

The prehistoric extinction of south pacific birds: catastrophe versus attrition

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Introduction

Nearly four decades ago, a landmark paper by Paul Martin developed the concept of prehistoric overkill. He suggested that the massive extinction of large mammals in North America (and smaller ones in the West Indies) was due to overhunting by humans in radiocarbon time (last 35,000 years) rather than to changes in climate and habitat associated with the glacial to interglacial transition (Martin 1958). The cause or causes of late Quaternary extinctions have been debated intensively ever since, with evidence from many disciplines and all continents except Antarctica contributing to the debate. At one extreme are Martin and other defenders of overkill. At the other extreme are proponents of non-human causes who usually incorporate some aspect of changing climate and habitat to explain most or all late Quaternary extinctions of mammals.

To accommodate the radiocarbon chronology indicating a catastrophic extinction in North America, Mosimann and Martin (1975) developed a model of "blitzkrieg" that portrays a rapidly advancing "front" of skilled hunters who kill animals beyond their actual needs and respond to their unlimited food supply with rapid population growth. A special type of catastrophe, the blitzkrieg model proposes that human colonization and megafaunal collapse could have swept across both North and South America in a matter of several centuries (Martin 1984, 1990).

Whatever the fate of blitzkrieg on continents, a model of explosive, human-induced extinction has intuitive appeal on oceanic islands, where even small vertebrates often are more susceptible to extinction than on continents because of small land areas, small population sizes, low rates of increase, and naïveté to predators. During historic times (the past several hundred years), written observations and scientific specimens have corrob-

rated numerous blitzkrieg-like events -the rapid extinction of multiple indigenous species - after the arrival of humans on a previously uninhabited island. I use “rapid” here in a geochronological sense to mean time intervals of several centuries or less, which are difficult or impossible to measure precisely by radiocarbon (^{14}C) dating.

Most oceanic islands, including those of the tropical Pacific (Fig. 1), were colonized by humans well before the past few centuries. Between 3200 to 3000 years ago, people of the Lapita Cultural Complex moved rapidly from an undetermined part of island Southeast Asia into Remote Oceania, settling on islands as far east as Samoa (Kirch and Hunt 1988, Irwin 1992, Kirch 1995). “Remote Oceania” refers to Pacific islands east of the Solomons and north of the Bismarcks, i.e., all of Polynesia and Micronesia as well as Vanuatu, New Caledonia, and Fiji; see Green 1991. The Lapita peoples were agriculturalists (Kirch 1989) as well as hunters and fishers who exploited a wide range of marine and terrestrial animals (Nagaoka 1988, Dye and Steadman 1990).

The rapid movement of Lapita peoples to islands spread across thousands of kilometers of ocean is the sort of colonization event one might expect to be associated with a catastrophic extinction. In fact, thousands of populations (especially seabirds, rails, pigeons, and parrots) and species (especially flightless rails) of birds have become extinct on tropical Pacific islands during the past several millennia of human presence (Steadman 1993, 1995a). At the species level, this is the largest single extinction event ever detected for vertebrates.

The exact timing of these extinctions, however, especially as compared to the first arrival of people (Lapita or otherwise), has been difficult to determine in most cases. From a cultural perspective or from the standpoint of conservation biology, it is important to determine how long it took for these extinctions to occur. In other words, after the arrival of people on a previously uninhabited island, was the extinction of various indigenous species of birds accomplished in years, decades, centuries, or millennia? From the standpoint of evolution or biogeography, the speed of extinction is somewhat less important to know, given that all of these time scales are short and that extinction is virtually guaranteed for most indigenous species of birds once humans colonize an oceanic island.

To study the timing and extent of extinctions that may have occurred in Oceania in prehistoric times requires identifying bones from dated contexts. Obtaining such evidence might seem to be straightforward, but complications often arise in such areas as: finding relatively old prehistoric sites with good bone preservation; determining just when humans arrived; obtaining large enough samples of bones to represent the indigenous fauna in a comprehensive way; and doing the difficult, species-level identifications of bones. These limitations can be severe. Among the numerous Lapita sites, for example, only site TK-4 from Tikopia and two sites in Tonga (Faleloa on Foa Island, Tongoleleka on Likufa Island) have yielded more than 100 bird bones that have been identified to species (Nagaoka 1988, Steadman *et al.* 1990, see Discussion herein). In some Lapita sites with excellent overall bone retrieval, such as the ECA site on Mussau (Bismarck

Archipelago; Steadman and Kirch in press), the scarcity of bird bones might be attributable to a genuine paucity of available birds because of earlier human impact. In many cases, however, poor field recovery methods or the unavailability of collected bones has limited the study of birds that were exploited by Lapita peoples.

In this paper I will outline some of the factors that can be considered, on an island-by-island basis, in evaluating the speed and extent of vertebrate extinction on oceanic islands. Following this I will examine some preliminary faunal data from Lapita sites in the Ha`apai Group of Tonga.

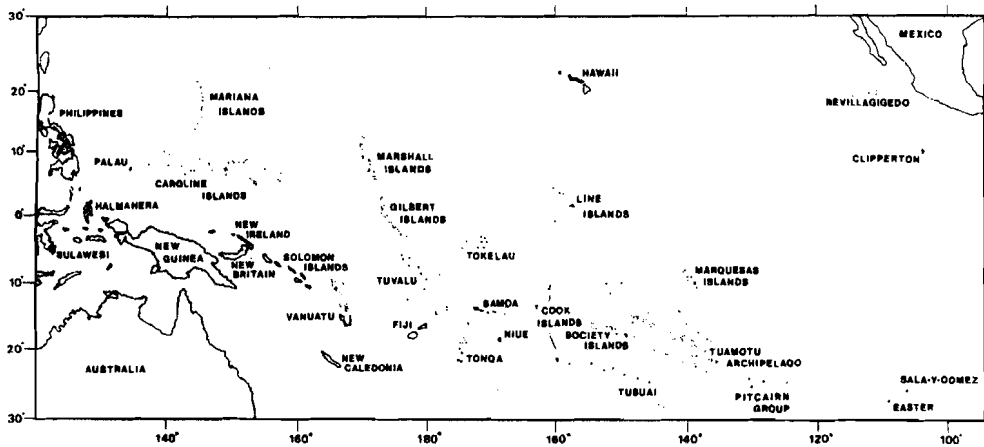


Figure 1
The main island groups of the tropical Pacific Ocean.

Factors that affect extinction on islands

At least three categories of factors influence the speed and extent of anthropogenic extinction of vertebrates on oceanic islands. These factors are outlined here as generalizations (with certain or possible exceptions) rather than absolute rules. This brief, preliminary compilation can be applied to any class of vertebrates on any oceanic island or island group, although my primary goal is to establish criteria for assessing extinction of birds on tropical Pacific islands. Most of these factors are not mutually exclusive but influence one another, both within and between categories.

■ Intrinsic Physical Factors

These characteristics are inherent to an island and thus provide the background for biological and cultural factors.

1. Island size (land area). The influence of island area on a variety of biological phenomena is legendary (MacArthur and Wilson 1967). As island area increases, for example, it should take longer for an anthropogenic impact to spread across the entire island. In the cases of some introduced predators (such as rats) or pathogens (such as avian malaria or pox), the differences in dispersal times across large vs. small islands may be minor.
2. Topography (relief). This factor is influenced by elevation, although extreme steepness (high relief) may deter human impacts related to deforestation, cultivation, and hunting more than large but gradual increases in elevation. Examples of areas where topography constrains human activities include “knife-edge” eroded volcanics (as in the Marquesas and Hawai`i), limestone cliffs (as in parts of the Cook Islands, Tonga, Vanuatu, and Palau), and pinnacle karst (as on Henderson Island). Topographic constraints on human activities tend to be greater on large islands than on small islands or atolls.
3. Bedrock types. This factor influences topography and soil types.
4. Soil types. Indigenous plant communities are more likely to be altered or removed where soils are well suited for cultivation.
5. Isolation. More isolated islands tend to have more depauperate plant and animal communities. Increased isolation also leads to a more strict dependence by people on that island alone for natural resources, such as the resource sink on Easter Island (Flenley *et al.* 1991, Steadman *et al.* 1994, Steadman 1995a). These phenomena together facilitate overexploitation of indigenous species. Repopulation of the island by conspecifics from neighboring islands is hindered by increased isolation.

■ Intrinsic Biological Factors

Each of these factors pertains to the indigenous plant and animal communities that exist on an island at first human contact.

1. Floral diversity. Having more species available, a richer flora might be exploited in a more generalized way that spreads the human impact across many species. On the

other hand, such floras may have naturally rare species that, if subjected to specialized exploitation, could be easy to exterminate. In either case, sustained exploitation of rich plant communities eventually will extirpate or make rare more species than in depauperate communities.

2. Faunal diversity. As with floral diversity, being part of a relatively rich fauna can work either for or against a given species. Faunal diversity includes pathogens; one would expect indigenous vertebrates from islands with minimal pathogenic diversity to be more vulnerable to disease when non-native pathogens arrive.

3. Presence/absence of non-volant terrestrial mammals. Indigenous rodents are absent from Remote Oceania. Birds and reptiles on these islands have evolved in the absence of terrestrial mammals, and thus tend to be relatively easy targets for predation by humans, rats, dogs, and pigs.

4. Marine resources, including access. Rich marine resources would lessen the short-term human dependence on terrestrial resources, and thus potentially reduce the speed with which terrestrial species would become overexploited. On the other hand, rich marine resources would help to sustain long-term human populations, whose activities eventually would lead to vanishing terrestrial species. Regardless of how rich the marine life may be, human access to marine resources is dictated by shoreline configurations and weather (beaches, cliffs, bays, fringing reefs, windward vs. leeward coasts, storms, rough seas, etc.).

5. Species-specific ecological, behavioral, or morphological traits. Species of birds that nest and forage in the forest canopy, for example, are more difficult to hunt than those living in the forest understory or on the ground. Flightlessness has rendered most species of rails highly vulnerable to predation from humans or non-native mammals (Steadman 1995a), with the result that nearly all species that once inhabited Oceania are extinct. Although volant, most species of seabirds nest on the ground and therefore are extremely vulnerable to predation at that crucial stage in their life history. The presence of colorful feathers, bones well suited for making into tools, or especially tasty meat are some morphological traits that might increase the rate at which humans hunt a species (Steadman 1996).

■ Human Factors

This set of closely interrelated factors concerns the socio-economic structure, demography, and cultural ecology of prehistoric peoples.

1. Permanent vs. temporary occupation. Permanent settlement would be expected to result in the introduction of more non-native species of plants and animals, especially

among horticulturalists. Temporary occupation means using an island as an occasional hunting and fishing outpost. This would not necessarily preclude the introduction of non-native species of plants or animals, or of burning forest in the dry season, but these activities probably would occur less often than on permanently inhabited islands.

2. Horticulturalists vs. hunter-fisher-gatherers (h-f-g). Lapita and later peoples in Remote Oceania were horticulturalists (with significant h-f-g activities as well). Related to the previous factor, horticulturalists would be expected to develop larger populations and to alter more forest than those with an exclusively h-f-g economy.

3. Introduced plants. Prehistoric voyagers transported a diverse set of food and other economically important plants across Remote Oceania (Kirch 1994). Deforestation, especially through burning in the dry season, was necessary to provide tillable land to sustain these crops.

4. Introduced animals. Four species of vertebrates were transported prehistorically across much of Remote Oceania: chicken (*Gallus gallus*), Pacific rat (*Rattus exulans*), dog (*Canis familiaris*), and pig (*Sus scrofa*). While all four were capable of forming wild as well as captive populations, only the rat did so consistently.

5. Settlement pattern. The earliest habitation sites in Remote Oceania are coastal (Kirch 1986). The interior of an island, although exploited for game and/or cultivation, may not have been settled until later in prehistory, perhaps as a response to increased human population (Kirch 1982, Kirch and Ellison 1994).

6. Population growth. Evidence from islands with extensive archaeological records point to population increases with time, even though prehistoric controls on population variably included resource shortages, disease, warfare, and others (Dye and Steadman 1990, Kirch 1990, Kirch and Weisler 1994). Higher populations lead logically to increased resource consumption.

7. Hunting preferences or avoidances. As mentioned above, certain species of birds were either favored or avoided by hunters because of their taste, plumage, bones, spiritual meaning, or other traits (Steadman 1996). A greater emphasis on exploiting terrestrial than marine species would ensue if access to the sea were restricted by the threat of violence (Dye 1990b) or by a rugged coastline.

■ An example from Tonga

Preliminary data from three fairly small, low islands in the Ha`apai Group of Tonga suggest that extinction of many species of birds occurred rapidly, i.e., within time intervals too short to be characterized by ^{14}C dating. The Lapita colonization of the nearby, inter-visible islands of Foa (13,3 km², 20 m elev.), Lifuka (11,4 km², 16 m elev.), and Ha`ano

(6,6 km², 12 m elev.) occurred at ca. 3000 yr BP (Dye 1990a, Dye and Steadman 1990, Burley 1994, 1996, in press, Burley *et al.* 1995, Dickinson *et al.* 1994, Shutler *et al.* 1994). Eight AMS ¹⁴C dates on wood charcoal from Lapita and Polynesian Plainware sites on these islands have been determined (Burley *et al.* 1995; Table 1 herein). The two dates from Polynesian Plainware sites are subsumed within the age spread of the six dates from Lapita sites. The Lapita sites have yielded abundant bones of extinct species of birds; such bones have not been found in the Polynesian Plainware sites (Table 2 p. 385). This suggests that many species of landbirds were lost from these islands within a time interval equal to or less than the statistical error inherent in very similar ¹⁴C dates, i.e., probably about 300 years or less. By either evolutionary or cultural standards, this is a very short period of time.

Island	Site	Ceramics	CAMS no.	1 sigma cal BP
Lifuka	Holopeka	Plainware	12918	2940-2790
Lifuka	Holopeka	Plainware	12919	2720-2460
Foa	Faleloa	Lapita	7145	3130-2930
Foa	Faleloa	Lapita	7146	2690-2430
Foa	Faleloa	Lapita	8074	2690-2440
Ha`ano	Pukotala	Lapita	7147	2750-2500
Ha`ano	Pukotala	Lapita	7148	3020-2840

Table 1
AMS radiocarbon dates (wood charcoal) from archaeological sites in the Ha`apai Group, Tonga. Data reported more fully in Burley *et al.* (1995).

Looking at the factors that affect extinction on islands, the three islands in Ha`apai seem well disposed as places where rapid and extensive extinction might occur. Most importantly they are small, flat, and have excellent soils for cultivation. The first colonists probably were horticulturalists who introduced non-native plants and animals and initiated a human presence that has continued to today.

The chronology of extinction for native landbirds in Ha`apai could be improved by determining accelerator-mass spectrometer (AMS) ¹⁴C dates on individual bones of extinct species such as megapodes and large pigeons. It would be ideal to date bones from both the highest and lowest stratigraphic occurrences of the extinct species. Such AMS ¹⁴C dates would suggest which species of birds survived for the longest time after

human arrival, as well as which were among the first to die out. I predict that there will be little if any difference in age between the stratigraphically highest and lowest dated bones from extinct megapodes and pigeons on Foa, Lifuka, or Ha`ano.

Discussion

Rapid extinction of birds on previously uninhabited Tongan islands would support the overkill and even "blitzkrieg" models of extinction (Martin 1990, Martin and Stuart 1995). Elsewhere in Polynesia, however, estimates for the amount of time that elapsed between the first arrival of humans and the extinction of most species of birds are more varied. On large, high islands in East Polynesia (>50 km², >100 m elevation), these estimates vary from several centuries to more than 1500 years. Many species of birds became extinct in East Polynesia from 900 to 600 yr BP (Steadman and Kirch 1990, Steadman 1995a, 1995b, Kirch *et al.* 1995, Steadman and Rolett 1996). The discrepancies in estimates of the rapidity of extinction arise from differing opinions on when humans first arrived in East Polynesia, ranging from 2500 to 1000 yr BP (Kirch 1986, 1996, Hunt and Holsen 1991, Spriggs and Anderson 1993, Anderson 1994, 1995, Kirch and Ellison 1994). The younger age estimates of human arrival are compatible with a blitzkrieg model of extinction. The older ones are not, and invite explanations of how species could survive so long in human presence.

The information now available for evaluating the chronology and extent of extinction in South Pacific birds may be inadequate for detailed comparisons between island groups. We simply need more bone-rich excavations at well stratified sites using laborious sieving methods (most or all sediment sieved through 3 mm mesh or finer, with subsampling to 1 or 2 mm mesh), followed by extensive radiocarbon dating and a major effort to identify bird bones to the species level. All of this adds up to a huge investment of time, money, and cooperative research - an exciting challenge and opportunity for the talented archaeological and biogeographic community of the tropical Pacific.

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DOMESTICATES	Lapita sites	Polynesian Plainware and later sites
Gallus gallus (i) Chicken	X	X*
SEABIRDS		
*Puffinus pacificus	X	X
Wedge-tailed Shearwater		
*Puffinus lherminieri	-	X
Audubon's Shearwater		
*Pterodroma sp. petrel	X	-
*Phaethon lepturus	X	-
White-tailed Tropicbird		
*Anous stolidus	X	X
Brown Noddy		
*Anous minutus	X	-
Black Noddy		
*Gygis candida	X	-
Common Fairy-Tern		
SHOREBIRDS		
Pluvialis dominica (m)	X	-
Lesser Golden-Plover		
Heteroscelus incanus (m)	X	-
Wandering Tattler		
Numenius tahitiensis (m)	X	-
Bristle-thighed Curlew		
LANDBIRDS		
Anas superciliosa	X	-
Gray Duck		
ÅMegapodius alimentum	X	-
Consumed Megapode		
ÅMegapodius molistructor	X	-
Giant Megapode		
*Megapodius pritchardii	X	-
Niuafou'ou Megapode		
*Porzana tabuensis	-	X
Sooty Crake		
Gallirallus philippensis	X	X
Banded Rail		
Gallirallus new sp. flightless rail	X	-
Porphyrio porphyrio	X	X
Purple Swampphen		
*Gallicolumba stairii	X	-
West Polynesian Ground-Dove		
ÅDidunculus new sp.	X	-
Large Tooth-billed Pigeon		
ÅCaloenas cf. canacorum	X	-
Large «Nicobar» Pigeon		
Ptilinopus porphyraceus	X	-
Purple-capped Fruit-Dove		
Ptilinopus perousii	X	-
Many-colored Fruit-Dove		
Ducula pacifica	X	-
Pacific Pigeon		
*Ducula latrans	X	-
Peale's Pigeon		
ÅDucula david	X	-

David's Pigeon		
À Ducula new sp.	X	-
Immense Pigeon		
Eudynamis taitensis (m)	X	X
Long-tailed Cuckoo		
Tyto alba	X	-
Common Barn-Owl		
Halcyon chloris	X	-
Collared Kingfisher		
*Halcyon sp. 2 small kingfisher	X	-
Lalage maculosa	X	-
Polynesian Triller		
*cf. Clytorhynchus vitiensis	X	-
Fiji Shrikebill		
Foulehaio carunculata	X	-
Wattled Honeyeater		
Aplonis tabuensis	X	-
Polynesian Starling		
Total NISP	~500	~200
Total species		
All	34	8
Non-native	1	1
Native	33	7
Seabirds	6	3
*Seabirds	6	3
Migratory shorebirds	3	0
Landbirds	24	4
À/* Landbirds	12	1

Table 2 (suite)

Birds from four archaeological sites on Lifuka and Foa islands, Ha'apai Group, Tonga. The Lapita sites are Faleloa and Tongoleleka. The later sites are Holopeka (Polynesian plainware) and Toumu'a Well (aceramic).

À, extinct species;

*, extirpated on Lifuka and Foa but survive elsewhere;

i, introduced species;

m, migratory species;

NISP, number of identified specimens.

Site details are reported in Burley (1994), Burley *et al.* (1995), Dickinson *et al.* (1994), and Shutler *et al.* (1994). Faunal data are modified from Steadman (1989, MS submitted), Steadman *et al.* (MS submitted). Several hundred bones from these sites, especially Tongoleleka, remain unidentified.

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