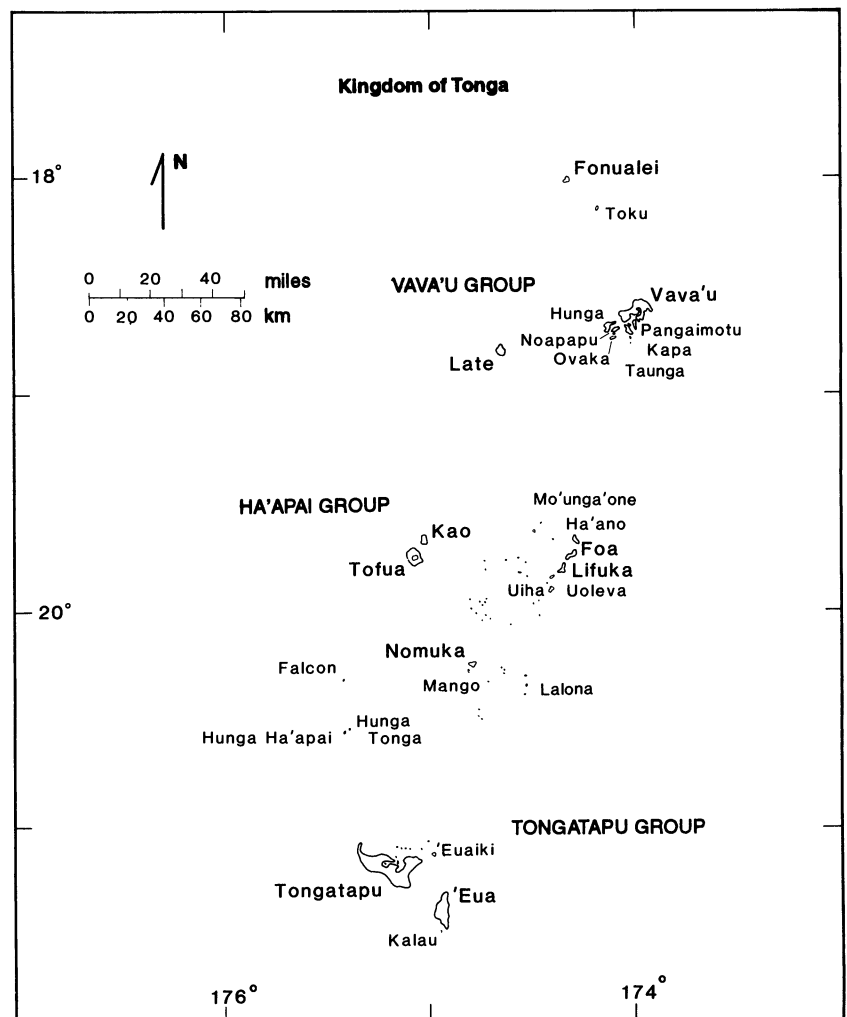


Fig. 3. The Kingdom of Tonga. Informative sites with bones of prehistoric birds are on the islands of 'Eua, Lifuka, and Foa.

related extinction elsewhere. When undisturbed by humans, the natural processes of dispersal, colonization, and evolution may result in a very low rate of extinction for vertebrates on tropical oceanic islands.

On continents, especially the Americas, Australia, and northern Eurasia, human hunting has been implicated in the late Pleistocene extinction of mammoth and other large mammals (52). A debate has focused on human activity versus changing climate and habitat as the primary or sole cause of megafaunal extinctions, although a

blend of the two factors is plausible (53). Unlike the situation on continents, most scientists readily accept that prehistoric humans were involved in the loss of island

species, probably because we have seen so many extinctions on Pacific islands in recent centuries (11). Even though islands are subject to natural disasters including

Table 5. Chronology and community ecology of indigenous resident land birds from 'Eua, Tonga. Chronologic and systematic data from (8). Prehuman record, more than 3000 yr B.P.; archaeological record, 3000 to 200 yr B.P.; historic record, 19th-century specimen. Daggers indicate extinct species; asterisks indicate extirpated species; x, present; dash, no records. Feeding guild categories are defined in Fig. 4.

Birds	Pre-human record	Archaeological record	Historic record	Extant in 1988	Feeding guild
Hérons					
<i>Egretta sacra</i>	—	x	x	x	NF
† <i>Nycticorax</i> sp. nov.	x	—	—	—	GP
Ducks					
<i>Anas superciliosa</i>	—	—	x	x	NF
Hawks					
* <i>Accipiter</i> cf. <i>rufitorques</i>	x	—	—	—	DR
Megapodes					
† <i>Megapodius alimentum</i>	x	x	—	—	GF
* <i>Megapodius pritchardi</i>	x	—	—	—	GF
† <i>Megapodius</i> sp. nov.	x	x	—	—	GF
Rails					
† <i>Gallirallus</i> sp. nov.	x	—	—	—	GO
<i>Gallirallus philippensis</i>	—	x	—	x	NF
* <i>Porzana tabuensis</i>	—	x	x	—	NF
† <i>Gallinula</i> sp. nov.	x	—	—	—	GO
<i>Porphyrio porphyrio</i>	—	x	x	x	NF
Pigeons and doves					
* <i>Gallicolumba stairi</i>	x	x	—	—	GF
† <i>Didunculus</i> sp. nov.	x	x	—	—	MF
<i>Ptilinopus porphyraceus</i>	x	x	x	x	CF
<i>Ptilinopus perousii</i>	x	x	—	x	CF
† <i>Ducula david</i>	x	x	—	—	CF
† <i>Ducula</i> sp. nov.	x	x	—	—	CF
<i>Ducula pacifica</i>	—	x	x	x	CF
Parrots					
* <i>Vini solitarius</i>	x	—	—	—	CN
* <i>Vini australis</i>	x	x	x	—	CN
† <i>Eclectus</i> sp. nov.	x	x	—	—	CF
Barn owls					
<i>Tyto alba</i>	—	x	x	x	NR
Swifts					
<i>Collocalia spodiopygia</i>	—	x	x	x	AI
Kingfishers					
<i>Halcyon chloris</i>	x	x	x	x	MI
Trillers					
<i>Lalage maculosa</i>	x	x	x	x	MI
†*cf. <i>Lalage</i> sp.	—	x	—	—	MI
Whistlers, robins					
†* <i>Eopsaltria</i> sp.	x	—	—	—	MI
Monarchs					
* <i>Clytorhynchus vitiensis</i>	x	x	x	—	MI
* <i>Myiagra</i> sp.	x	x	—	—	MI
Warblers					
†* <i>Cettia</i> sp.	x	—	—	—	MI
Thrushes					
* <i>Turdus poliocephalus</i>	x	x	—	—	MF
Starlings					
<i>Aplonis tabuensis</i>	x	x	x	x	MF
Honeyeaters					
* <i>Myzomela cardinalis</i>	x	x	—	—	CN
<i>Foulehaio carunculata</i>	x	x	x	x	CN
White-eyes					
† <i>Zosteropidae</i> sp. nov.	x	—	—	—	CO
Total species	27	26	14	13	
Total extinct and extirpated species	21	14	3	0	
No. of sites / no. of bird bones	1/401	14/888	—	—	

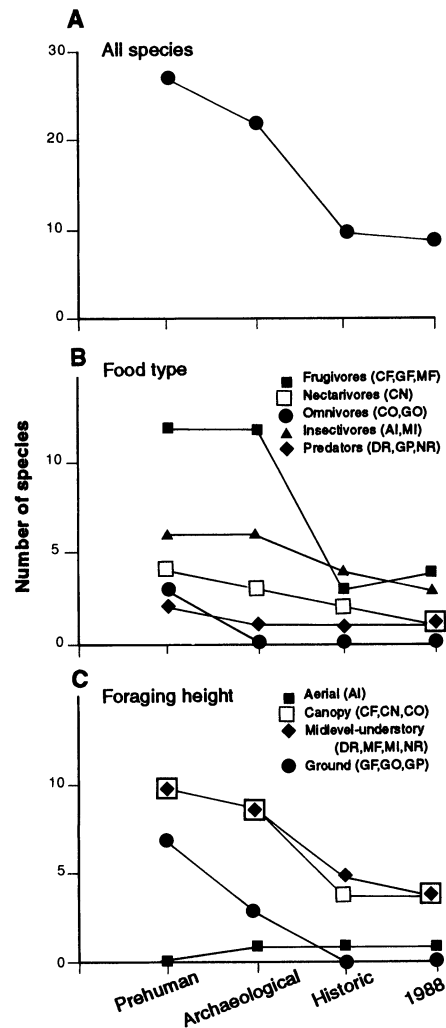


Fig. 4. Long-term changes in the species richness of forest birds on 'Eua, Kingdom of Tonga. The horizontal scale (chronology) corresponds to Table 5. (A) All species. (B) Dietary category or preference. (C) Foraging height. Feeding guild categories are as follows: AI, aerial insectivore; CF, canopy frugivore-granivore; CN, canopy nectarivore; CO, canopy omnivore; DR, diurnal raptor; GF, ground frugivore-granivore; GO, ground omnivore; GP, ground predator; MF, midlevel-understory frugivore-granivore; MI, midlevel-understory insectivore; NF, nonforest species; and NR, nocturnal raptor. There may be overlap between canopy and midlevel-understory habitats; some species were assigned arbitrarily to one or the other.

drought, fire, and severe cyclonic storms, to date the fossil record has revealed no major loss of species from natural causes.

Once people occupy an island, human predation, habitat loss, and introduced predators, competitors, or pathogens appear to be responsible for the extinctions of birds, whether modern or prehistoric (54). Finding the bones of extinct species in a cultural context does not prove that people caused the extinctions, even when evidence of butchery, cooking, or consumption is present. Such bones do indicate human predation on the extinct species which, based on modern analogy, probably was a factor leading toward extinction. Direct evidence for prehistoric habitat changes comes not from the bones themselves but from paleobotanical and geological studies (24, 37, 38).

The rate of extinction for island birds need not be a matter of two or three centuries only, as proposed for North American mammals (52). On Mangaia, the rugged *makatea* limestone that covers 56% of the island provided a forested refuge that allowed many species of birds to survive for more than 1000 years after human arrival. The forest disturbance portrayed in the Mangaian sediment cores reflects mainly what occurred on the inner volcanic hills, not on the *makatea*, where exploitation of plants and birds intensified only after the volcanic hills had been deforested. Even today, the most inhospitable areas of Mangaia's *makatea* sustain a predominately native forest (55). During the initial period of Mangaian prehistory, from about 2500 to 1600 years B.P., there may have been little or no permanent settlement. Mangaia may have been an occasional outpost for fishermen who ate birds and fruit bats and set fires in the dry season. Probably no nonnative mammals were introduced. From about 1600 to 1000 years B.P., Mangaia may have been visited more frequently, with settlements made along the coast. Rats were introduced. Fires increased and some forest was cleared for agriculture. Settlement expanded to the island's interior at around 1000 years B.P., resulting in further deforestation and in the occupation of sites such as MAN-44.

We expect extinction after people arrive on an island. Survival is the exception. The time required, whether 10^2 or 10^3 years, for a species to become extinct is of interest ecologically as well as from a cultural (22) or conservational (56) perspective. For time that exceeds the 50,000-year range of radiocarbon, these differences are lost within the inherent imprecision of dating methods.

Chronology aside, the loss of Pacific island birds is part of a global anthropogenic extinction event in which certain species may be targeted (41) although no major groups of organisms are immune (2). Cur-

tailoring this event has been and will be difficult (57). For thousands of years we have devastated naïve faunas and have found it difficult to manage scarce resources in a sustainable way. It appears that the Earth's biota, already much depleted because of human activity, will continue to decline in the foreseeable future.

REFERENCES AND NOTES

- O. L. Phillips and A. H. Gentry, *Science* **263**, 954 (1994).
- E. O. Wilson, *The Diversity of Life* (Norton, New York, 1992); N. Myers, *Biodivers. Conserv.* **2**, 2 (1993).
- J. M. Diamond, *The Third Chimpanzee* (Harper-Collins, New York, 1992); S. L. O'Hara, F. A. Street-Perrott, T. P. Burt, *Nature* **362**, 48 (1993); W. Denman, *Assoc. Am. Geogr. Ann.* **82**, 369 (1992).
- S. Wickler and M. Spriggs, *Antiquity* **62**, 703 (1988).
- G. Irwin, *The Prehistoric Exploration and Colonization of the Pacific* (Cambridge Univ. Press, Cambridge, 1992). The chronology of archaeological sites is determined most often by radiocarbon dating of wood charcoal, marine shell, bone, and other organic materials.
- D. W. Steadman, *J. Archaeol. Sci.* **16**, 177 (1989). Bones from paleontological and archaeological sites on 40 Pacific islands provide estimates of prehistoric avifaunas and of the magnitude of extinction. No bone assemblage represents all species that once lived on a given island. The relation between the fossil sample and the actual avifauna is influenced by the number of identified bones, the agent that deposited the bones (humans, other predators, or natural trap activity, for example), age of the bone sample (by late prehistoric times, most species of birds were already gone), and methods of sampling (screen sizes popular before the past decade were too coarse to recover bones of small species).
- At the time of European contact, such tameness was noted on a number of uninhabited oceanic islands. Darwin's finches and other resident land birds on most of the Galápagos Islands are still remarkably tame.
- D. W. Steadman, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 818 (1993).
- M. J. Williamson, *Philos. Trans. R. Soc. London Ser. B* **325**, 457 (1989).
- P. V. Kirch, *Archaeol. Oceania* **18**, 26 (1983).
- N. J. Collar and P. Andrew, *Int. Counc. Bird Preserv. Tech. Publ.* **8** (1988); T. H. Johnson and A. J. Statfield, *Ibis* **132**, 167 (1990); D. A. Burney, *Am. Sci.* **81**, 530 (1993); P. Craig, T. E. Morrell, K. So'oto, *Pac. Sci.* **48**, 344 (1994).
- R. C. Murphy, *Oceanic Birds of South America* (Macmillan, New York, 1936), vol. 1, pp. 59–81; C. J. R. Robertson and B. D. Bell, *Int. Counc. Bird Preserv. Tech. Publ.* **2**, 573 (1984).
- D. W. Steadman, in *Global Climate Change and Life on Earth*, R. L. Wyman, Ed. (Routledge, Chapman and Hall, New York, 1991), p. 156.
- D. W. Steadman and D. S. Pahlavan, *Geoarchaeology* **7**, 449 (1992).
- S. L. Olson and H. F. James, *Science* **217**, 633 (1982); H. F. James et al., *Proc. Natl. Acad. Sci. U.S.A.* **84**, 2350 (1987).
- S. L. Olson and H. F. James, *Ornith. Monogr.* **45** (1991); H. F. James and S. L. Olson, *ibid.* **46** (1991).
- T. H. Worthy, *Nat. Mus. N. Z. Misc. Ser.* **17** (1988); A. Anderson, *Prodigious Birds: Moas and Moa-hunting in Prehistoric New Zealand* (Cambridge Univ. Press, Cambridge, 1989); R. N. Holdaway, *N. Z. J. Ecol.* **12** (suppl.), 11 (1989); A. Anderson and R. McGovern-Wilson, *N. Z. Arch. Assoc. Monogr.* **18** (1991).
- P. V. Kirch, *Feathered Gods and Fishhooks* (Univ. of Hawaii Press, Honolulu, 1985).
- T. H. Worthy and R. N. Holdaway, *J. R. Soc. N. Z.* **23**, 147 (1993).
- D. W. Steadman, P. Vargas, C. Cristino, *Asian Perspect.* **16**, 79 (1994).
- W. S. Ayres, *J. Soc. Océanistes* **80**, 103 (1985).
- T. Dye and D. W. Steadman, *Am. Sci.* **78**, 209 (1990).
- P. Bahn and J. R. Flinley, *Easter Island, Earth Island* (Thames and Hudson, London, 1992).
- J. R. Flinley et al., *J. Quat. Sci.* **6**, 85 (1991).
- D. W. Steadman and S. L. Olson, *Proc. Natl. Acad. Sci. U.S.A.* **82**, 6191 (1985); S. E. Schubel and D. W. Steadman, *Atoll Res. Bull.* **325** (1989), p. 1; G. Wragg and M. I. Weisler, *Notornis* **41**, 61 (1994).
- D. W. Steadman and M. C. Zarriello, *Proc. Biol. Soc. Wash.* **100**, 518 (1987); D. W. Steadman, S. E. Schubel, D. S. Pahlavan, *ibid.* **101**, 487 (1988); *Nat. Hist. Mus. Los Angeles Cty. Sci. Ser.* **36**, 329 (1992).
- B. V. Rolett, *J. Polynesian Soc.* **101**, 86 (1992); D. W. Steadman and B. V. Rolett, *J. Archaeol. Sci.*, in press.
- D. W. Steadman, *Pac. Sci.* **40**, 27 (1987); M. S. Allen and D. W. Steadman, *Archaeol. Oceania* **25**, 24 (1990); D. W. Steadman, *Pac. Sci.* **45**, 325 (1991).
- D. W. Steadman and P. V. Kirch, *Proc. Natl. Acad. Sci. U.S.A.* **87**, 9605 (1990); P. V. Kirch, J. R. Flinley, D. W. Steadman, F. Lamont, S. Dawson, *Nat. Geogr. Res. Explor.* **8**, 166 (1992); P. V. Kirch, D. W. Steadman, V. Butler, J. Hather, M. I. Weisler, *Archaeol. Oceania*, in press. The numbering system for Mangaia's more than 100 archaeological sites includes the prefix MAN to distinguish these from sites elsewhere in the Cook Islands. The Tangataua Rockshelter is the 44th site in this system.
- D. W. Steadman, *Univ. Calif. Archaeol. Res. Fac. Contrib.* **51**, 217 (1993).
- _____, *Proc. Biol. Soc. Wash.* **102**, 537 (1989).
- J.-C. Balouet and S. L. Olson, *ibid.* **100**, 769 (1987); D. W. Steadman, D. S. Pahlavan, P. V. Kirch, *Occas. Pap. Bernice P. Bishop Mus.* **30**, 118 (1990).
- G. K. Pregill, *Pac. Sci.* **47**, 101 (1993); K. F. Koopman and D. W. Steadman, *Am. Mus. Nov.*, in press.
- G. H. Adler, *Evol. Ecol.* **6**, 296 (1992).
- J. Franklin and D. W. Steadman, *Conserv. Biol.* **5**, 506 (1991).
- P. V. Kirch, *J. Polynesian Soc.* **95**, 9 (1986).
- J. C. Ellison, *Pac. Sci.* **48**, 1 (1994); P. V. Kirch and J. Ellison, *Antiquity* **68**, 310 (1994).
- D. Lepofsky, H. C. Harries, M. Kellum, *J. Polynesian Soc.* **101**, 299 (1992).
- D. A. Burney, *Quat. Res.* **40**, 98 (1993); _____, L. P. Burney, R. D. E. MacPhee, *J. Archaeol. Sci.* **21**, 273 (1994).
- W. E. Rainey and E. D. Pierson, *U.S. Fish Wildl. Serv. Biol. Rep.* **90**, 111 (1992).
- K. H. Redford, *Bioscience* **42**, 412 (1992); M. S. Alvard, *Hum. Ecol.* **21**, 355 (1993).
- D. W. Steadman, *Micronesica* **25**, 71 (1992).
- _____ and M. Intoh, *Pac. Sci.* **48**, 116 (1994).
- T. F. Flannery and J. P. White, *Nat. Geogr. Res. Explor.* **7**, 96 (1991).
- F. Hannecart and Y. Letocart, *Oiseaux de Nouvelle Calédonie et des Loyautés* (Les Éditions Cardinalis, Nouméa, New Caledonia, 1980, 1983), vols. 1 and 2; J.-C. Balouet and S. L. Olson, *Smithson. Contrib. Zool.* **469** (1989).
- There are about 260 islands and atolls in Polynesia, 120 in Micronesia, and 430 in Melanesia. G. Douglas, *Micronesica* **5**, 327 (1969); L. S. Motteler, *Bishop Mus. Misc. Publ.* **34** (1986); B. G. Karolle, *Atlas of Micronesia* (Bess Press, Honolulu, HI, 1993).
- J. M. Diamond, *Auk* **108**, 461 (1991).
- E. Mayr, *Birds of the Southwest Pacific* (Macmillan, New York, 1945); R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ, 1967); E. Mayr, *Evolution and the Diversity of Life: Selected Essays* (Harvard Univ. Press, Cambridge, MA, 1976).
- N. Oreskes, K. Shrader-Frechette, K. Belitz, *Science* **263**, 641 (1994).
- W. R. Dickinson, D. V. Burley, R. Shutler Jr., *Geoarchaeol.* **9**, 85 (1994).
- D. W. Steadman, *Smithson. Contrib. Zool.* **413** (1986); _____, T. W. Stafford Jr., D. J. Donahue, A. J. T. Jull, *Quat. Res.* **36**, 126 (1991).
- P. S. Martin, in *Quaternary Extinctions*, P. S. Martin and R. G. Klein, Eds. (Univ. of Arizona Press, Tucson, AZ, 1984), p. 354; P. S. Martin, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **82**, 187 (1990).
- P. S. Martin and R. G. Klein, Eds., *Quaternary Extinctions* (Univ. of Arizona Press, Tucson, AZ, 1984); A.

- J. Stuart, *Biol. Rev.* **66**, 453 (1991).
54. J. M. Diamond, *Int. Counc. Bird Preserv. Tech. Publ.* **3**, 17 (1985); D. W. Steadman, E. C. Greiner, C. S. Wood, *Conserv. Biol.* **4**, 398 (1990).
55. J. Franklin and M. Merlin, *J. Veg. Sci.* **3**, 3 (1992).
56. S. L. Pimm, H. L. Jones, J. Diamond, *Am. Nat.* **132**, 757 (1988); ———, M. P. Moulton, L. J. Justice, *Philos. Trans. R. Soc. London Ser.* **344**, 27 (1994).
57. D. Ludwig, R. Hilborn, C. Walters, *Science* **260**, 17 (1993).
58. Supported by the National Geographic Society (grants 2088 and 4001-89), NSF (grants BSR-8607535 and BNS-9020750), the Smithsonian Institution, the U.S. Fish and Wildlife Service, and the

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RESEARCH ARTICLE

Head-On Collision Between a DNA Replication Apparatus and RNA Polymerase Transcription Complex

Bin Liu and Bruce M. Alberts*

An in vitro system reconstituted from purified proteins has been used to examine what happens when the DNA replication apparatus of bacteriophage T4 collides with an *Escherichia coli* RNA polymerase ternary transcription complex that is poised to move in the direction opposite to that of the moving replication fork. In the absence of a DNA helicase, the replication fork stalls for many minutes after its encounter with the RNA polymerase. However, when the T4 gene 41 DNA helicase is present, the replication fork passes the RNA polymerase after a pause of a few seconds. This brief pause is longer than the pause observed for a codirectional collision between the same two polymerases, suggesting that there is an inherent disadvantage to having replication and transcription directions oriented head to head. As for a codirectional collision, the RNA polymerase remains competent to resume faithful RNA chain elongation after the DNA replication fork passes; most strikingly, the RNA polymerase has switched from its original template strand to use the newly synthesized daughter DNA strand as the template.

The *Escherichia coli* genome is arranged in a curious way, inasmuch as most of the heavily transcribed genes are oriented in the direction of the leading strand of the DNA replication fork (1, 2). A similar nonrandom gene organization is found in other bacteria (3), plasmids, and bacteriophages (1). These observations suggest that a codirectional collision between RNA and DNA polymerases is less disadvantageous to an organism than an oppositely oriented (head-on) collision.

Using a highly purified in vitro system, we previously examined the consequences of a collision between a DNA replication fork and codirectionally moving RNA polymerase (4, 5). We found that the replication fork can pass the RNA polymerase ternary complex even in the absence of a DNA helicase; surprisingly, the bypassed RNA polymerase ternary complex remained bound at its original place on the

DNA template, and it was fully competent to resume RNA chain elongation.

We have now examined the consequences of an oppositely oriented collision between a replication fork and an RNA polymerase ternary transcription complex. We found that the replication fork stalls for a long time during such a head-on collision with RNA polymerase when no DNA helicase was present. However, when the DNA helicase was added, the replication fork passed the RNA polymerase after a brief pause. We have investigated the consequences of this bypass reaction and found that the RNA polymerase switched its template strand, requiring that its RNA-DNA helix break up and re-form with a new DNA partner.

A head-on collision between a replication fork and RNA polymerase. A singly nicked circular DNA molecule containing an appropriately oriented *E. coli* σ^{70} promoter was used as a DNA template that supports oppositely directed DNA replication and DNA transcription (in this molecule, the nick that primes leading-strand DNA synthesis is located in the DNA

strand that serves both as the template for transcription and as the template for lagging-strand DNA synthesis). We began our reaction by adding purified *E. coli* RNA polymerase and ribonucleoside triphosphates (NTPs) to this DNA; because we omitted cytidine triphosphate (CTP), the RNA polymerase began synthesis at the promoter but stopped at the first G nucleotide on the template. This created a stable ternary transcription complex composed of RNA polymerase, an 18-nucleotide (nt) nascent RNA transcript, and the DNA template (6). After purifying this ternary complex on Sepharose Cl-2B to remove a few other, less stable ternary complexes and any RNA polymerase molecules bound to DNA without a transcript (4), we added the proteins and nucleotides required to start DNA synthesis. Because the σ factor and NTPs were removed by the treatment with Sepharose Cl-2B, new RNA chains could not be initiated during the DNA replication reaction (4).

For DNA synthesis, we used an in vitro replication system composed of seven highly purified bacteriophage T4-encoded proteins that catalyze efficient leading-strand DNA synthesis. The proteins were the T4 DNA polymerase holoenzyme (consisting of the products of T4 genes 43, 44, 62, and 45), a helix-destabilizing single-stranded DNA-binding protein (gene 32 protein), the highly processive DNA helicase (gene 41 protein), and the gene 59 protein that greatly facilitates the loading of the gene 41 protein onto DNA at a replication fork (7). An eighth protein, the gene 61 protein (DNA primase), interacts with the gene 41 protein to form the primosome that makes primers for lagging-strand (Okazaki fragment) DNA synthesis; in some experiments, this protein was added to complete the T4 replication apparatus that catalyzes coupled leading- and lagging-strand DNA synthesis at a rate comparable to that observed in vivo (7).

Using alkaline agarose gel electrophoresis (8), we determined the effect of stalled RNA polymerase ternary complexes on the movement of oppositely oriented replication forks by analyzing the rate of increase in DNA strand lengths during replication. We used either naked DNA or purified ternary complexes as the DNA template in side-by-side reactions. In the absence of the gene 41 DNA helicase, the replication fork

The authors are in the Department of Biochemistry and Biophysics, University of California, San Francisco, CA 94143-0448, USA.

*On leave as president of the National Academy of Sciences, Washington, DC 20418, USA.