



The late Quaternary extinction and future resurrection of birds on Pacific islands

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Abstract

People have lived on tropical Pacific islands over the past 30,000 years (Bismarcks, Solomons) or 3000 to 1000 years (the rest of Oceania). Their activities have led to the loss of many thousands of populations and as many as 2000 species of birds that probably otherwise would exist today. This extinction event is documented by avian fossils from archaeological (cultural) and paleontological (noncultural) sites from nearly 70 islands in 19 island groups. Extinction of birds in Oceania rivals the late Pleistocene loss of large mammals in North America as the best substantiated rapid extinction episode in the vertebrate fossil record. Some avian extinctions in Oceania occurred within a century or less after human arrival, while others required millennia or even tens of millennia. Any of these time frames is rapid in an evolutionary or geochronological sense. Inter-island differences in the speed and extent of extinction can be explained by variation in abiotic (A), biotic (B), and cultural (C) factors. Levels of extinction on large, near islands can be comparable to those on small, remote islands when C factors (such as high human population density and introduction of invasive plants and animals) override A factors (such as large land area or little isolation) or B factors (such as rich indigenous floras and faunas). An innovative, proactive conservation strategy is needed not only to prevent further extinctions of birds in Oceania, but also to restart evolution of some of the lineages that have suffered the most loss, such as flightless rails. This strategy should focus on islands with ABC traits that retard rather than enhance extinction. © 2003 Elsevier Science B.V. All rights reserved.

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1. Introduction

Islands are renowned as sites of both prehistoric and modern anthropogenic extinction. Species on oceanic islands tend to be more prone to extinction than those

on continents or continental islands because of small land areas and population sizes, low rates of increase, and naïveté to predators (Diamond, 1985). The late Quaternary fossil record suggests that many thousands of populations of birds (especially seabirds such as petrels, shearwaters, boobies, and terns, and landbirds such as megapodes, rails, pigeons, parrots, and passerines) and as many as 2000 avian species (especially rails) were lost on tropical Pacific islands after the arrival of people (Steadman, 1995a, unpublished data). “Extinction” refers to taxon-level losses, whereas

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“extirpation” refers to loss of an island population of a species that survives elsewhere. The massive loss of birdlife in Oceania is a sobering example of “human domination of earth’s ecosystems” (Vitousek et al., 1997).

A model of rapid, anthropogenic late Quaternary extinction, often known as “overkill” (Martin, 1984, 1990), resonates on oceanic islands. Gathering evidence for the timing and extent of extinctions on islands that were inhabited prehistorically requires finding early (first human contact) sites with well-preserved fossil bones, determining when people arrived, obtaining large enough fossil samples to represent most of the indigenous avifauna, and identifying the fossils to species (Steadman, 1993; Kirch et al., 1995; Steadman and Rolett, 1996). The radiocarbon (^{14}C) chronology of avian extinction on islands has improved considerably over the past decade. Conventional ^{14}C dates are reported in years before present [AD 1950] or “year BP”; if calendrically calibrated for atmospheric variation in ^{14}C , they are reported as “Cal BP.” Accelerator-mass spectrometer (AMS) ^{14}C dating can determine the age of a single fossil bone. Only 0.5–1 mg of purified carbon, commonly obtained from a mere 50–150 mg of whole bone, is enough to yield an accurate AMS ^{14}C date (Stafford et al., 1990, 1999). With good collagen preservation, one can obtain high-quality AMS ^{14}C

dates from a single diagnostic skeletal element of a bird with a total body mass as small as ~ 10 g.

In this paper, we first briefly review the late Quaternary (especially the late Holocene) extinction of birds on a few exemplary islands in Oceania from a chronological, cultural, and paleoecological rather than taxonomic perspective. Then, we present a model that can be used anywhere in Oceania to evaluate the abiotic, biotic, and cultural factors that may accelerate or retard the speed and extent of extinction on a particular island. Finally, we show how this model can be applied to modern as well as prehistoric situations in an effort to restart the evolution of certain extinct taxa.

2. Description, methods, and materials

Large samples of Holocene fossils from the Galápagos Islands suggest that the background (pre-human) rate of extinction for reptiles, birds, and mammals during the past 8000 years was hundreds of times less than the rate after people first arrived several centuries ago (Steadman et al., 1991). This concept is supported further by data from the Hawaiian Islands (James, 1987), Tonga (Steadman, 1993), and New Zealand (Holdaway et al., 2001). Unlike in the Galápagos, most tropical Pacific islands (Fig. 1)

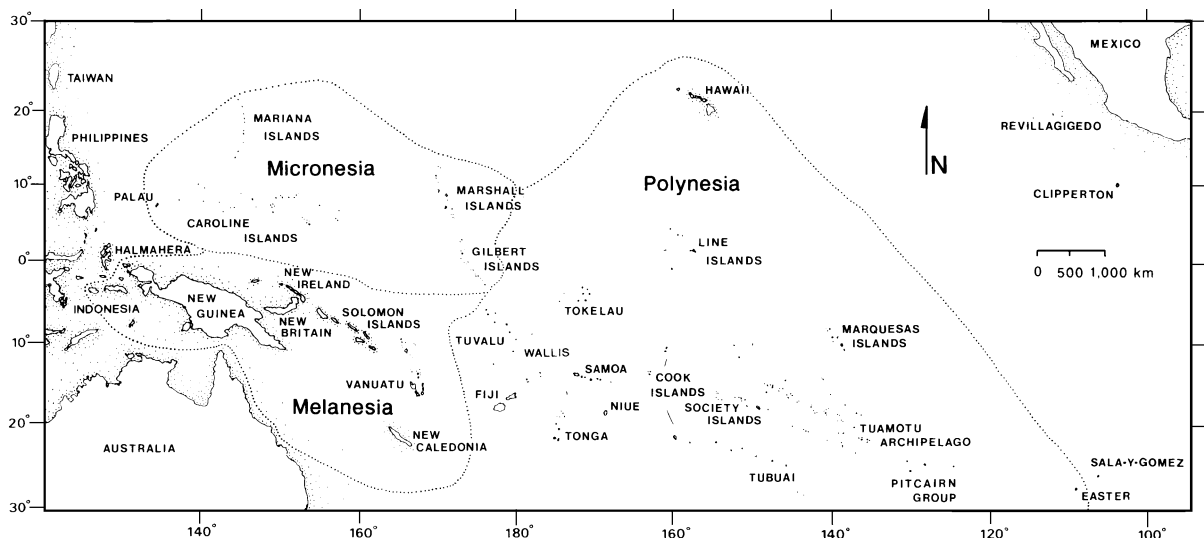


Fig. 1. The main island groups of the tropical Pacific Ocean.

were or had been inhabited before European discovery. About 3000 years ago, people of the Lapita Cultural Complex became the first settlers of Remote Oceania, colonizing rapidly from island southeast Asia eastward to Tonga and Samoa (Irwin, 1992; Kirch, 1997; Spriggs, 1997) (“Remote Oceania” refers to islands east of the Solomons and north of the Bismarcks, i.e., Polynesia, Micronesia, Vanuatu, New Caledonia, and Fiji, whereas “Near Oceania” refers to the main islands of the Bismarcks and Solomons, first colonized by people ca. 30,000 years ago; see Green, 1991). The Lapita peoples were horticulturalists as well as hunters and fishers who exploited a wide range of marine and terrestrial animals (Kirch, 1997, 2000; Steadman, 1999b). The name “Lapita” is taken from a site in New Caledonia where their distinctively decorated pottery was first discovered. Lapita sites range in age from 3500–3350 Cal BP in the Bismarcks to 2850–2750 Cal BP near its eastern limit in Tonga (Kirch, 1997; Burley, 1999; Dickinson and Shutler, 2000; Burley and Dickinson, 2001; Steadman et al., 2002).

Lapita pottery is lacking on islands east of Tonga and Samoa (Kirch, 1997), although sedimentological and palynological evidence of fire, deforestation, and plant introductions suggests that humans arrived as early as 2500 Cal BP in the Cook Islands and 1500 Cal BP in the Society Islands (Ellison, 1994; Kirch and Ellison, 1994; Lepofsky et al., 1996). Nevertheless, artifact-bearing archaeological sites are rare in this region before 1000 Cal BP (Rolett, 1998; Kirch, 2000). On many islands east of the Cook Islands, people may have been absent or only sporadically present before Polynesian settlement at ca. 1000 Cal BP. This pertains as well to the outlying Hawaiian Islands, Easter Island, and New Zealand, also colonized by Polynesians (Kirch, 2000).

Knowing whether the loss of a certain species required years, decades, centuries, or millennia is important to infer patterns of exploitation. This is less critical from an evolutionary or geological standpoint because all of these time scales are short. One cannot be certain that an archaeological site, even one that represents initial human occupation and yields abundant bird fossils, has sampled all of the indigenous species that existed at first human contact. The most vulnerable species may have been lost within decades of exposure to people, leaving behind few if any

fossils to be recovered and identified. In such instances, precultural fossil assemblages reveal which species were present at human arrival.

From New Ireland (Steadman et al., 1999a,b) to Easter Island (Steadman, 1995a), DWS has studied 26,000+ avian fossils from >60 islands across Oceania. Most fossil samples are small (<100 identified specimens per island), although the number exceeds 500 on 17 islands in seven archipelagos. On no one island it is likely that the fossils represent all species that existed at first human contact. Faunal completeness probably is being approached (>80% of species) on five islands with >1000 identified bird fossils (Henderson, Pitcairn Group; Ua Huka, Marquesas; Mangaia, Cook Islands; and Lifuka and 'Eua, Tonga). An exceedingly rich fossil record of birds is also available from the two very large but highly isolated Pacific island groups settled in post-Lapita times, namely the Hawaiian Islands (James, 1987; James and Olson, 1991; Olson and James, 1991; James and Burney, 1997) and New Zealand (Anderson, 1989; Worthy and Holdaway, 1994; Holdaway, 1999; Holdaway et al., 2001).

On the Tongan island of 'Eua (87 km², 325-m elevation), at least 22 species of landbirds (herons, megapodes, rails, pigeons, parrots, passerines, etc.) have been lost since human arrival at ca. 2850 Cal BP (Steadman, 1993, 1995a). Twelve species of landbirds survive on 'Eua. A cave named 'Anatu has a cultural stratum (Layer I) underlain by sediment (Layers II and III) that predates human presence. Layer I is a fossil-rich midden deposited by humans and barn owls (*Tyto alba*), with ¹⁴C dates from 570 ± 70 years BP (670–500 Cal BP) at 20-cm depth to 2710 ± 70 years BP (2970–2710 Cal BP) at 36-cm depth. Beneath Layer I is 100–140 cm of calcareous pebbly silt (Layers II and III) regarded as pre-human because it lacks the cultural features, charcoal, artifacts, or bones of chickens (*Gallus gallus*), Pacific rats (*Rattus exulans*), pigs (*Sus scrofa*), dogs (*Canis familiaris*), or humans found in Layer I. Layers II and III are separated from each other by calcite flowstone 2–5 cm thick, with three uranium-series dates ranging from 78.8 ± 2.7 to 60.0 ± 3.0 ka. Layers II and III yielded fossils from 46 species of extinct or extirpated vertebrates (26 landbirds, 12 seabirds, 5 bats, and 3 lizards); only 13 (38%) of these still occur on 'Eua (Steadman, 1993, unpublished data; Pregill, 1994; Koopman and Stead-

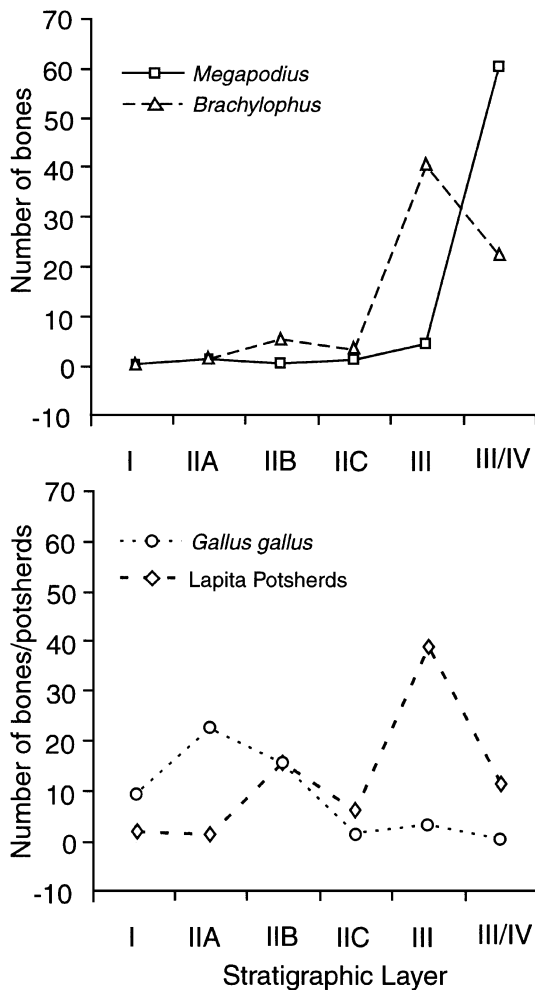


Fig. 2. Distribution of fossil bones of extinct megapode (*Megapodius alimentum*), extinct iguana (*Brachylophus* undescribed sp.), chicken (*Gallus gallus*), and decorated (Lapita) potsherds in each major stratigraphic layer, Excavation Unit 10, Tongoleleka archaeological site, Lifuka, Tonga. From Steadman et al. (2002).

man, 1995). Deposited before human arrival, Layers II and III yielded no evidence of extinctions.

About 120 km north of 'Eua, in the Ha'apai Group of Tonga, the extinction of most species of birds occurred almost too rapidly to be resolved by ^{14}C dating. On the five small (1.8–13.3 km²), low (elevation 10–20 m) islands of Foa, Lifuka, Ha'ano, 'Uiha, and Ha'afeva, Lapita colonization at 2850–2750 Cal BP left behind rich deposits of pottery, other artifacts, charcoal, shell, and bone on leeward beaches of calcareous sand (Dickinson et al., 1994; Shutler et

al., 1994; Burley et al., 1995; Burley, 1999; Steadman et al., 2002). Based on the ca. 1800 bird fossils that DWS has identified thus far from these sites, at least 22–26 species of landbirds lived on each of these five islands at human contact, more than twice the 9–11 species living on individual islands in Ha'apai today and equivalent to the 26 species known from pre-cultural deposits on the much higher, larger island of 'Eua (Steadman, 1993, 1998, unpublished data). At the most extensively studied archaeological site in the Ha'apai Group, Tongoleleka on Lifuka Island, fossils of extinct or extirpated birds and iguanas are common in lower strata along with Lapita potsherds, but are rare or absent in the overlying strata where the predominate pottery style is Polynesian Plainware (Fig. 2). "Polynesian Plainware" is a nondecorated pottery style that replaced the more ornate Lapita pottery in Fiji, Tonga, and Samoa at ca. 2700 Cal BP (Burley, 1999; Kirch, 2000).

AMS ^{14}C dates from Polynesian Plainware contexts (Layers I and II) at the Tongoleleka site average only 100–150 years younger than (and usually overlap at 1σ or 2σ) those from Lapita contexts (Steadman et al., 2002; Table 1 herein). This suggests that most species of landbirds were lost from islands in the Ha'apai Group within a time period equal to or less than the

Table 1

Stratigraphic and taxonomic sets of weighted mean averages of AMS ^{14}C dates from excavation Unit 10, Tongoleleka archaeological site, Lifuka Island, Tonga

| Stratum/species | Number of AMS ^{14}C dates | Weighted mean average conventional ^{14}C age (years BP) | Weighted mean average calibrated ^{14}C age (Cal BP) |
|-------------------------------------|-------------------------------------|---|---|
| IIA | 2 | 2690 ± 30 | 2850–2760 |
| IIB/IIC | 5 | 2700 ± 20 | 2840–2760 |
| III | 3 | 2660 ± 20 | 2780–2750 |
| III/IV | 8 | 2760 ± 20 | 2880–2790 |
| <i>Gallus gallus</i> | 5 | 2650 ± 20 | 2780–2750 |
| <i>Megapodius alimentum</i> | 7 | 2790 ± 20 | 2940–2850 |
| <i>Brachylophus</i> undescribed sp. | 6 | 2700 ± 20 | 2840–2760 |

The calibrated ^{14}C ages are presented at 2σ (95.4% confidence). Each AMS ^{14}C date is on an individual, identified fossil of a chicken (*Gallus gallus*), extinct megapode (*Megapodius alimentum*), or extinct iguana (*Brachylophus* undescribed sp.). From Steadman et al. (2002).

statistical error (2σ ; 95.4% confidence) inherent in the similar ^{14}C dates, i.e., less than 150 years. After this short period of intense depletion, the avifauna assumed a modern composition that has remained largely unchanged for 2700 years. The five islands in Ha'apai with Lapita pottery are small (ca. 1.8–13.3 km²), flat, low (10–20-m elevation), and covered with fertile soils (Dickinson et al., 1999). Apart from bats, native mammals were absent. The Lapita colonists surely hunted and fished, as seen from the 100,000+ bones of fishes, reptiles, birds, and mammals recovered from the five archaeological sites. They also brought nonnative plants (28 species listed in Kirch, 1997: Table 7.2) and animals (chicken, Pacific rat, dog, and pig), cut and burned the forest, and initiated a permanent and overwhelming human presence that continues today. That the fossil record reveals rapid and extensive extinction in the Ha'apai Group is not surprising.

On East Polynesian islands, with respectable fossil samples and radiometric dates, most extinction of landbirds occurred from 1000 to 600 Cal BP, roughly 2000 years later than in Tonga and corresponding to the archaeological evidence of first permanent human occupation at ca. 1000 Cal BP (Steadman, 1995a; Wragg, 1995; Kirch, 1996). The environmental, cultural, and chronological contexts for these losses are particularly revealing on Mangaia, Cook Islands. Within a framework of nearly 50 conventional and AMS ^{14}C dates, the rich cultural deposits at Tangata-tau Rockshelter (site MAN-44) depict the decline of landbirds on Mangaia from 20 to 5 species over the past 1000 years. Most extinction had taken place by 700–600 Cal BP, a period of little perceptible change in material culture (Steadman and Kirch, 1990; Steadman, 1995b, unpublished data; Kirch, 1996; Steadman et al., 2000; Fig. 3 herein). Lost were a heron (*Nycticorax* undescribed sp.), four rails (*Porzana rua*, *Porzana* undescribed sp., *Gallirallus ripleyi*, *Gallinula/Porphyrio* undescribed sp.), a sandpiper (*Proso-bonia* undescribed sp.), five pigeons and doves (*Ducula aurorae*, *D. galeata*, *Ptilinopus rarotongensis*, *Gallinolumba erythroptera*, *G. nui*), three parrots (*Vini kuhlii*, *V. vidivici*, *V. sinotoi*), and a swift (*Collocalia manuoi*). The survivors are heron (*Egretta sacra*), duck (*Anas superciliosa*), rail (*Porzana tabuensis*), kingfisher (*Halcyon mangaia*), and warbler (*Acrocephalus kerearako*), the first three widespread in Oceania and the last two endemic to Mangaia.

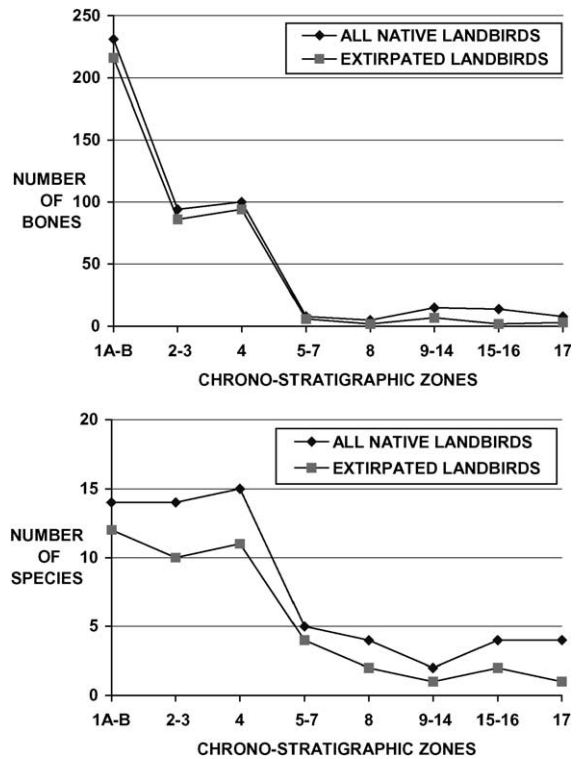


Fig. 3. Time-series of native landbird fossils by chrono-stratigraphic zones at Tangata-tau Rockshelter, Mangaia, Cook Islands. Zones 1A–B are oldest (pre-cultural). Zones 2–3 are the earliest cultural levels (up to 900–1000 years old). The avifaunal collapse between zones 4 and 5 is 700–600 years old. Zone 17 is the youngest (ca. 200 years old). The decline in number of species between zones 1–4 and zones 5–17 is not a function of smaller sample sizes of bird fossils because those of other taxa (fish, rats, dogs, pigs, humans) do not decrease in number during this same time. Modified from Kirch et al. (1995).

The chronology of avian extinction in the Marquesas Islands, based on bird fossils at the Hanamiai archaeological site (Steadman and Rolett, 1996; Rolett, 1998), is very similar to that on Mangaia. Lost on Tahuata were seven species of rails, pigeons and doves, and parrots (Table 2). The stratigraphic distribution of bird fossils at Hanamiai shows that exploitation of indigenous landbirds was intense only during Phase I (ca. 925–650 Cal BP). Four of the seven extinct or extirpated species are not recorded at Hanamiai after Phase I. By ca. 500 Cal BP or even earlier, six of the seven extirpated species of landbirds (and, undoubtedly, others not recorded in the small fossil sample) either had been eliminated from the

Table 2
Bird fossils from the Hanamiai Dune archaeological site, Tahuata, Marquesas

| Species | Phase | | | | | Total |
|---|-------|----|-----|----|---|-------|
| | I | II | III | IV | V | |
| <i>Rails</i> | | | | | | |
| <i>Gallirallus</i> undescribed sp. ^a | 19 | 3 | 2 | – | – | 24 |
| <i>Porphyrio paepae</i> ^a | 9 | 1 | 1 | – | – | 11 |
| [<i>Gallirallus/Porphyrio</i> ^a] | 1 | – | – | – | – | 1 |
| <i>Pigeons, doves</i> | | | | | | |
| <i>Gallinocolumba rubescens</i> ^a | 5 | – | – | – | – | 5 |
| <i>Ptilinopus dupetithouarsii</i> | 1 | – | 1 | – | – | 2 |
| <i>Ducula galeata</i> ^a | 6 | – | – | – | – | 6 |
| <i>Parrots</i> | | | | | | |
| <i>Vini ultramarina</i> ^a | – | – | 1 | 3 | – | 4 |
| <i>Vini vidivici</i> ^a | 4 | – | – | – | – | 4 |
| <i>Vini sinotoi</i> ^a | 3 | – | – | – | – | 3 |
| [<i>Vini</i> sp. ^a] | 2 | – | – | – | – | 2 |
| <i>Kingfishers</i> | | | | | | |
| <i>Halcyon godeffroyi</i> | – | 1 | – | – | – | 1 |
| <i>Warblers</i> | | | | | | |
| <i>Acrocephalus mendanae</i> | – | – | – | 2 | – | 2 |
| <i>Total fossils</i> | | | | | | |
| All native landbirds | 50 | 5 | 5 | 5 | 0 | 65 |
| Species ^a | 49 | 4 | 4 | 3 | – | 64 |
| % ^a | 98 | 80 | 80 | 60 | – | 92 |
| <i>Total species</i> | | | | | | |
| All native landbirds | 7 | 3 | 4 | 2 | – | 10 |
| Species ^a | 6 | 2 | 3 | 1 | – | 7 |

Approximate ¹⁴C chronology (from Rolett, 1998) is as follows: Phase I—925–650 Cal BP; Phase II—925–650 Cal BP; Phase III—650–500 Cal BP; Phase IV—500–150 Cal BP; Phase V—150–100 Cal BP. Taxa in brackets are not necessarily different from those listed more specifically. Modified from Steadman and Rolett (1996).

^a Extinct or extirpated species.

island or had become uncommon enough to elude archaeological sampling.

3. Results and analyses: factors that affect extinction rates on islands

The factors that influence the speed and extent of anthropogenic extinction of birds on islands can be divided into three major categories (Steadman, 1999c).

Here we designate these categories as abiotic (A), biotic (B), and cultural (C). The various ABC factors can interact, both within and between categories, either to delay or to promote extinction. We now propose a model, based on these factors, which can be used to evaluate the late Quaternary fossil record of birds in Oceania and on other oceanic islands. Discussed below and outlined in Table 3, the ABC model can be applied to any oceanic island or island group. Our examples focus on Oceania, where islands can differ profoundly from one another in any of these factors.

3.1. Abiotic factors

These inherent characteristics of an island provide the physical background for biological and cultural factors.

3.1.1. A1. Island size (land area)

As island area increases, it should take longer for an anthropogenic impact to spread. For some introduced predators (such as rats or snakes) or pathogens (such as avian malaria or pox), the differences in dispersal times across large vs. small islands may be decades or less. By itself, large island size does not prevent extinction.

3.1.2. A2. Topography

Extreme steepness (high relief) or roughness (karstification) may deter deforestation, cultivation, nonnative predators, and other agents of extinction. This is why so many endangered species of Hawaiian plants live only on virtually inaccessible cliff-sides. With many exceptions, topographic constraints on human activities tend to be greater on large islands than on small islands or atolls, simply because large islands are more likely to have more relief.

3.1.3. A3. Bedrock

This factor influences topography and soil types. Karst limestones often feature pinnacles, crevices, sinkholes, and cliffs (see Stoddart et al., 1985; Pandolfi, 1995) that stifle human activities, including hunting and deforestation, and thus delay extinction. Oceanic basalts may weather into “knife-edge” ridges (see Duncan et al., 1994; Thompson et al., 1998) that are too steep to cultivate.

Table 3

A summary of the ABC model (factors that influence extinction of vertebrates on oceanic islands after human arrival)

| | Promotes extinction | Delays extinction |
|-----------------------------------|---|---|
| <i>Abiotic factors</i> | | |
| A1. Island size | small | large |
| A2. Topography | flat, low | steep, rugged |
| A3. Bedrock | sandy, or noncalcareous sedimentary | limestone or knife-edge volcanics |
| A4. Soils | nutrient-rich | nutrient-poor |
| A5. Isolation | no adjacent islands | many nearby islands |
| A6. Climate | seasonal aridity | reliably wet |
| A7. Sea level | high stands (atolls only) | low stands (atolls only) |
| <i>Biotic factors</i> | | |
| B1. Plant diversity | depauperate | rich (short-term delay only) |
| B2. Faunal diversity | depauperate | rich (short-term delay only) |
| B3. Terrestrial mammals | absent | present |
| B4. Marine resources | depauperate; difficult access | rich (temporary delay only); easy access |
| B5. Species-specific traits | ground-dwelling; flightless; large; tame; palatable; colorful feathers; long and straight bones for tools | canopy-dwelling; volant; small; wary; bad taste; drab plumage; short and curved bones |
| <i>Cultural factors</i> | | |
| C1. Occupation | permanent | temporary |
| C2. Settlement pattern | island-wide | restricted (coastal) |
| C3. Population growth and density | rapid; high | slow; low |
| C4. Subsistence | horticulture as well as h–f–g | h–f–g only, especially if marine-oriented |
| C5. Introduced plants | many species; invasive | few species; noninvasive |
| C6. Introduced animals | many species; feral populations | few or no species; no feral populations |

See text for further explanation. The cultural factors are presented graphically in Fig. 4.

3.1.4. A4. Soils

Indigenous plant communities are unlikely to endure where soils are well suited for cultivation.

3.1.5. A5. Isolation

Remote islands tend to have depauperate plant and animal communities. Greater isolation increases dependence on that island alone for natural resources, resulting in a resource sink as on Easter Island (Flenley et al., 1991; Steadman et al., 1994; Steadman, 1995a). These factors intensify the overexploitation of indigenous species.

3.1.6. A6. Climate

To the detriment of indigenous biota, forests on seasonally dry islands are easier to burn. Conversely, unpredictable droughts on such islands can restrict agriculture and thus limit human populations. Both long-term (Lea et al., 2000; Tudhope et al., 2001) and short-term (Wigley and Raper, 2001) variation in climate can influence the agricultural potential of, and the ability to, clear forest.

3.1.7. A7. Sea level

Changes in sea level were drastic (ca. 118–135 m) during the glacial–interglacial transition from ca. 20 to 8 Cal BP (Clark and Mix 2000; Hanebuth et al., 2000). The much more subtle mid- to late Holocene changes in sea level (ca. 1–2 m) were nevertheless important from a standpoint of coastal geomorphology and initial human settlement (Dickinson, 1999, 2001; Dickinson et al., 1999). In compromising the richness of the terrestrial biota, neither of these rises in sea level would have had nearly as profound an ecological consequence on high islands as on atolls or low limestone islands.

3.2. Biotic factors

These factors refer to an island's native plant and animal communities at first human contact.

3.2.1. B1. Plant diversity

Having more species available, a richer flora might be exploited in a more generalized way, spreading human impact across many species. On the other hand, such floras may include rare species that, if subjected to specialized exploitation, would be

easy to exterminate. In either case, sustained exploitation of rich plant communities eventually will deplete more species in rich than in depauperate communities.

3.2.2. B2. Faunal diversity

As with plants, being part of a relatively rich fauna can work either for or against survival of a species. Faunal diversity includes pathogens; one would expect indigenous birds from islands with few pathogens to be more vulnerable to disease if nonnative pathogens arrive through human agency (Steadman et al., 1990).

3.2.3. B3. Presence/absence of nonvolant terrestrial mammals

On islands lacking indigenous, nonvolant terrestrial mammals (which includes all islands in Remote Oceania; Flannery, 1998), native birds may be more susceptible to predation when nonnative mammals such as humans, rats, dogs, pigs, etc. are present.

3.2.4. B4. Marine resources

Rich marine life might lessen the short-term human dependence on terrestrial resources. In the long run, however, renewable marine resources subsidize population growth, thereby intensifying use of terrestrial resources. People may emphasize terrestrial rather than marine resources if access to the sea were restricted by intertribal violence (Dye, 1990) or by coastal geology and weather (cliffs, fringing reefs, windward coasts, storms, rough seas, etc.).

3.2.5. B5. Species-specific ecological, behavioral, or morphological traits

Birds of the forest canopy are more difficult to hunt than those in the understory or on the ground. Flightless species are so vulnerable to nonnative predators that nearly all are extinct (Steadman, 1995a). Although superb flyers, most species of seabirds are ground-nesters that are clumsy on land and thus highly vulnerable to predation. Certain birds may be favored (megapodes, pigeons) or avoided (herons, warblers) by hunters because of differences in taste, plumage color, shape and size of bones (for making tools and ornaments), song, spiritual meaning, or other traits (Burley, 1996; Steadman, 1997a). Rarity of favored

species in Oceania probably did not prevent them from being hunted.

3.3. Cultural factors

These closely interrelated factors concern the socio-economic structure, demography, and cultural ecology of prehistoric peoples (Fig. 4). Levels of sociopolitical complexity (see Kirch, 1990, 2000) influence these factors.

3.3.1. C1. Occupation (permanent vs. temporary)

Permanent settlement leads to the introduction of nonnative species of plants and animals, and to regular burning in the dry season to sustain horticulture. These activities would be less extensive if occupation were transitory, such as an island used as a seasonal hunting/fishing outpost.

3.3.2. C2. Settlement pattern

Even though island interiors undoubtedly were used early for hunting and/or cultivation, the oldest habitation sites in Remote Oceania are coastal (Kirch, 1986). When island interiors were settled centuries later, perhaps as a response to increased human population, exploitation of natural resources became intense island-wide (Kirch and Ellison, 1994).

3.3.3. C3. Population growth and density

Prehistoric settlement data suggest population increases with time, in spite of resource shortages, disease, warfare, infanticide, and other prehistoric controls on population (Kirch, 1990). Population growth intensifies resource consumption.

3.3.4. C4. Subsistence (horticulturalists vs. hunter–fisher–gatherers [h–f–g])

Lapita and later peoples in Remote Oceania were horticulturalists as well as h–f–g. Horticulturalists might develop larger populations, have different settlement patterns, and alter more forest than peoples with an exclusively h–f–g economy.

3.3.5. C5. Introduced plants

Prehistoric people transported many species of plants across Oceania (Kirch, 1994, 1997). Deforestation, especially through dry-season burning, provided tillable land for cultivation (Athens, 1997).

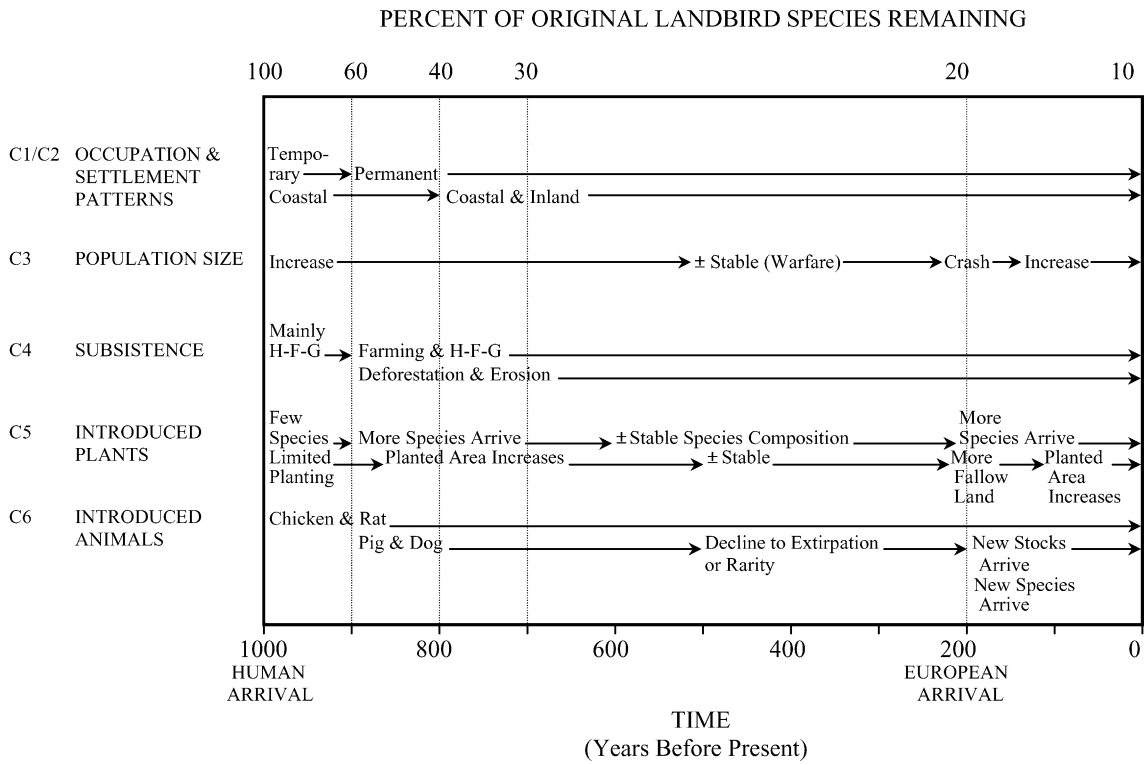


Fig. 4. A hypothetical example of the cultural (C) factors, taken from the ABC model (Table 3), that drive anthropogenic extinction on Pacific oceanic islands. This example is based in part on data from East Polynesia. See text for additional details.

3.3.6. C6. Introduced animals

Rats, dogs, pigs, and chickens accompanied the first colonists of Remote Oceania. Each of these animals can establish feral populations, although only rats did so consistently. Chickens may transmit disease to native birds, whereas nonnative mammals prey on birds (Atkinson, 1985; Hunt et al., 1996) and are seed-predators that may disrupt forest succession.

4. Discussion and conclusions

4.1. Prehistoric extinctions: continents vs. islands

The overkill model attributes the catastrophic late Quaternary extinction of large (>44 kg) mammals in lands of human colonization to overhunting rather than changes in climate and habitat associated with the glacial to interglacial transition (Martin, 1984, 1990).

To accommodate the ^{14}C chronology for extinction of North American large mammals at ca. 13,000 Cal BP, Mosimann and Martin (1975) developed the blitzkrieg model—a rapidly advancing front of skilled hunters who killed preferred prey beyond their needs and responded to an unlimited food supply with rapid population growth. The blitzkrieg model proposes that human presence and megafaunal collapse could have swept across North and South America in several centuries, equivalent to only 5–10 human lifetimes or 10–20 human generations. In ^{14}C time, a few hundred years is essentially instantaneous. An improved version accomplishes much the same result with a much smaller human population (Alroy, 2001).

Two items stand out in the late Quaternary extinction of vertebrates on continents. First is that, with rare exception, only large species of mammals (and their commensals, scavengers, and parasites) were affected (Martin, 1984; Steadman and Martin, 1984; Martin and

Steadman, 1999). Second is that where the losses were greatest (North America, South America, Australia), the faunal collapse post-dated the arrival of people onto a previously uninhabited landscape (Alroy, 1999; Miller et al., 1999). By contrast, humans and other large mammals evolved side-by-side through the Quaternary (last 1.8 million years) in Africa and Eurasia, where late Pleistocene mammalian extinctions were less extensive and occurred over a much longer time (tens of millennia; Martin and Stuart, 1995).

The late Pleistocene arrival of humans in North America, South America, and Australia is comparable to the late Pleistocene and late Holocene human colonization on oceanic islands. In both cases, vertebrate faunas unaccustomed to people were suddenly subjected to earth's most ingenious predator. Whether large mammals on continents or birds on oceanic islands, most species were unable to cope with becoming the preferred prey of bipedal invaders, or at least were unable to survive other ecological changes brought on by people. Another similarity between late Quaternary extinctions on islands and those in North America, South America, and Australia is that no other fossil-based vertebrate extinction event of this magnitude has been found prior to human colonization (James, 1987; Steadman et al., 1991; Alroy, 1999; Martin and Steadman, 1999). These losses are unique. When considered in geological rather than ecological time scales, their coincidence with human arrival is by itself overwhelming evidence for cause and effect.

The rapid loss of birds (and iguanas) on Tongan islands suggests an insular version of the blitzkrieg model. The short period of time (<150 years) between Lapita and Polynesian Plainware contexts in Ha'apai resembles that which separates Clovis from Folsom contexts in North America (Taylor et al., 1996) ("Clovis" and "Folsom" are the two types of stone projectile points found early in the North American cultural sequence). Collapse of the North American large mammal fauna occurred during Clovis rather than subsequent Folsom times, just as the avifauna of Ha'apai collapsed during the brief tenure of Lapita peoples and attained an essentially modern species composition by Polynesian Plainware times. In both cases, a vertebrate fauna that had not known humans was invaded by skilled hunters. Among factors in the ABC model that would have promoted

the extinction of birds in the Ha'apai Group are A1–A4, A7, B3, and C1–C6.

Elsewhere in Polynesia, estimates are more varied for how much time elapsed between first human arrival and the loss of most species of birds. On large islands in East Polynesia (>50 km², >100-m elevation), estimates range from a few centuries to >1500 years. Most East Polynesian species of birds became extinct from 1000 to 600 Cal BP (Steadman, 1995a; also see above). When humans first arrived in East Polynesia, however, is not well resolved within the late Holocene, with estimates ranging from ca. 2500 Cal BP (Kirch, 1986; Kirch and Ellison, 1994) to 1000 Cal BP (Anderson, 1995). The younger estimates of human arrival are compatible with blitzkrieg-type extinction. The older ones are not, and invite explanations of how island species could survive so long in human presence. Steadman (1995b) and Kirch (1996) propose that human habitation was in temporary, coastal settlements before 1000 Cal BP, with permanent, island-wide settlement only thereafter.

Here, the ABC model (Table 3, Fig. 4) provides some guidance. Acting in concert, factors A2, A3, and C1 through C6 could be especially important in delaying extinction on high East Polynesian islands. In other regions of Oceania, local variation in factors such as A1, A6, B3, B4, and C1–C6 might help further to delay extinctions from centuries to a millennium or more. Even on the large, topographically rugged, mostly forested, malarial island of New Ireland in the Bismarcks, at least 12 species of birds have been lost since human arrival at ca. 32,000 years BP (Steadman et al., 1999a,b). That these losses occurred both in the late Pleistocene (>10,000 years BP) and in the Holocene (<10,000 years BP) might be attributed to traits on New Ireland that have retarded extinction rates, such as factors A1, A2, A6, B1–B3, C2, and C3.

4.2. Restorations and mitigations

Most species and populations of Pacific island birds that existed at human contact already are gone, and losses continue to take place. One of the goals of Quaternary geology, especially from a standpoint of global change, is to use information from the past to help to understand the present and predict the future

(Dickinson, 2000). This concept has strong and direct application to birds in Oceania, where some future extinction might be offset by moving birds to certain islands where late Quaternary fossils indicate that they once occurred (Franklin and Steadman, 1991). Two such translocations show initial signs of success.

The first is moving the endangered Marquesas Lorikeet (*Vini ultramarina*) from Ua Huka (the only remaining large population) to Fatu Hiva, Marquesas in 1992–1994 (Kuehler et al., 1997). The Ua Huka population itself is based on birds brought from Ua Pou in 1941. Prehistoric bones show that *V. ultramarina* was widespread in the Marquesas at human arrival (Steadman, 1995a). The second involves the Polynesian megapode (*Megapodius pritchardii*), chicks and eggs of which were moved in 1992–1993 from its last stand on the inhabited, volcanic Tongan island of Niuafo'ou to the well-forested, uninhabited, volcanic Tongan islands of Late and Fonualei (see Göth and Vogel, 1995; Jones et al., 1995, p. 148), where they still survived in 1999 (C. Matavalea, personal communication). Fossils from archaeological and paleontological sites indicate that *M. pritchardii* was widespread in Tonga at human arrival (Steadman, 1993, 1999b, unpublished data).

The conditions to consider in evaluating translocations (see Franklin and Steadman, 1991; Armstrong and McLean, 1995) are reflected in the ABC model. We would add that small islands should not be overlooked. Substantial landbird populations persist, for example, on many very small (0.1–10 km²) forested islands in Fiji, Tonga, and Samoa (Steadman and Freifeld, 1998; Steadman et al., 1999a,b; Freifeld et al., 2001, DWS unpublished data). Small islands with favorable ABC factors (such as being uninhabited, mainly forested, and with few or no introduced species of plants and animals) may provide some of our best opportunities to save remnants of Oceania's depleted avifauna. We will describe three situations where new translocations would stand a decent chance of success.

The first example would be to release the Polynesian megapode (*M. pritchardii*) and tooth-billed pigeon (*Didunculus strigirostris*) on the steep, uninhabited, forested, volcanic island of Tofua (46.6 km², 558-m elevation) in Tonga. Tofua is uninhabited primarily because the single possible landing place is bouldery, steep, very dangerous even under the

calmest conditions, and lacks an anchorage or wharf. Bones of *M. pritchardii* occur in archaeological sites on nearby smaller islands (Tofua has no prehistoric record of birds), as do bones of an undescribed species of *Didunculus* (Steadman, 1999c). The living *D. strigirostris* survives only in Samoa where it is threatened by massive deforestation (Beichle, 1987, DWS personal observation). The current species richness and relative abundance of landbirds on Tofua exceed that of any inhabited island in the region (Steadman, 1998). This reflects its lower level of human impact, epitomized in a magnificent rainforest that is protected from logging by rugged terrain. From an ABC standpoint, Tofua excels in factors A2, A3, B1, B2, and all of C.

A second example would be to release the Guam Rail (*Gallirallus owstoni*) on Aguiguan, an uninhabited, cliffy, mostly forested limestone island (7 km², 157-m elevation) 150 km NNE of Guam. The Guam Rail was lost in the wild in the 1980s but thrives in captivity (Haig and Ballou, 1995). Since 1990, several attempts on nearby Rota (81 km², 459-m elevation) have failed to establish another wild population. Aguiguan looks good in its ABC factors, differing from Rota in lacking black rats (*Rattus rattus*), cats (*Felis catus*), dogs, people, highways, vehicles, a wharf, an anchorage, etc., i.e., the important primary and secondary sources of anthropogenic rail mortality.

It is also just a matter of time before Rota becomes infested with the brown tree snake (*Boiga irregularis*), which has devastated Guam's avifauna in recent decades (Savidge, 1987). Lacking shipping facilities and accessible (with difficulty) only by very small boats, Aguiguan will not be colonized by this snake. At Pisonia Rockshelter, a cultural site on Aguiguan (¹⁴C dates ranging from 1870–1530 to 660–500 Cal BP), the most common species of bird recovered was a flightless rail (*Gallirallus* undescribed sp.) similar to the Guam Rail (Steadman, 1999a). In the absence of snakes, black rats, cats, dogs, and people, Guam Rails would have an excellent chance of surviving on Aguiguan, which still sustains healthy populations of many other landbirds including the ground-dwelling Micronesian megapode *Megapodius laperouse* (Engbring et al., 1986; Craig, 1992).

The third example concerns Mangaia (52 km², 169-m elevation), Cook Islands, where all five indig-

enous species of columbids are gone. One is extinct (*Gallinucolumba nui*; Steadman, 1997b). Three others (*D. aurorae*, *D. galeata*, and *G. erythroptera*) now exist only outside of the Cook Islands (Steadman, 1995a), with populations so small that obtaining propagules may not be possible. The fifth species is the Cook Island fruit-dove (*P. rarotongensis*), a canopy frugivore that survives only on the nearby islands of Rarotonga and Atiu (Franklin and Steadman, 1991). These same two islands sustain another canopy frugivore, the Pacific pigeon (*Ducula pacifica*), which is an ecological analog of Mangaia's extirpated population of *D. aurorae*. If protected from hunting, *P. rarotongensis* and *D. pacifica* would stand a reasonable chance of reestablishment on Mangaia, where much of the rugged karst landscape (factors A2 and A3) sustains forest with native fruiting trees such as *Ficus*, *Elaeocarpus*, *Guettarda*, *Pipturus*, *Canthium*, and *Homalium* (Merlin, 1991). Mangaia's rats, cats, dogs, and pigs (factor C6) preclude consideration of understory species for translocation. In December 1997, various Mangaian men told DWS of their desire to establish and protect populations of pigeons and doves, thereby restoring some of the auditory and visual enchantment that these forests once offered.

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