Radiocarbon dates on bones of extinct birds from Hawaii

(tandem accelerator mass spectrometer/archeology/faunal turnover)

HELEN F. JAMES*, THOMAS W. STAFFORD, JR.[†], DAVID W. STEADMAN[‡], STORRS L. OLSON*,
PAUL S. MARTIN[§], A. J. T. JULL[¶], AND PATRICK C. MCCOY[∥]

*National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; [†]Carnegie Institution of Washington, Geophysical Laboratory,
2801 Upton St., NW, Washington, DC 20008; [‡]New York State Museum, The State Education Department, Albany, NY 12230; [§]Department of
Geosciences, University of Arizona, Tucson, AZ 85721; [¶]Department of Physics, University of Arizona, Tucson, AZ 85721;
[∥]Bernice Bishop Museum, P.O. Box 19000-A, Honolulu, HI 96819

ABSTRACT Bones from a stratified sedimentary deposit
in the Puu Naio Cave site on Maui, Hawaiian Islands, reveal the
late Holocene extinction of 19 species of birds. The age of the
sediment and associated fauna was determined by direct
radiocarbon dating (tandem particle accelerator–mass spec-
trometer; TAMS) of amino acids extracted from bones weigh-
ing as little as 450 mg. The ^{14}C dates indicate that sediment has
been accumulating in the lava tube for at least the last 7750
years, a suitable time frame for testing the hypothesis that
Holocene extinction on islands began after human colonization.
Despite growing evidence that a worldwide wave of extinctions
coincided with human colonization of oceanic islands, little
radiometric data have been available to date the extinction of
most small fossil vertebrates on islands. The TAMS technique
of dating purified collagen from the bones of small vertebrates
could lead to vastly improved chronologies of extinction for
oceanic islands where catastrophic mid- to late-Holocene ex-
tinction is expected or known to have occurred. Chronologies
derived from nonarcheological sites that show continuous
sedimentation, such as the Puu Naio Cave deposit, may also
yield key evidence on the timing of earliest human settlement
of Oceania.

To a much greater degree than previously suspected, recent
paleontological research has implicated prehistoric humans
in the rapid degradation of insular ecosystems, with accom-
panying extinctions of organisms. Extensive Holocene ex-
tinctions of vertebrates occurred on oceanic islands as
diverse and distant as Madagascar (1), New Caledonia (2),
New Zealand (3, 4), the Chatham Islands (R. Cassels in 1984;
ref. 3), the Cook Islands (5), Henderson Island (6), the
Hawaiian Islands (7–9), the Galapagos (10), Antigua in the
Lesser Antilles (11), and the Balearic Islands in the Medi-
terranean (12). These extinctions were not coincident with
any climatic or geological upheavals that might have triggered
them, and most are known or thought to postdate the arrival
of *Homo sapiens*. Some combination of human-related pre-
dation, habitat alteration, or introduced pathogens, preda-
tors, or herbivores is thought to be the cause.

At least for birds, the worldwide impact of these extinc-
tions was catastrophic. No fewer than 80 species disappeared
from New Zealand and the Hawaiian Islands alone, severely
reducing the richness of their native avifaunas. If this pattern
holds for the numerous oceanic islands that are still
paleontologically unexplored, then the species richness of
birds before the spread of *Homo sapiens* in Oceania must
have been much greater than current estimates of slightly
more than 9000 avian species in the world (13).

Although fossils of extinct insular vertebrates have often
been found in archeological contexts (3, 5, 6, 8, 14), estab-
lishing the exact causes leading to extinction is rarely
possible. This is no less true for historic extinctions. The
cause of decline may be indeterminable or debatable even for
endangered species currently threatened with extinction (15,
16). Christensen and Kirch (17) point out that two alternative
hypotheses for the cause of extinction in Hawaii—Holocene
climatic change and undocumented effects of colonization by
western peoples—while not well supported, nevertheless
have not been rejected by a rigorous test.

Competing hypotheses for the cause of Late Pleistocene
megafaunal extinctions in North America have been tested by
comparing the predictions of each hypothesis to the chro-
nology of extinction derived from ^{14}C dating of extinct
animals (18). A similar approach could be used to test the
association of human impacts and island extinctions if bones
of small vertebrates could be reliably dated.

In the past, direct dates on fossil bone have often been
impossible to obtain because the bones were either too small
or too unique and valuable for ^{14}C dating. Another way to
estimate the age of extinct vertebrates is to date charcoal,
wood, or other suitable organic material found in stratigraph-
ic association with fossil bone. The application of this
technique is limited because, in many insular fossil sites, (*i*)
no organic material suitable for conventional ^{14}C dating is
found, (*ii*) datable organic material is found only in one or a
few strata, or (*iii*) the chronostratigraphic association of the
fossil bones and datable material is open to doubt. The
amount of reliable ^{14}C data pertaining to extinct island
vertebrates is consequently very little.

The tandem particle accelerator–mass spectrometer
(TAMS) may remove the obstacles to ^{14}C dating of insular
fossil vertebrates by enabling us to date milligram-sized
amino acid residues from small bones of the extinct animals
themselves. We obtained TAMS ^{14}C dates from bones
weighing between 0.45 and 11.6 g (Fig. 1). The bones were
excavated from a stratified sedimentary deposit in a lava tube
on the Hawaiian island of Maui. The importance of this site,
and potentially of many other island fossil sites, was greatly
enhanced by the ability to date small bones.

Puu Naio Cave is a lava tube located at 305 m (1000 feet)
elevation above La Perouse Bay on the southwestern slope
of Haleakala Volcano (20°37′ N, 156°24′ W; state archeolog-
ical site 50-50-14-1009; Bishop Museum archeological site
Ma-B2-3). The tube occurs within a lava flow that is probably
less than 10,000 years old, which was erupted from a vent
along the southwest rift zone of Haleakala Volcano [D. R.
Crandell in ref. 19 (1983) and personal communication
(1986)]. After the lava tube formed, part of its roof collapsed
and created a large pit with a vertical depth of 10 m and a

Evolution: James *et al.*

Proc. Natl. Acad. Sci. USA 84 (1987) 2351

FIG. 1. Fossil bones used for radiocarbon dates. (*A*) Seven bones of Pacific rat, *Rattus exulans* (AA-760, 0.45 g). (*B*) Femur of juvenile flightless ibis, *Apteribis* sp. (AA-761, 1.84 g). (*C*) Femur of flightless goose, *Thambetochen* sp. (AA-762, 11.6 g). (Bars = 2 cm.)

mouth roughly 8.5 by 5.5 m in diameter at ground level (Fig. 2).

During heavy rains, sediment was transported by water through this opening into the gently sloping ascending portion of the tube (upper cave), where it was deposited in roughly horizontal layers of pebbly, sandy muds that included various concentrations of volcanic cinders from nearby cinder cones (Figs. 3 and 4). The present surface of the sediment in the upper cave is a level floor extending 25 m from the entrance. Water was able to flow into the upper cave because of the
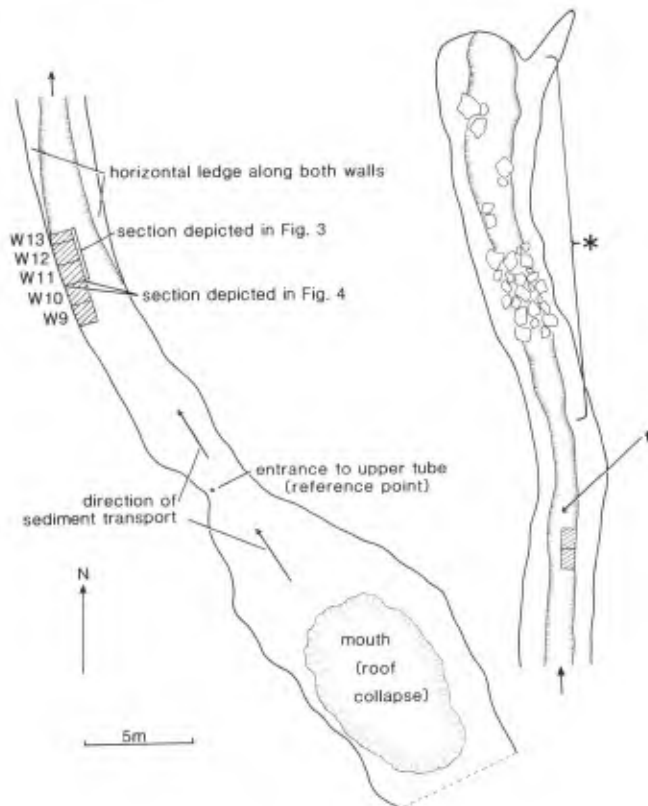

FIG. 2. Map of the upper part of Puu Naio Cave, showing the 1984 excavation (hatched area). The asterisk indicates the floor of the lava tube without sediments; the dagger indicates the end of the fine-grained sediments.

slope created by the mound of boulders left below the mouth of the cave after the ceiling collapsed. Sediment also washed into the steeper, downslope portion of the tube, where it accumulated in several shallower, less-stratified deposits extending 108 m from the entrance.

During February 1984, we removed approximately 4.5 m³ of sediment from two locations in the upper cave (Fig. 2), leaving most of the deposit undisturbed for future excavation. The excavated sediment was washed through 1/16-inch (0.16 cm) mesh screens, and the remaining concentrate was dried and sorted under a binocular microscope. In this way, we recovered about 1000 bones per cubic meter of sediment, about 580 of which were identifiable at the species level (quantities are based on grid square W9, Table 1). The bones are generally in an excellent state of preservation, and many delicate bones such as ibis mandibles, goose skulls, and small passerine long bones are unbroken.

The finely stratified, roughly horizontal bedding seen in the upper cave excavation (Figs. 3 and 4) is unique in our extensive experience with lava tube deposits. We designated four major stratigraphic units in the upper cave sediments, based on observed differences in particle size distribution, compaction, color, and bedding (Figs. 3 and 4). The upper and lower contacts of each of these units are distinct and abrupt. Within units I, III, and IV, subunits were designated to define stratigraphic breaks that represent minor changes in lithology.

The sediment consists mainly of volcanic ash, basaltic cinders, and basaltic roof spall from the tube, or their weathering products. The sand and pebble-sized particles are subrounded to angular, suggesting brief transport over a short distance. Sheetwash seems to be the main mode of deposition of the sediments in Puu Naio Cave. Ponding may also have occurred during intense rains (Fig. 3). Since the sediment in the tube has been deposited over a gently upward-sloping floor, we expect that as we excavate nearer the mouth of the cave, we will find deeper and older sediment, perhaps representing the entire Holocene.

Unit II is particularly interesting because its ¹⁴C age is contemporaneous with the Polynesian occupation of Maui. Although the area below the ceiling collapse was a Polynesian habitation site, the scarcity of artifacts in the excavation suggests that the upper cave was not used for long-term habitation. Six rounded, polished stones, presumably brought in by humans, were found in units I and II. These are the only evidence in the excavated sediments of earlier human presence in the upper cave. The higher degree of compaction in unit II than in units I or III (Fig. 3) may reflect a period of rapid infilling by silts and clays from soil erosion associated with clearing of the native forest in the region or from human habitation of the area below the ceiling collapse. Human trampling was not an important factor in the compaction of unit II because the sediment is compact even against the wall where humans would have been unable to walk.

Material suitable for conventional ¹⁴C dating included charcoal dispersed through unit II and a well-preserved piece of wood in unit IV. The latter turned out to be a modern root (Smithsonian Radiation Biology Laboratory number 6504). Four bone samples were selected for TAMS dating. Detailed procedures for pretreatment of the fossil bones are given by Stafford *et al.* (20); results are reviewed in Table 1. Each bone was first analyzed for percent nitrogen to determine the maximum amount of protein remaining. Compared to the 4–4.5% nitrogen in modern bone, only the bone of *Thambetochen* (AA-762), with 0.3% nitrogen, had a marginal amount of collagen remaining.

The fossils were ultrasonically washed in deionized water and decalcified in distilled, 4°C 0.6 M HCl. Decalcified specimens of *Rattus* (specimen no. AA-760) and *Apteribis*
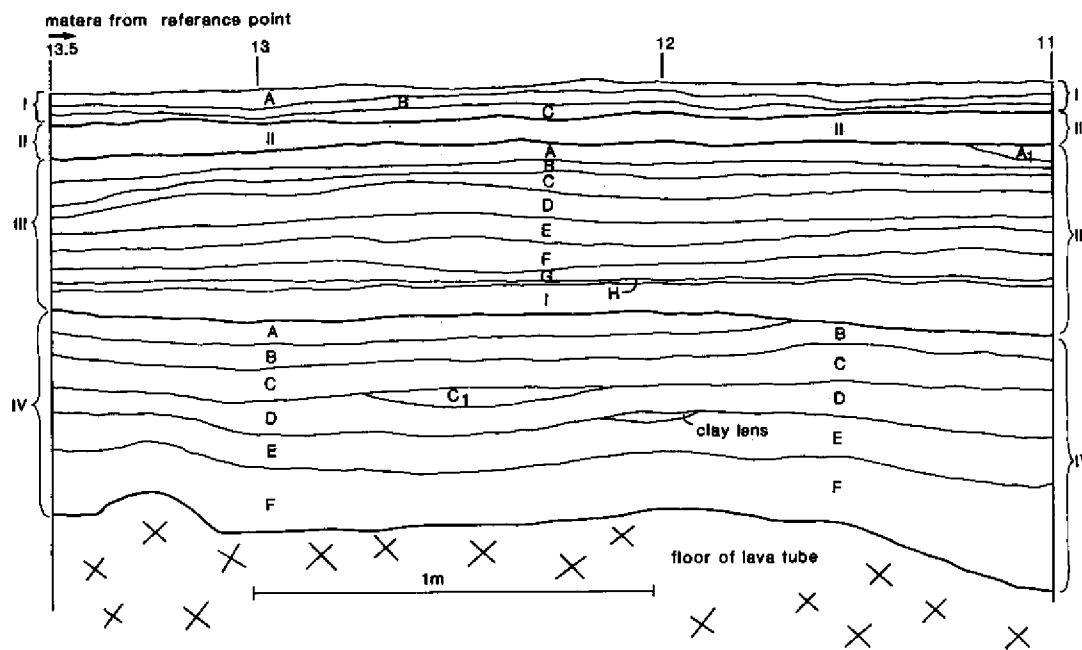
FIG. 3. Stratigraphic section of the east side of the trench along the west wall of the upper cave (squares W11–W13.5, Fig. 2). The vertical scale is the same as the horizontal scale. Roman numerals indicate the major stratigraphic units; letters indicate the subunits. In each unit, both the sands and pebbles are mainly very fine to medium. Unit I is composed of reddish brown-to-dark grayish brown, poorly bedded-to-well bedded, loose, sandy, clayey silt to sandy, silty clay that has been somewhat disturbed by modern trampling. Subrounded calcareous particles (up to 5-mm diameter), which might represent degraded shells of land snails, occur in a band in subunit B. Organic material, mainly from plants, is common. The maximal observed thickness of unit I is 8 cm. Unit II is a brown, firm, moderately well-bedded, sandy, very clayey silt, with a higher clay component than unit I. Subrounded calcareous particles and pieces of charcoal are common in the upper half but rare in the lower half. The maximal observed thickness of unit II is 9 cm. Unit III is composed of yellowish brown-to-brown, moderately well-to-very poorly bedded, soft, very pebbly, sandy, clayey silt to very sandy, silty clay with various concentrations of calcitic particles (subrounded and platy; up to several millimeters in diameter) and occasional land-snail fragments. Within most subunits of unit III, there is a downward increase in pebble concentration. The maximal observed thickness of unit III is 46 cm. Unit IV consists of dark grayish brown, poorly bedded, soft-to-firm, sandy, silty clay within which the subunits are darker, more clayey, and more compacted with increasing depth. Platy and subrounded calcitic particles and land-snail shells are rare. The maximal observed thickness of unit IV is 86 cm.

(AA-761) gave exact pseudomorphs of the whole bone, while the *Thambetochen* (AA-762) and the older *Apteribis* (AA-
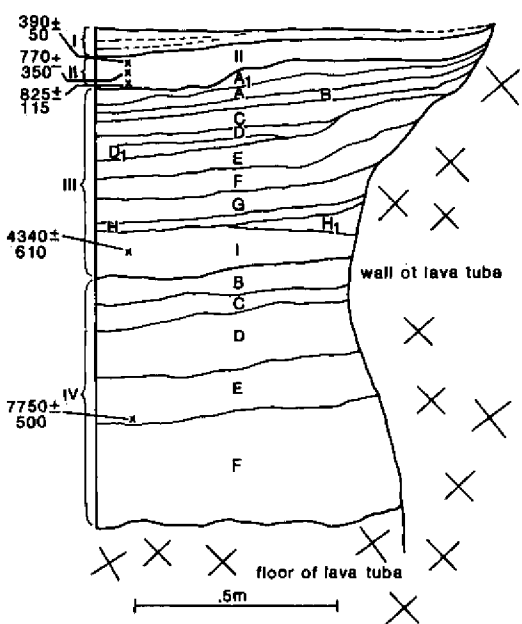

FIG. 4. Stratigraphic section of the south wall of square W11, 11 m from the reference point (Fig. 2). Roman numerals indicate the major stratigraphic units; letters indicate the subunits. The radiocarbon dates are from squares W9, W11, and W12. The vertical scale is the same as the horizontal scale.

763) fossils gave gelatinous residues after decalcification. The acid-insoluble collagen was washed with water, lyophilized, and hydrolyzed in distilled 6 M HCl for 24 hr at 110°C. The protein hydrolysate was filtered and passed through XAD-2 resin to remove fulvic acid residues. The XAD-2-purified hydrolysate was combusted to CO_2, which was reduced to amorphous carbon before mixing with iron and conversion to an iron-carbide bead for accelerator dating (21). The samples were ^{14}C-dated at the University of Arizona National Science Foundation facility for radioisotope analysis.

The accuracy of the dates for these samples is considered excellent because the two youngest fossils were well preserved and contained minimal amounts of humate contamination. Additional dating of these bones would require <500 mg of total bone. Although the two older specimens were contaminated with substantial amounts of humates, it has been shown that treatment with XAD resins will yield accurate ^{14}C dates for bone having >0.2% nitrogen and collagen-like amino acid compositions (20). The poor preservation of the two older bird fossils required greater amounts of bone for dating, thus revealing the difficulty in estimating collagen content with percent nitrogen analyses. The *Thambetochen* and the older *Apteribis* fossils yielded the same percent extractable gelatin despite the 5-fold difference in percent nitrogen between these bones. Future dating of bird bones will be significantly improved because sample pretreatment losses will be smaller and dating precision will be improved to 1% by the use of graphite targets (22, 23).

The ^{14}C dates indicate that sediment has been accumulating in Puu Naio Cave during most of the Holocene (Table 2). A tarsometatarsus of an extinct flightless ibis (*Apteribis*) from near the bottom of the excavated sediment, 90–100 cm below

Table 1. Faunal analysis of bones from 1 m³ of sediment (W9) in Puu Naio Cave

Stratigraphic context	Bones identified,* no.	Percentage of bones belonging to species in each category			
		Historically introduced[†]	Prehistorically introduced[‡]	Native, extant on Maui[§]	Native, extinct on Maui[¶]
Unit I	162 (115, 37, 10)	70.4	29.6	0.0	0.0
Unit II	168 (123, 30, 15)	9.5	89.3	0.6	0.6
Unit III					
17–30 cmbs	61 (8, 53, 0)	0.0	14.7	1.6	83.6
30–60 cmbs	37 (1, 36, 0)	0.0	0.0	10.8	89.2
Unit IV					
60–120 cmbs	149 (4, 144, 1)	0.0	0.7[‖]	3.4	96.6

The analysis is based on the evidence of faunal remains, ¹⁴C dates, and cultural artifacts; unit I correlates with the historic period, unit II correlates mainly if not entirely with the prehistoric Polynesian period, and unit IV was deposited before humans colonized the archipelago. The lower part of unit III is also a prehuman deposit, whereas the upper part of unit III is coeval with human occupation of the island.
*The three figures in parentheses are the number of identified bones belonging to mammals, birds, and lizards, in that order.
[†]The fauna from the 1984 excavation includes the following historically introduced taxa: house mouse (*Mus musculus*), larger rats (mostly *Rattus rattus* but possibly including some *R. norvegicus*), Spotted Dove (*Streptopelia chinensis*), and Common Myna (*Acridotheres tristis*).
[‡]The prehistorically introduced taxa in the excavation are: Pacific rat (*Rattus exulans*), Short-eared Owl (*Asio flammeus*), and small lizards (Scincidae and Gekkonidae).
[§]The native taxa in the excavation that are still extant on Maui are: Hawaiian bat (*Lasiurus cinereus semotus*), Dark-rumped Petrel (*Pterodroma phaeopygia*), Po'ouli (*Melamprosops phaeosoma*), Maui Parrotbill (*Pseudonestor xanthophrys*), Nukupu'u (*Hemignathus lucidus*), Maui Creeper (*Paroreomyza montana*), 'Apapane (*Himatione sanguinea*), and Crested Honeycreeper (*Palmeria dolei*).
[¶]The extinct fossil taxa in the excavation are: a small bat (presumed extinct), a flightless ibis (*Apteribis* sp.), a Nene-like goose (*Branta* sp.), a flightless goose (*Thambetochen* sp.), a small flightless rail, a long-legged owl, the Hawaiian Crow or 'Alala (*Corvus hawaiiensis*), a thrush (*Myadestes* sp., a large Meliphagid) at least six finch-billed drepanidines [*Psittirostra* (*Telespiza*) related to (aff.) small species, *P.* aff. (*Loxioides*) bailleui, *P.* (*Rhodacanthis*) aff. *palmeri*, *P.* (*Rhodacanthis*) aff. *flaviceps*, *P.* (*Chloridops*) sp., and the "ridge-billed finch"], two new thin-billed drepanidine species, and one species of "icterid-like gaper."
[‖]This figure is derived from a single tiny lizard bone which is clearly out of context. cmbs, Centimeters below surface.

the surface, had a ¹⁴C age of 7750 ± 500 years before present (B.P.) (AA-763). Fifty to 60 cm below the surface, a femur of an extinct flightless goose (*Thambetochen*) had a ¹⁴C age of 4340 ± 610 years B.P. (AA-762). A pooled sample of seven bones of the Polynesian-introduced Pacific rat (*Rattus exulans*) taken from unit II, 3–20 cm below the surface, had a ¹⁴C age of 770 ± 350 years B.P. (AA-760). These three dates are separated from each other by more than 3 standard deviations, even though the standard deviations are large. The fourth bone date of 1850 ± 270 years B.P. (AA-761) for a femur of *Apteribis*, collected 10–20 cm below the surface in square E24, comes from another part of the excavation. While stratigraphically consistent with the other dates, it was not collected in the grids illustrated in Figs. 3 and 4. In unit

II, the two charcoal dates of 390 ± 50 and 825 ± 115 years B.P. are separated from each other by more than 2 standard deviations, yet the date on rat bones of 770 ± 350 years B.P. overlaps with both charcoal dates at 1 standard deviation.

While most of the vertebrates from our excavations are endemic Hawaiian species, the rodents, lizards, and a few of the birds were introduced by humans (see the list in Table 1). The presence of these introduced species in the sediments indicates stratigraphic levels postdating prehistoric human arrival (8, 17). The historic (post-Polynesian) period on Maui correlates mainly with unit I, in which historically introduced taxa predominate. These also occur in the upper part of unit II. Prehistorically introduced taxa first appear in the upper part of unit III and are predominant in unit II. The ¹⁴C dates

Table 2. Radiocarbon dates from the 1984 excavation at Puu Naio Cave

Sample	Bone analysis				Provenience	Date, years B.P.
	Weight, g	% N	Extracted gelatin, mg	% extractable gelatin		
Charcoal, SI-6503	—	—	—	—	W12, unit II	390 ± 50
Introduced Pacific rat (*Rattus exulans*)						
7 bones, AA-760	0.45	2.1	39.4	8.8	W12, unit II	770 ± 350
Charcoal, SI-6502	—	—	—	—	W9, unit II	825 ± 115
Extinct flightless ibis (*Apteribis* sp.)						
Femur, AA-761	1.84	2.8	246.7	13.4	E24, 10–20 cmbs	1850 ± 270
Extinct flightless goose (*Thambetochen* sp.)						
Femur, AA-762	11.6	0.3	109.0	0.9	W11, unit III, subunit 1, 50–60 cmbs	4340 ± 610
Extinct flightless ibis (*Apteribis* sp.)						
Tarsometatarsus, AA-763	1.74	1.6	15.4	0.9	W11, unit IV, 90–100 cmbs	7750 ± 500

Collagen from small bone samples was dated with University of Arizona TAMS. Charcoal was dated at the Smithsonian Radiation Biology Laboratory. The depth of dated material in the excavation is given as centimeters below surface (cmbs).

(Table 2) indicate that unit II accumulated during a period of expansion of the Polynesian population (24). In our faunal analysis of one m³ of sediment, 90% of the 241 animal bones identified from units prior to Polynesian impact (III to IV) represent extinct species, mostly birds and a few bats. Afterward, virtually all (99.4%) of the 330 identified bones represent introduced species, mostly rodents (Table 1). Our sample of bird bones from the upper units that are associated with man is thus very small, yet it includes three species that are extinct on Maui (a flightless goose, *Thambetochen* sp.; the Hawaiian Crow, *Corvus hawaiiensis*; and the "ridge-billed finch"). We expect to be able to expand this list by enlarging the excavation.

Only 10 endemic Hawaiian species of land birds are known historically from Maui, all belonging to the Drepanidini, a tribe of carduelinc finches that underwent extensive adaptive radiation in the archipelago. The excavated sediment from Puu Naio Cave contained remains of at least 23 species of endemic land birds, including 1 flightless ibis, 2 or 3 geese (1 or 2 of them flightless), 1 flightless rail, 1 owl, 1 crow, 1 thrush, 1 honeyeater (Meliphagidae), and at least 15 drepanidines (see the list in Table 1). According to our current taxonomic assessment, 11 of these species are undescribed, 6 are new records for Maui, and 6 are still extant on Maui. Bones of 2 additional undescribed species, a flightless goose and a flightless rail, were found lying amidst the rubble on the floor of the lava tube in areas beyond the sediment deposit. Thus, Puu Naio Cave has already added 19 endemic land birds to the avifauna of Maui, tripling the number known before the fossil discoveries.

Maui was ignored by ornithological collectors for the first century after European discovery, making it difficult to distinguish between prehistoric extinctions and those that may have occurred early in the historic period. Small passerines are more likely than large flightless species to have survived unnoticed into the historic period, but the weight of the evidence suggests that most extinctions of Hawaiian birds documented by fossils occurred prehistorically (8, 17).

While the sample sizes and ¹⁴C dates from our preliminary excavation are not sufficient to establish exactly when individual species disappeared from leeward Haleakala, we have demonstrated the feasibility of obtaining precise chronological data for island extinctions by combining stratigraphic excavation and ¹⁴C dating of small bones. By applying these techniques to a more extensive excavation at Puu Naio Cave, it should be possible to study faunal turnover and extinction on Maui during most of the Holocene.

The widely accepted view that human settlement of Polynesia began about 4000 years ago has recently been challenged on the grounds that rising sea levels may have submerged earlier coastal archeological sites (25). Estimates of the time of human colonization independent of the archeological record can potentially be obtained by dating the earliest occurrence of Pacific rats (*Rattus exulans*) or other prehistorically introduced organisms in inland nonarcheological deposits that show continuous sedimentation, such as in Puu Naio Cave. Therefore, this kind of deposit may become increasingly important to the study of human prehistory in Oceania.

1. Dewar, R. E. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ), pp. 574–593.
2. Balouet, J. C. (1984) *La Recherche* 15, 390–393.
3. Cassels, R. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ), pp. 741–767.
4. Trotter, M. M. & McCulloch, B. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ) pp. 708–725.
5. Steadman, D. W. (1985) *Bull. Br. Ornithol. Club* 105, 58–66.
6. Steadman, D. W. & Olson, S. L. (1985) *Proc. Natl. Acad. Sci. USA* 82, 6191–6195.
7. Olson, S. L. & James, H. F. (1982) *Science* 217, 633–635.
8. Olson, S. L. & James, H. F. (1982b) *Smithson. Contrib. Zool.* 365, 1–59.
9. Olson, S. L. & James, H. F. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ), pp. 768–780.
10. Steadman, D. W. (1986) *Smithson. Contrib. Zool.* 413, 1–103.
11. Steadman, D. W., Pregill, G. K. & Olson, S. L. (1984) *Proc. Natl. Acad. Sci. USA* 81, 4448–4451.
12. Alcover, J. A., Moya, S. & Pons, J. (1981) *Institució Catalana D'Història Natural filial de l'Institut D'Estudis Catalans*, Memòria núm. 11. (Editorial Moll, Ciutat de Mallorca, Spain).
13. Bock, W. J. & Farrand, J. (1980) *Am. Mus. Nov.* 2703, 1–29.
14. Anderson, A. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ), pp. 728–740.
15. Greenway, J. C. (1958) *Extinct and Vanishing Birds of the World*, (Am. Comm. Int. Wild Life Prot., New York), Spec. Pub. 13.
16. Diamond, J. M. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ), pp. 824–862.
17. Christensen, C. C. & Kirch, P. V. (1986) *Occas. Pap. Bernice Puahi Bishop Mus.* 26, 52–80.
18. Martin, P. S. (1986) in *Dynamics of Extinction*, ed. Elliott, D. K. (Wiley, New York), pp. 107–130.
19. Crandell, D. R. (1983) *US Geol. Surv. Misc. Invest. Ser.* Map I-1442.
20. Stafford, T. W., Jr., Jull, A. J. T., Brendel, K., Duhamel, R. C. & Donahue, D. J. (1986) *Radiocarbon* 28, in press.
21. Jull, A. J. T., Donahue, D. J. & Zabel, T. H. (1983) *Nuclear Instrum. Methods Phys. Res.* 218, 509–514.
22. Jull, A. J. T., Donahue, D. J., Hatheway, A., Linick, T. W. & Toolin, L. J. (1986) *Radiocarbon* 28, 191–197.
23. Linick, T. W., Jull, A. J. T., Toolin, L. J. & Donahue, D. J. (1986) *Radiocarbon* 28, 522–533.
24. Kirch, P. V. (1985) *Feathered Gods and Fish Hooks: An Introduction to Hawaiian Archaeology and Prehistory* (Univ. of Hawaii Press, Honolulu).
25. Gibbons, J. R. H. & Clunie, F. G. A. U. (1986) *J. Pac. Prehist.* 21, 58–82.