

Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i

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Abstract

Pre-contact avifaunal extinctions in Hawai'i generally have been attributed to human predation and/or landscape alteration by colonizing Polynesians. However, until recently there have been insufficient data for evaluating most of the important variables involved in this issue. This situation has changed with recent archaeological, paleontological, and wetland coring research conducted on O'ahu's 'Ewa Plain, a hot, dry emerged limestone reef characterized by numerous sinkholes. The main evidence obtained from this research includes (1) wetland coring data that stratigraphically demonstrate forest decline before any burning, (2) radiocarbon dating of bones of rats and extinct birds that provides a time frame for their occurrence unavailable from stratified deposits, and (3) the radiocarbon-based history of human settlement of the 'Ewa Plain.

Based on this evidence the argument is made that (1) at least some major avian extinctions occurred within the period immediately following Polynesian colonization, (2) these extinctions were due primarily to the rapid decline of their native lowland forest habitat, (3) human settlement of the 'Ewa Plain occurred after native forest collapse, not coincident with it, and (4) the main source of destruction of the native forests was the introduced Polynesian rat, *Rattus exulans*, not Hawaiian agricultural clearing and burning. This model also explains the absence of large quantities of bird bone in early sites (in contrast to other places in Polynesia and Micronesia), and the absence in early middens of many plants (notably *Kanaloa kahoolawensis*) that were common in the native forest.

Introduction

The cause of Holocene avifaunal extinctions in Hawai'i has been a topic of intense interest since the first detailed investigation of subfossil paleontological remains almost two decades ago demonstrated that Hawai'i once had a much richer species inventory of birds than previously suspected (Olson and James, 1982, 1991; James and Olson, 1991). Recent interdisciplinary investigations on the 'Ewa Plain of southwest O'ahu (Fig. 1) provide new insights into the process of extinction and environmental change in the Hawaiian lowlands (Athens et al., 1999).

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The new data 1) document the unexpected rapidity of vegetation change, 2) provide detailed information on the chronology of human settlement on the 'Ewa Plain, and 3) provide detailed paleontological evidence, particularly as concerns the chronology of avian remains and vegetation change. These data indicate that avian extinctions and extirpations were the result of habitat destruction in the form of lowland forest decline. However, there is strong evidence that forest decline followed Polynesian colonization of Hawai'i but preceded dispersal, suggesting that direct human activity such as burning or gardening had nothing to do with the general decline. We propose that the main cause of forest decline was the Polynesian rat, Rattus exulans, brought by early colonists.

Problem of avifaunal extinctions and extirpations

Some 35 to 57 extinct avian species have been identified from subfossil remains in Hawai'i, the number depending upon classification (James, 1995). Considering that historically known avifauna numbered from 40 to 55 endemic species, then about 100 avian species were present in Hawai'i prior to the archipelago's settlement by Polynesians (James and Olson, 1991), which occurred between about AD 700-800.1 Chronological data from a stratified assemblage of avian subfossils on Maui (James et al., 1987) indicate a strong association of a major extinction event with the period of Polynesian settlement. Other studies of subfossil birds in the tropical Pacific follow a similar pattern, indicating that long periods passed with few extinctions despite major climatic oscillations with the last ice age (Steadman, 1995). However, with the spread of humans throughout tropical Oceania beyond Melanesia during the late Holocene,

^{1.} The chronology of Polynesian settlement of Hawai'i is a hotly debated topic with some investigators suggesting settlement occurred as early as the first century AD (Hunt and Holsen, 1991). Kirch's standard textbook on Hawaiian archaeology cites a date of AD 300 (Kirch, 1985:58, 68), and he more recently (2000:291–292) suggests a range between AD 300 and 600. However, we see the chronological data supporting a settlement range of AD 700–800 (Athens, 1997; Masse and Tuggle, 1998; Tuggle and Spriggs, 2000).

wholesale avifaunal extinctions and extirpations frequently occurred, and the decline to extinction is often evident in early archaeological middens (Dye and Steadman, 1990; Steadman, 1995).

For Hawai'i, habitat alteration by humans is regarded as the leading candidate for extinction of at least the smaller forest avian species, but other factors have been considered, including human predation, predation by the prehistorically introduced Polynesian rat (R. exulans), and introduced diseases (James and Olson, 1991). Research has provided little evidence to support any significant role in avian extinction by disease or by human or rat predation. Archaeological studies have shown there was major habitat alteration from human action, and that by AD 1600 eighty percent of lands below about 460 m elevation had been extensively changed as a result of agricultural development, with fire thought to have been the chief agent of destruction (Kirch, 1982a, 1982b). It had been reasonably argued that Hawaiian agricultural expansion was the primary source of native forest destruction (Kirch, 1982a:8 and 1985:291; Dye, 1994a:9). However, the 'Ewa Plain research indicates that agricultural modification of the landscape (including the use of fire) occurred following an initial early postsettlement forest change. The significant alteration of the natural landscape immediately after Polynesian colonization has been demonstrated by a number of wetland coring studies on O'ahu during the last decade that provide detailed information on the lowland vegetation both before and after Polynesian arrival (Athens and Ward, 1993; Athens et al., 1992, Athens, 1997).

There is little doubt that the advent of human settlement in Hawai'i and the loss of the native forests are inextricably linked with avian extinctions and extirpations. The problem, however, is to better specify exactly what these linkages are. Our recent investigations on the 'Ewa Plain provide data for a model of these linkages.

The 'Ewa Plain: environment and human occupation

The arid 'Ewa Plain is situated on an emerged limestone reef west of Pearl Harbor (Fig. 1 - environment discussed in Athens et al., 1999; Davis, 1990; Tuggle, 1997). It is roughly 5 x 15 km (75 km²) and rises from sea level to about 15 m elevation. Thick primary and secondary alluvium/colluvium eroded from the Wai'anae Mountains has been deposited on the inland part of the plain, where commercial sugarcane was cultivated until recent years. The limestone exposed in the more shoreward locations is punctuated by numerous sinkholes. Annual rainfall is quite limited, averaging 508 mm and mostly falling during winter. Actual rainfall, however, frequently deviates significantly from monthly, seasonal, and annual averages; often most of what falls during the year occurs as a result of two or three downpours from winter cyclonic storms. Surface water is absent on the 'Ewa Plain, though prior to the advent of sugarcane plantations in the latter part of the 19th century, some sink-

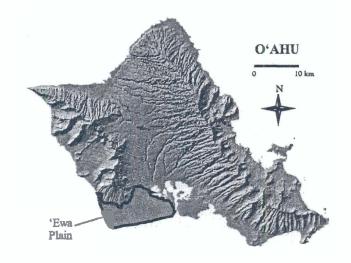


Figure 1. Relief map of O'ahu showing location of the 'Ewa Plain (map from Hawai'i State Historic Preservation Division; geographical designation follows Atlas of Hawaii, 1983).

holes may have retained fresh water. For colonizing Polynesians, the 'Ewa Plain must have been a marginal and unreliable agricultural environment, a point underscored by observations of the earliest western visitors (e.g., Vancouver [1798–II:217] called it "one very barren waste" when he saw it in 1792).

Modern vegetation on the Plain reflects its generally hot and dry conditions. Dominant post-contact introductions include *Prosopis pallida* (kiawe) and Leucaena leucocephala (koa haole) along with a variety of shrubs, grasses, and vines. Native species are represented only by dry-adapted *Erythrina sandwicensis* (wiliwili) trees (in certain areas these may be relatively common) and occasional isolated plants of *Cordyline fruticosa* (ti) and *Morinda citrifolia* (noni).

Numerous archaeological studies have been conducted on the 'Ewa Plain during the last several decades (for review and synthesis see Tuggle, 1997; Tuggle and Tomonari-Tuggle, 1997a). As of 1995 most of the only 6 to 10 percent of the 'Ewa Plain (4.5 to 7.5 sq. km) that was undisturbed by modern development had been archaeologically surveyed (for documentation see Tuggle & Tomonari-Tuggle, 1997a:45). Archaeological findings indicate that Hawaiian settlement consisted of small. scattered communities that relied heavily on fishing, but also carried out limited cultivation. Settlements were concentrated around limestone sinkhole clusters, and included C-shaped structures, thick-walled rectangular houses, small high platforms, low walls or alignments enclosing sinkholes, cobble mounds, and piles of firecracked limestone (Tuggle, 1997; Tuggle and Tomonari-Tuggle, 1997a).

Archaeological research on the 'Ewa Plain has long involved a substantial paleoenvironemental component. The focus was initially on the collection and study of extinct and extirpated subfossil avian remains in sinkhole

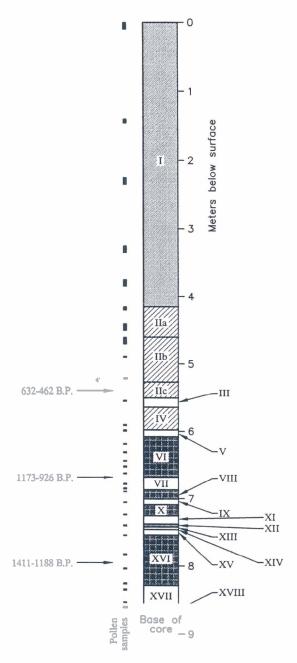
deposits (Sinoto, 1976, 1978; Olson and James, 1982; Davis, 1990), but subsequently included non-marine snails (Christensen and Kirch, 1986). More recently, however, paleoenvironmental studies have also included the coring of wetland deposits with associated palynological investigations and related studies. The following sections summarize the new data and analyses from our research (Athens et al., 1999). The findings indicate a rapid decline of the native lowland forest almost immediately following Polynesian colonization, the relatively late human settlement of the environmentally marginal 'Ewa Plain, and the chronology of avian extinctions. The evidence suggests that both many land birds and the dryland forest had disappeared by the time humans arrived on the 'Ewa Plain.

Paleoenvironmental Cores

Wetland cores recovered and analyzed from the 'Ewa Plain (Athens *et al.*, 1999) include two from an evaporite pan and one from a large sinkhole basin known as Ordy Pond. The evaporite pan is located about 500 m from the coast at an elevation of 4.6 m. Ordy Pond is about 700 m from the coast and has an elevation of about 1.5 m. It is 70 m across, with 5.5 m of standing, slightly brackish, water. Ordy Pond is just over 1 km east of the evaporite pan.

The two evaporite pan cores document a maximum of 3.76 m of mostly finely laminated sediments on top of limestone bedrock. Two radiocarbon determinations show that most of the stratified sediments encompass all but the earliest part of the Holocene, extending back to around 7200 cal BP.² However, there is an undated lower sedimentary unit in one of the cores. Because of the abundance of terrestrial snails in the sediments (presumably indicative of a time of lowered sea levels), this layer is thought to pertain to the Late Pleistocene.³

The single Ordy Pond core record, comprising a mostly laminated sediment column of 8.7 m, dates back from the present to about 1500 cal BP (AD 450); the sediments extend between 4.0 and 12.7 m *below* sea level (Fig. 2).⁴ Because of its relatively high resolution record



Sediment Groupings

Loosely consolidated greenish to greenish—gray gelatinous algal material with occasional fine carbonate laminae.

Light brown and pale tan gelatinous silt; some subtle banding.

Groupings of predominantly greenish and brown algal laminae interspersed with generally thin white laminae of calcite/aragonite.

Groupings of predominantly thick white laminae of calcite/aragonite interspersed with generally thin laminae of algal material.

Figure 2. Profile of Core 1, Ordy Pond. Note radiocarbon determinations (calibrated, 2 sigma range) and distribution of pollen samples. See Athens *et al.* (1999:54–63) for detailed description of sediments.

^{2.} The radiocarbon dates and pollen analysis (Athens et al., 1999:69–79) together suggest the possibility of a sedimentary unconformity in the evaporite pan sequence during the middle Holocene, perhaps coinciding with a high stand at this time (see Fletcher and Jones, 1996; Grossman and Fletcher, 1998). However, more detailed investigations are needed before any conclusions can be drawn regarding this important sequence.

^{3.} Similar snails at the base of Ordy Pond subsequently were dated to the Late Pleistocene — see footnote 4.

^{4.} A subsequent project by the senior author under the direction of Jane Tribble (Dept. of Oceanography, Univ. of Hawai'i) raised a 17.4 m sediment column from Ordy Pond (Tribble *et al.*, 1999). Like the evaporite pan, it appears to document a full Holocene sequence besides extending into the Late Pleistocene (¹⁴C determinations to 25,750 BP).

for the period of interest (i.e., the period immediately prior to Polynesian colonization through to the end of the prehistoric Polynesian period), analyses were primarily concentrated on the Ordy Pond core.

Although the organic laminations of Ordy Pond were not analyzed, similar laminations in the evaporite pan

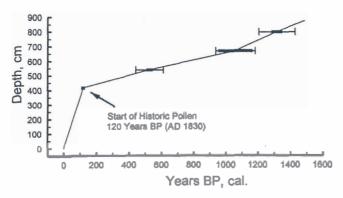


Figure 3. Depth-age plot of radiocarbon determinations for Ordy Pond derived from terrestrial plant material. Determinations are shown with 1 and 2 sigma calibration ranges.

consisted of mats of two types of freshwater filamentous algae (possibly either Mougeotia or Spirogyra and Vaucheria). The inorganic carbonate laminations of Ordy Pond consist mostly of fine-grained calcite and/or aragonite of apparent authigenic origin (Tribble et al., 1999). It is believed that the organic laminae provide a record of major rainfall events prior to about 590 cal BP (AD 1360). Clusters of algal mats suggest a tendency during which either seasonally increased rainfall or isolated (but repeated) major rainfall events occurred over a period of several decades or more (allowing the algae to grow in the freshwater lens at the surface). These alternated with clusters of non-organic laminae, presumably indicative much drier spells of both longer and shorter duration (during which there was no freshwater lens, and saline conditions of the pond water became increasingly concentrated). Detailed analyses of these laminae and their implications for past climatic patterns is currently ongoing by Jane Tribble and colleagues at the University of Hawai'i.

The chronology of the Ordy Pond sequence is based on three AMS radiocarbon determinations derived from terrestrial plant material (a piece of wood and two seeds) found in the sediments. Use of terrestrial plant

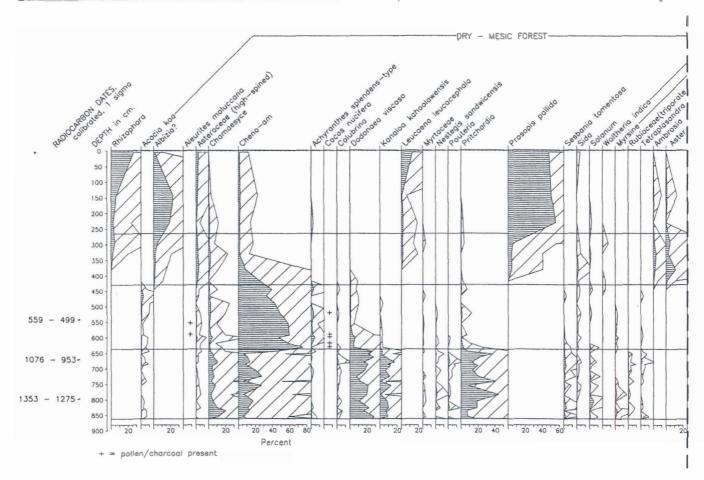


Figure 4. Pollen diagram from Ordy Pond, plotted in silhouette style (hatching is tenfold exaggeration). Two pollen sums were used in calculating percentages for the curves. For all types except the sedges, the curves are based on a sum excluding sedge pollen from the total, while the sedge curve is based on total pollen and spores.

material for dating was critical to avoid an old carbon effect from life forms that metabolized carbon derived from the dissolved limestone of the sink (the dating of algal mat samples was attempted, but the results were obviously invalid). In addition, the advent of pollen from historically introduced species in the sediment column provides an important chronological marker for more recent sediments. Based on historical information concerning the introduction and spread of particular plants (e.g., Wagner et al., 1990), the earliest historical pollen is estimated to have begun appearing in significant quantities about AD 1830, corresponding to 120 BP using 1950 as a reference. A depth-age curve based on the dating information is illustrated in Figure 3. This curve allows the derivation of specific dates by linear interpolation for any interval of the core (see Athens et al., 1999:71 for dates of all analyzed intervals); all interpolated ages must be understood to have an unspecified error range similar to the radiocarbon determinations on which they are based.

Thirty-two pollen samples were processed from the

Ordy Pond core in accordance with standard protocols for Pacific lowland sediments (for details see Athens et al., 1999:70, Moore et al., 1991). A pollen percentage diagram with graphs for pollen and charcoal concentrations and pollen sums for each interval is presented in Figure 4. Charcoal particles were counted using an eyepiece graticle with a 10 x 10 grid square pattern (Patterson et al., 1987); exotic marker Lycopodium spores were counted along with them. Charcoal was counted in grid square size classes and the total area in mm² was determined, from which concentrations could be calculated.

The Figure 4 pollen diagram illustrates only the most common pollen and spores along with charcoal particle counts. In interpreting this diagram, it is important to note the special nature of this record, including the fact that most pollen, other microfossils, and sediments derive from the immediate vicinity of Ordy Pond (i.e., Ordy Pond does not receive water-borne sediments from distant sources within a fluvial watershed). Thus, Ordy Pond contains a largely local paleoenvironmental record

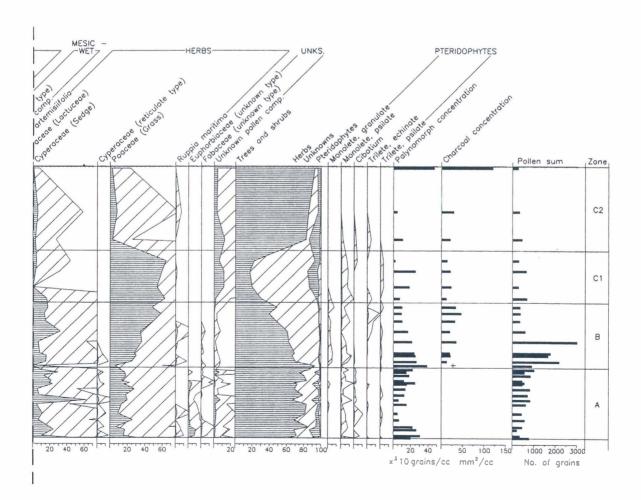


Figure 4 continued.

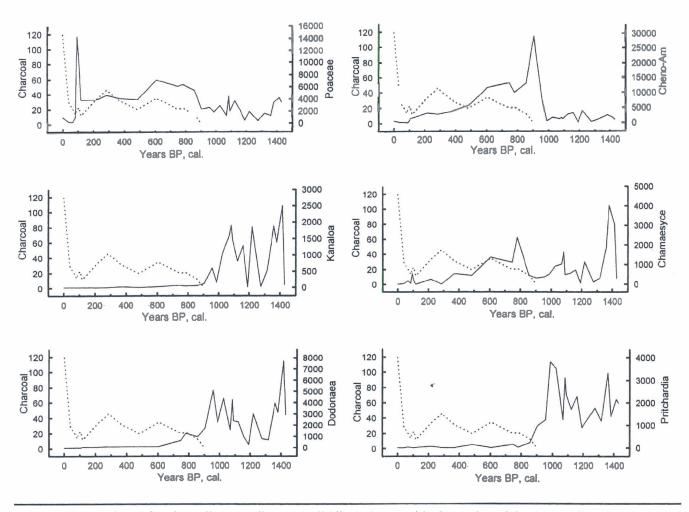


Figure 5. Comparison of major pollen contributors (solid line) shown with charcoal particles (dotted line) in Ordy Pond core. Concentration values are given for both charcoal (mm²/cc) and pollen (#/cc). Some of the high variation in the pollen values in the pre-1000 cal. BP part of the core is possibly due to oscillating climatic patterns.

(though the presence of extra-regional wind transported pollen is clearly evident from the very sparse presence of a highly diverse assemblage of mesic-wet forest types in the pre-Polynesian intervals — these are mostly derived from the higher elevation areas of the Wai'anae and Ko'olau Mountains). Secondly, the laminae tend to insure the stratigraphic integrity of the analyzed samples, minimizing chances for any mixing of sediments as a result of biotic activity. What this means is that any "blurring" of the pollen results (or other microfossil evidence) as a result of the mixing of sediments from closely sampled intervals (i.e., time periods) is minimized.

An assumption critically important for our interpretation of the Ordy Pond pollen sequence is that the sedimentary record is intact and that there are no periods during which sediment did not accumulate. If there were an unconformity (or multiple unconformities), we would potentially expect to see a gradual pollen transition foreshortened into what could appear in the pollen record as an abrupt change. Although we do see an abrupt transition between Zones A and B (as will be discussed below), there are reasons to believe it is not the result of

a sedimentary unconformity. First, the diatom record (Blinn, 1999), which indicates an alkaline to brackish water environment of moderate to high salinity, shows that a water column was continuously present in the Ordy sinkhole. Thus, erosion or lack of sediment accumulation for a protracted period seems unlikely. This finding also appears logical in view of the nearness of the sinkhole to the coast (700 m) and the depth of the sediments below mean sea level (4 to 12.7 m), suggesting the likely infiltration of seawater into the sinkhole. Secondly, the sedimentary and isotopic evidence do not suggest that the pond ever dried following the postglacial rise in sea level (J. Tribble, pers. comm., 2001). Third, although the pollen diagram shows widely fluctuating values over time for some of the more common pollen types, which might suggest preservation problems due to drying of the sinkhole, a close inspection of the pollen diagram indicates that the timing of the fluctuations is not precisely the same for the different taxa (see Figs. 4 and 5). Thus, Pritchardia values seem to change out of phase with most of the other types, possibly suggesting short-term climate fluctuations rather than a drying out of the sinkhole.

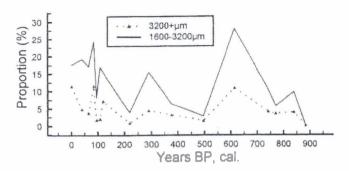


Figure 6. Large particle proportions of charcoal in Ordy Pond core. The graphs are based on the largest two size categories $(3200+\mu m \text{ and } 1600-3200\mu m)$ divided by the smallest size category $(100-199\mu m)$.

For purposes of this study, one of the most interesting features of the pollen diagram concerns the very abrupt transition in pollen values separating the lower pre-Polynesian Zone A from the later Zone B, which pertains to the prehistoric Polynesian period (Fig. 4).

The pollen of Zone A is indicative of a mixed dryland forest, Pritchardia palms and Dodonaea viscosa (a small tree or shrub) are apparently common among the larger taxa, and there are more limited representations of Nestegis sandwicensis, Pouteria, Colubrina, and other types whose counts are too limited to represent in the diagram (Diospyros, Elaeocarpus, Erythrina sandwicensis, Nothocestrum, and others). The understory seems to have been dominated by Kanaloa kahoolawensis, chenoams (probably Chenopodium oahuensis), and Chamaesyce along with other less numerous pollen types (Achyranthes splendens-type, Asteraceae (high-spined), Sesbania tomentosa, Sievos, Solanum sandwicense, grass, possibly a non-aquatic sedge, and others). The analysis of pollen from the earlier evaporite pan produced similar results for the pre-Polynesian middle to fate Holocene, though there were some interesting differences in the early Holocene (see Athens et al., 1999).

The transition from Zone A to Zone B is interpreted as marking the appearance of humans on O'ahu. Charcoal particles and Cocos nucifera (coconut), both anthropogenic indicators, occur in the lowermost interval of Zone B. However, what is striking is the abruptness of the floristic change that occurs at the end of Zone A and the start of Zone B. The dryland forest seems to disappear almost at once and there is a concurrent surge in the cheno-am pollen type (i.e., Chenopodiaceae and/or Amaranthaceae pollen, which cannot be distunguished palynologically) and a more limited surge in grass pollen (Poaceae). The latter pollen types are considered diagnostic of an open canopy or disturbance. There can be no doubt that we are witnessing the wholesale and rapid disappearance of the native forest on the 'Ewa Plain.

The interpolated depth-age dates and the stratigraphic data suggest that the landscape underwent a transforma-

tion of its vegetation within a period of perhaps no more than 50 to 100 years starting at about 930 cal BP (AD 1020; interpolated date). Such a rapid change is not a peculiarity of the Ordy Pond core. Subsequent coring investigations at Weli Pond, close to Ke'ehi Lagoon in Honolulu, also documented the very rapid replacement of the native forest by disturbance or open canopy flora (Athens and Ward, 2000). However, in this case the timing of this change appears to have been slightly earlier, at about 1074 cal BP (AD 876; interpolated).

Microscopic charcoal particles in the Ordy Pond sediments display two interesting features. First, their earliest occurrence is one or two sampling intervals after the beginning of precipitous declines in *Pritchardia*, Kanaloa, and Chamaesyce, and after the start of the surge of cheno-ams (Fig. 5). On the basis of the Ordy Pond stratigraphic data alone, therefore, forest loss must have begun prior to any direct evidence for humans on the 'Ewa Plain. Humans clearly could not have been directly responsible for the forest decline through burning or agricultural activities.

Second, the particle size distribution graph indicates that there is a prevalence of small-size charcoal particles in the earliest sampling intervals in which they appear (Fig. 6). As Morrison (1994;675) observes, "charcoal particles in different size categories do not always covary in the core, reflecting differences between more local and more regional fire histories." This is because the smallest particles are more likely to be suspended by wind and transported long distances (Clark, 1988). Thus, a prevalence of the smallest particles in the earliest intervals where charcoal particles occur in the Ordy Pond core suggests a relatively distant origin of anthropogenic fires and hence settlement (this supposition is consistent with the direction of the prevailing northeast trade winds in Hawai'i). The opposite, of course, would indicate the occurrence of local fires and proximal settlement, as seems to have first occurred on the 'Ewa Plain around 700 cal BP or shortly thereafter (see Fig. 6).

In sum, both the stratigraphic position of the earliest charcoal particles with respect to pollen changes, and also the particle size data imply that forest decline on the 'Ewa Plain preceded human presence. In light of this evidence, it is worth exploring further the question of the chronology of human settlement on the 'Ewa Plain.

Chronology of human settlement

The Ordy Pond charcoal particle size data (see Fig. 6) do not indicate settlement and use of the 'Ewa Plain until after about 700 cal BP (AD 1250; interpolated), with the first large particle peak indicative of significant occupation or land use about 606 cal BP (AD 1344; interpolated). This conclusion is consistent with the chronology of human settlement based on archaeological radiocarbon dates from the 'Ewa Plain.

There are 194 charcoal (or material attributed to be charcoal) radiocarbon age determinations from cultural

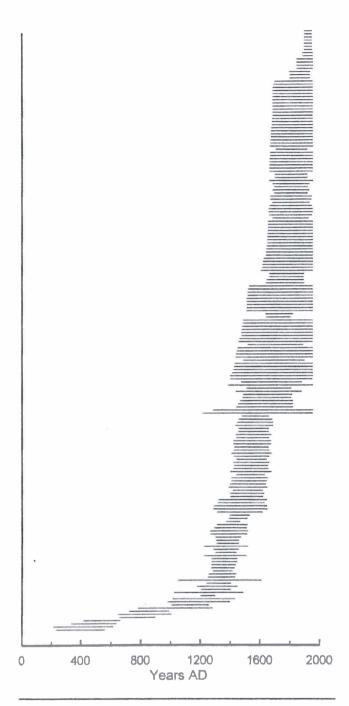


Figure 7. Compilation of charcoal radiocarbon dates from archaeological sites on the 'Ewa Plain. Dates are calibrated and depicted at 2 standard deviations. "Modern" dates are indicated by the convention of using a histogram bar spanning from AD 1900 to 1950.

contexts on the 'Ewa Plain, and these are displayed in a histogram in Figure 7 (data summarized in Athens et al., 1999:260–265). Analysis of these dates indicates that some very limited human activity may have occurred on the 'Ewa Plain in the AD 1000–1250 period, but that activity (and inferred population growth) began to dramatically increase in the AD 1250–1300 period (Athens et al., 1999; Tuggle, 1997; Tuggle and Tomonari-Tuggle, 1997a). Another useful way to view the aggregate radio-

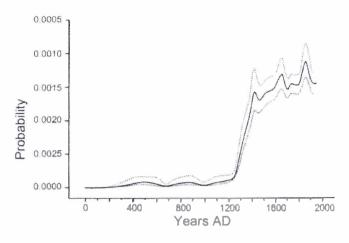


Figure 8. Cumulative probability curve of radiocarbon charcoal dates from the 'Ewa Plain. The y-axis scale, called "intensity" by Stolk *et al.* (1994), is the annual frequency distribution of the dates (see also Dye and Komori, 1992b).

carbon data is in the form of a cumulative probability curve in Figure 8, which can be interpreted as a population growth curve (see Dye and Komori, 1992a; based on method described by Dye and Komori, 1992b). This pattern is consistent with the population curve and history of Hawaiian cultural growth based on radiocarbon dates developed by Dye and Komori (1992b) and Dye (1994a), in which the "growth phase" begins about AD 1150, or some 100 years before the start of the 'Ewa Plain "growth phase."

The combined paleontological and archaeological data indicate that the collapse of the native forest on the 'Ewa

- 5. Two dates of 4480±80 and 5030±50 BP were eliminated from graphical representation because they obviously pertain to a pre-human time period; the samples likely were not charcoal but if so, they represent the burning of very old wood in the environment.
 - The activity is most likely confined to the latest part of this range. As indicated by Figure 7, there are only seven radiocarbon dates that fall within the pre-AD 1000 range. These have been evaluated and discussed at length elsewhere (Tuggle and Tomonari-Tuggle, 1997a; Athens and Tuggle. 2001). These dates suffer from a number of problems related to questionable methods of sample excavation and data analysis and none are considered reliable measures of cultural chronology. Reviews of the "tails" of radiocarbon sequences consistently demonstrate these difficulties (see, for example Dye, 2000a; Masse and Tuggle, 1998; Tuggle, 1997). The causes may be due to old undecayed wood in the environment, old driftwood, interior wood from longlived species, confusion of non-cultural anaerobically blackened wood with charcoal, and questionable sample selection (see Murakami, 1992; Strong and Skolmen, 1963). In general, treatment of radiocarbon samples by archaeologists in Hawai'i has a very poor history, lacking protocols and controls commonly found elsewhere in Polynesian research (e.g., Davidson, 1992).

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Passeriformes	Corvus (large sp.)	ebb			******	I	1	4		1	100	Ţ	1	******
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	Passeriform, small	and a	269	70	2	1	2	1	6	1	, press.	∞	******	362
Other	Pluvialis fulva	mg	\sim	Seems	-		Xues	160	_		ession .	da.	· vana	m
	Numenius tahitiensis	gim	1	Access	-	***	10011		ą.	and the same of th	***		- 4	Monore
Total			5408	416	95	diane	3588	45	2278	611	88	28	7	12068
					California de la calega de la c				,					*

Table 1. Bird Bone (NISP, lowest taxon) from 'Ewa Plain Sinkholes; Distribution by Site and Feature. Key: epp = extinct prehuman/prehistorically; eh = extinct historically; pi = Polynesian introduction; mi = historic/modern introduction; p = presently surviving native; mig = migratory.

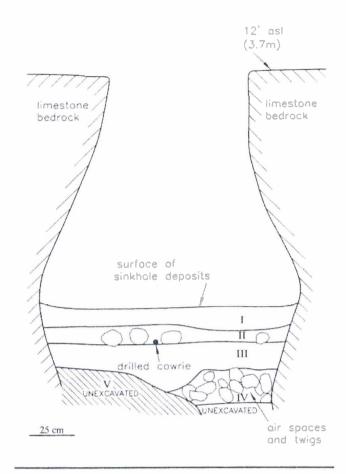


Figure 9. Profile of Feature 1 sinkhole at Site 5108.

Plain began after human colonization of the Hawaiian Islands, but prior to rapid population growth and expansion in Hawai'i in general (around AD 1150), and certainly before significant settlement of the 'Ewa Plain.

'Ewa Plain sinkholes: avian remains and chronology

Limestone sinks are a common natural feature of the 'Ewa Plain. They range in diameter from less than a meter to 400 m. The largest are known primarily from early maps. These natural features probably numbered in the thousands before historical filling for agriculture, military training, and development. Most remaining today are between 50 cm and 2 m in width, and contain deposits whose surfaces (the floors of the sinkhole) are from 50 cm to 2 m below the top of the limestone (Fig. 9). Excavation indicates that most deposits are 1 to 3 m in depth before the limestone base is encountered. Many sinkholes have been culturally modified, with such features as a ring of stones placed around the opening (usually indicating agricultural use of the sinkhole), attached platforms or pavings, and rock fill. Deposits often have some cultural debris, either as primary or secondary deposition. Sinkholes generally have no evidence of activity within the sinks themselves, except that a few were used for human burial. Most sinkholes are reposito-

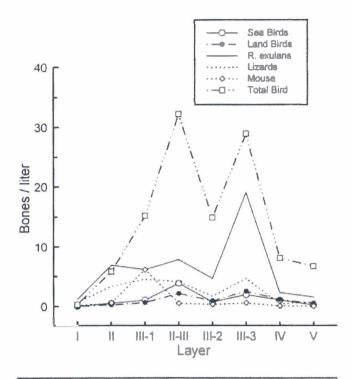


Figure 10. Densities of faunal bone remains from sinkhole at Site 5108–F1.

ries of paleontological remains (especially subfossil avian bones and terrestrial snails — for discussion of latter, see Dye and Tuggle, 1998, 2001; Athens et al., 1999:155–166, 209–211). The sinks served as natural traps for these remains, resulting primarily from deposition of surface sediments carried in by sheet wash from occasional heavy rain storms. As expected from this depositional process, skeletal elements of the subfossil remains rarely show any evidence of articulation.

A summary of the types, numbers, and survival status of avian remains recovered from sinkholes excavated during a recent project is presented in Table 1. These figures are representative of the 'Ewa Plain as a whole (see Table 2). The assemblages are dominated by sea birds (74 to 91 percent), with passeriforms and anseriforms making up the only other significant percentages (5 to 23 percent and 1 to 9 percent, respectively).

An example of the stratigraphic distribution of the types of paleontological and archaeological remains found in sinkholes is provided by the results of a sink excavated at Site 5108, Feature 1 (or -F1; Fig. 9; Table 3 — see Athens et al., 1999:275–276 for formal sediment descriptions and other details). This was a relatively small but rich paleontological repository. The drilled cowrie (Cypraea sp.) shell octopus lure found at the base of Layer II (see Fig. 9) is a clear indicator that sedimentary deposition of this strata began during the traditional Hawaiian time period. However, this does not mean that Layer II is a primary cultural deposit or that its deposits are stratigraphically intact. There are no animal domesticates (pig, dog, or chicken), and the relatively small fish

		Bird	6	Rattus exulans	IM	Mus musculus	R. 110.	R. norvegicus or R. rattus	-	Fish	Liz	Lizard, small	Vern	Vertebrate	Other	Shell	Charcoal Artifacts	Artifacts
Strata	п	3.0	п	5.0	ď	ac	а	0.0	=	ac	=	51)	п	ac		п	50	
-	47	1.26	174	3.07	25	0.25	CI	0.06	m	0.17	95	0.38	4		Herpestes	9	0.14	
															auropunctatus -1			
Η	612	612 31.17	712	12.55	63	0.55	2	29.0	30	0.72	353	76.0	136	68.0		7	0.29	сожпе
																	Proposition of the Control of the Co	lure
111-1	2483 107.04	07.04	1004	19.91	49	0.33	CI	0.10	47	0.35	741	1.26	973	2.97		33	0.25	
(III-III)	819	41.28	199	3.94	1	0.04			~	0.11	105	0.21	305	1.47		9	0.04	
Ш-2	808	508 15.16	159	2.72	=	80.08				0.07	58	0.16	184	76.0		ng.	0.07	
Ш-3	254	17.6	167	3.22	10	90.0			****	0.01	4	0.11	133	19.0	Vespertilionid	2	0.02	
															Bat 1			
2	78	4.07	22	0.56	-	0.03			0.00	1	4	0.05	∞	0.17	Vespertilionid Bat -1			
>	98	2,79	20	0.41	and the second	- interest			į		10	0.01	46	0.25				
Misc.	521 23.95	23.95	275	4.85	21	60.0			13	0.80	123	0.24	74	0.39		8	0.02	
Total	5408 236.43	36.43	2732	47.93	189	1.43	19	0.83	112	2.23	1530	3.39	1900	7.72		37	0.83	
Table 3. Site 5108-F1: Bone, Shell, and Artifacts.	le 5108	-FI: Bo	ne, She	II, and Ari	tifacts.													

AVES	NAS (1) % NISP	NAS (2) % NISP	Deep Draft (3) % NISP	West Beach (3) % NISP	
Procellariiformes	74	76	91	75	THE STATE OF THE S
Pelicaniformes	0	< !		()	
Anseriformes	1	9	1	6	
Falconiformes	0	0	<1	<1	
Galliformes	<1	<1	<1	1	
Gruiformes	1	2	< [1	
Columbiformes	1	<1	0	<1	
Strigiformes	<1	1	1	<1	
Passeriformes	21	10	5	16	
Other	<1	<1	<1	<1	
	100%	100%	100%	100%	
Total Identified NISP	1872	1782	5285	25373	
Total Bird Bone	1872	?	15134	72781	

Table 2. Percentages of Identified Bird Bone in 'Ewa Plain Sinkholes. NAS (1): Athens et al. (1999); NAS (2): calculated from Beardsley (2001: Table V-20); Deep Draft (3) and West Beach (3): Tuggle and Tomonari-Tuggle (1997b:Table 1).

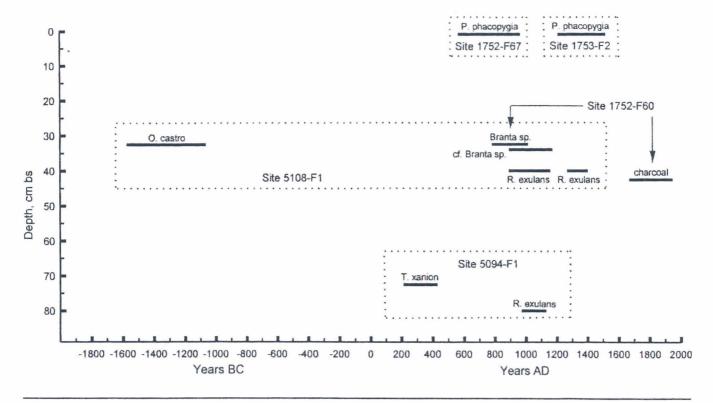


Figure 11. Radiocarbon age and depth of dated bones of bird and *Rattus exulums* from sinkholes. AMS sample preparation for the bone was undertaken by Thomas Stafford using the XAD resin protocol (Stafford *et al.*, 1991). This method helps to insure that the dated collagen protein is free from contamination.

ORDER	FAMILY	TAXON	_	=	11-1	(II-III) III-2	Ш-2	111-3	2	>	Misc.	total	total o
	The second secon		*										a)
Procellariiformes	Procellariidae	Puffinus newelli						_				_	0.3
		Puffinus sp.			0						_	4	8.0
		Pterodroma phaeopygia		50	21	13		_	_	_	6	51	6.6
		Indet. Procellariid, small		ic.	24	17	_	2	33		9	58	9.8
		Indet. Procellariid, medium	_	42		49	61	Ξ	5	2	41	296	9.98
	Hydrobatidae	Oceanodroma castro	_	7	∞	4	4	2	_			22	8.0
Anseriformes	Anatidae	Branta sp., cf. and/or Thambe. x.											
		Branta sp.					_					_	0.5
		Thambetochen xanion											
		Indet. Anatid, small											
		Indet. Anatid				_						_	0.1
Falconiformes	Accipitridae	Buteo solitarus											
Galliformes	Phasianidae	Gallus gallus											
Gruiformes	Rallidae	Porzana ziegleri				_		_			_	cc	0.1
		Porzana sp.											
		Indet. Rallid, medium											
Columbiformes	Columbidae	Streptopelia chinensis	_								Т	2	0.2
		Geopelia striata		0								2	0.1
Strigiformes	Strigidae	Asio flammeus											
		Strigid, medium				•							
Passeriformes	Corvidae	Corvus (large sp.)			_							_	0.2
	Meliphagidae	Chaetoptila sp.	_	_	Ξ	10		7	-		∞	34	2.8
	Indeterminate	small, or cf.	×	23	94	44	30	19	10	7	34	269	4.9
Other		Pluvialis fulva, cf.		7								2	0.1
		Numenius tahitiensis											
Indeterminate	Indeterminate	Bird	35	530	2210	999	453	215	57	76	420	4661	120.7
	(egg shell)		(3)	(4)	(12)	\equiv	(5)	(2)		(1)	(2)	(30)	
		Total number	47	612	2483	819	508	254	78	98	521		
		Grant Total										5408	236.7
Table 4. Site 5108-	-F1: Bird Bone D	Table 4. Site 5108-F1: Bird Bone Distribution (by count).											

Age, calibrated, Avi 2 sigma*	an Taxon	Location	Site No.	Deposit	Source	Radiocarbon Lab. No.
AD 1651-1950	Pterodroma phaeopygia	DDH	2706-18a	C	3A.	Beta-11710
AD 1549–1950 (1)	Pterodroma phaeopygia	DDH	2702-7	C	3A	Beta-11195
AD 1420-1880	Pterodroma phaeopygia	DDH	9659-1	N	3**	Beta-11192
AD 1508-1950	Pterodroma phaeopygia	DDH	2706-18a	C	3^	Beta-11709
AD 1390-1870	Pterodroma phaeopygia	DDH	2706-6e	C	3^	Beta-11707
AD 1360-1810	Pterodroma phaeopygia	DDH	2706-18a	C	3^	Beta-11708
AD 1320-1720	Pterodroma phaeopygia	DDH	27063q	C	3^	Beta-11706
AD 1300-1589	Pterodroma phaeopygia	DDHE	4903-C	C	4	SR-5079
AD 1290-1720	Pterodroma phaeopygia	DDH	2706-18c	C	3^	Beta-11711
AD 1280-1740 (2)	Pterodroma phaeopygia	DDH	2702-7	C	3^	Beta-11196
AD 1280-1660	Pterodroma phaeopygia	DDH	2706–3f	C	3^	Beta-11705
AD 1214–1520	Pterodroma phaeopygia	NASBP	1753-02	N	1	NSRL-2908
AD 1200-1540	Pterodroma phaeopygia	DDH	1710-1	N	3*	Beta-11188
AD 1150-1510	Pterodroma phaeopygia	DDH	9659-1	N	3*	Beta-11193
AD 1030-1339	Pterodroma phaeopygia	DDHE	4917-L 6°	N	4	SR-5314
AD 1010-1410	Pterodroma phaeopygia	DDH	1710-1	N	3*	Beta-11189
AD 942-1172	Branta sp.	NASBP	5108-1	N	1	NSRL-2855
AD 900-1159	Branta sp.	DDHE	4907-D 1	N	4	SR-5307
AD 890-1340	Pterodroma phaeopygia	DDH	9659-1	N	3*	Beta-11194
AD 890-1040	Chaetoptila angustipluma cf.	EM	CLST. B, EU-46	N	2	NSRL-2443
AD 810-1049	Med, or Large Anatid	DDHE	4907-D I	N	4	SR-5305
AD 783-1016	Branta sp.	NASBP	1752-60	N	1	NSRL-2861
AD 650-869	Porzana ziegleri	DDHE	4907-D 1	N	4	SR-5303
AD 580-1060	Pterodroma phaeopygia	DDH	1710-1	N	3*	Beta-11190
AD 569-971	Pterodroma phaeopygia	NASBP	1752-67	N	1	NSRL-2860
AD 440-639	Thambetochen xanion	DDHE	4907-D 2	N	4	SR-5306
AD 420-629	Thambetochen xanion	DDHE	4907-D 2	N	4	SR-5310
AD 211-429	Thambetochen xanion	NASBP	5094-1	N	2	NSRL-2857
AD 30-239	Branta sp.	DDHE	4907-D 5	N	4	SR-5312
AD 1-250	Thambetochen xanion	EM	CLST. F, EU-24	N	2	NSRL-2438
BC 51-AD399	Oceanodroma castro	DDHE	4917-L 3	N	4	SR-5317
BC 81-AD 399	Pterodroma phaeopygia	DDHE	4917-L 3	N	4	SR-5316
BC 200-AD 450	Pterodroma phaeopygia	DDH	1710-1	N	3*	Beta-11191
BC 341-AD 9	Thambetochen xanion	DDHE	4907-D 5	N	4	SR-5311
BC 371-82	Med. or Large Anatid	DDHE	4907-D 1	N	4	SR-5309
BC 367-275	Thambetochen xanion	EM	CLST. E, EU-15	N	1	NSRL-2402
BC 400-170	Thambetochen xanion	EM	CLST. E, EU-15	Name of the last	2	NSRL-2404
BC 761-391	Porzana ziegleri	DDHE	4907-D 2	N	4	SR-5308
BC 763-370	Thambetochen xanion	ЕМ	CLST. A, EU-9	N	2	NSRL-2441
BC 1573-1066	Oceanodroma castro	NASBP	5108-1	N	1	NSRL-2854

Age, calibrated. Av 2 sigma*	ian Taxon	Location	Site No.	Deposit	Source	Radiocarbon Lab. No.
BC 1680-1410	Thambetochen xanion	EM	CLST. F, EU-24	N	2	NSRL-2401
BC 1871-1522	Porzana ziegleri	DDHE	4917-L 2	N	4	SR-5315
BC 3350-2920	Thambetochen xanion	EM	CLST. G. EU-26	N	2	NSRL-2400
BC 5150-4840	Thambetochen xanion	EM	CLST. B, EU-46	N	2	NSRL-2442
BC 5630-5330	Thambetochen xanion	EM	CLST. G, EU-26	N	2	NSRL-2408
BC 6480-6210	Thambetochen xanion	EM	CLST. B, EU-48	N	2	NSRL-2440

Table 5. Radiocarbon Dates on Bird Bone from the 'Ewa Plain.

*Dates for Pterodroma phaeopygia and Oceanodroma castro calibrated using marine reservoir curve with Delta r = 110 ± 80 (Dye, 1994b). (1) This provenience also produced a charcoal radiocarbon date: AD 1410-1650 (Beta-9543; Davis, 1990). (2) This provenience also produced a charcoal radiocarbon date: AD 1280-1440 (Beta-9052, Davis, 1990). Location: EM = 'Ewa Marina; DDH = Deep Draft Harbor; DDHE = Deep Draft Harbor Expansion; NASBP = Naval Air Station, Barbers Point, Deposit, C = cultural deposit; N = natural deposit.

Sources, 1 = Athens et al. (1999:Appendix G; XAD resin protocol used — Stafford et al., 1991). 2 = Franklin et al. (1995:Table 8.23; XAD resin protocol used). 3* = Davis (1990) for original data, with marine reservoir correction in Dye and Tuggle (1998:123). 3^ = Davis (1990) for original data, with marine reservoir correction calculated for the present table. 4 = McDermott et al. (2000:Table 4.29; XAD resin protocol used).

bones were probably introduced by birds. Thus, Layer II seems to be a paleontological deposit probably dating to the prehistoric Hawaiian period despite the presence of historically-introduced *Mus musculus* (mouse) bones (see below). Its significance is that it fails to provide evidence for human contemporaneity with any of the extinct land birds, though procellariids are present (see Table 4).

The relative densities of total bird bone (much of it unidentifiable), procellariids, all native land birds, R. exulans, lizards, and mice in the sink at Site 5108-F1 are shown graphically (Fig. 10). It is perhaps significant that the density of R exulans bones in the sinkhole deposit makes up such a large proportion of the total bone, considering it is only a single species and its bones have had much less time to accumulate than the native avian bones.

As Table 3 suggests, there is little stratigraphic integrity in the subfossil deposits despite the evident layering of the sediments. R. exulans and the lizards, which are Polynesian introductions, occur throughout the deposits even though sediments almost certainly have been accumulating in the Site 5108–F1 sink since long before the arrival of Polynesians. Bones of M. musculus, an historic introduction, are also found in all but the lowest layer. Trace amounts of charcoal, associated with human activity, are also found in all but the lowest two layers.

The lack of stratigraphic integrity in the Site 5108-F1 deposits is confirmed when radiocarbon dates on bird bone and *R. exulans* bone from several excavations are plotted (Fig. 11; Athens et al., 1999). As may be seen, surface bone may be quite old (all dates calibrated, 2 sigma range). The Figure 11 graph illustrates surface dates of AD 569-971 and AD 1214-1520 (both Pterodroma phaeopygia) from Sites 1752-F67 and

1753-F2. Also, four bone samples from near the base of Layer III at Site 5108-F1 display strikingly different ages: 1573-1066 BC (Oceanodroma castro), AD 942-1172 (Branta sp.), AD 1268-1401 (R. exulans), and AD 892-1160 (R. exulans - probably a different individual). Note that for Site 1752-F60 there is an inversion of ages from samples deriving from the same strata (Layer III) but slightly different levels. The disparity of ages, however, is no less striking. Here dates were obtained of AD 783-1016 from the 30-35 cm level (Branta sp.) and AD 1669-1950 from the 40-45 cm level (charcoal - primarily Scaevola cf. coriacea). Finally, from Site 5094-F1, two of the deepest sinkhole samples produced dates of AD 211-429 (Thambetochen xanion) and AD 972-1179 (R. exulans). These results are also stratigraphically inverted, with the older T. xanion date deriving from Layer II at 70-75 cmbs, while the R. exulans date derives from Layer II at 75-85 cmbs. In sum, there are obviously major problems in regard to the stratigraphic integrity of the sinkhole paleontological deposits.

There seem to be several natural disturbance processes affecting most sinkholes (Athens et al., 1999:147-148; Hammatt and Shideler, 1995; Tuggle, 1997; Franklin et al., 1995; Beardsley, 2001). Surface flooding from occasional heavy rains is one such process because the water induces percolation as it drains into the sinkholes. These rainfall events may also lead to redeposition of outside surface bird bones and other materials into the sinkholes. The flooding problem is no doubt aggravated by the relatively coarsely textured sinkhole sediments, facilitating downward migration of materials that are either within the sinkhole or have been introduced from the outside the sinkhole. Although sinkhole deposits possess sedimentary layers, it is a mistake to assume that paleonto-

AD Age.	BP Age, calibrated,	Location	Site No.	Source	Radiocarbon
calibrated, 2 sigma	2 sigma			es.	Lab. No.
AD 850-1289	1100-661	DDHE	4907-D 5	3	SR-5082
AD 892-1160	1058-790	NASBP	5108-F1	1	NSRL-2920; CAMS-25560
AD 972-1179	978-771	NASBP	5094-F1	1	NSRL-2858; CAMS-26396
AD 1190-1399	760-551	DDHE	4907-D 2	2	SR-5080
AD 1268-1401	682-549	NASBP	5108-F1	1	NSRL-2922; CAMS-25561
AD 1280-1409	670-541	DDHE	4917-L 2	2	SR-5085
AD 1330-1629	620-321	DDHE	4907-D 2	2	SR-5081
AD 1450-1639	500-311	DDHE	4907–D 1	2	SR-5304

Table 6. Radiocarbon dates on bone of *Rattus exulans* from sinkhole deposits on the 'Ewa Plain. All samples processed using the XAD resin processing protocol (Stafford et al. 1991). Location: NASBP = Naval Air Station Barbers Point: DDHE = Deep Draft Harbor Expansion. Source: 1 = Athens et al. (1999); 2 = McDermott et al. (2000).

logical materials associated with R. exulans or other Polynesian horizon markers in sinkhole deposits have a coeval age (see also radiocarbon dating evidence below).

Another example of the dating problem concerns the finding of bones of two types of extinct geese associated with an archaeological hearth feature discovered inside a large sinkhole (Olson and James, 1982:28,31). A charcoal sample from the hearth dated to AD 1205-1299 (2 sig. cal. range). Bones of P. phaeopygia (a petrel that no longer occurs on O'ahu), Branta sp. (an extinct goose), another type of unnamed extinct goose, and R. exulans were found "in and around [the] hearth" (Olson and James, 1982:31). The difficulty is that paleontological remains extend to the surface of many sinkhole deposits (e.g., Franklin et al., 1995; Wickler and Tuggle, 1997). This suggests that mixing of archaeological and paleontological deposits of very different ages inside sinkholes is virtually a foregone conclusion. Without radiocarbon determinations performed directly on the bird bone samples to demonstrate contemporaneity, or other compelling evidence to confirm a human association (e.g., butcher marks on the bone or evidence of burning), it is unwarranted to assume that the land bird remains are anything other than a part of the natural pre-Polynesian paleontological assemblage. In this case the excavator of the sinkhole hearth, P. McCoy, has stated that the cultural context of the bird bone is uncertain (pers. comm. cited by Tuggle and Tomonari-Tuggle, 1997a:92).

In terms of the overall chronology of avian subfossil remains in the 'Ewa Plain sinkholes, there are a total of 46 usable radiocarbon determinations (Table 5). Although dating of such remains in the absence of meaningful stratigraphic context has obvious sampling problems, there are a number of important points that can be considered.

One is that a significant change occurs about AD 1000. Prior to this time a range of taxa is found, indicating a general accumulation of avian remains from the early mid-Holocene. However, after AD 1000 only

Pterodroma phaeopygia is present in the sinkholes. This is completely consistent with the archaeological record. Lowland archaeological deposits, if they contain any avian remains, have almost exclusively seabirds.

Further, the dating sequence for the 'Ewa Plain avian remains indicates the temporal overlap with the early period of Hawaiian settlement for some extinct taxa. Four individual Large Anatid (including three identified as Branta sp.), one flightless rail (Porzana ziegleri) and one passeriform (Chaetopila angustipluma) have radiocarbon dates that overlap the AD 800–1000 range that defines the Hawaiian colonization period, indicating that these taxa did not become extinct in the pre-Polynesian period. The problems of sampling and the statistical nature of radiocarbon dating ranges do not allow the conclusion that these birds necessarily became extinct during the early Polynesian period, but the evidence is consistent with this interpretation given the absence of such remains in later archaeological deposits.

'Ewa Plain archaeological sites and avian remains

Excavation of non-sinkhole habitation sites on the 'Ewa Plain has produced very little bird bone, despite good bone preservation. The few bird bones present are almost exclusively sea birds (procellariids; see summary in Tuggle and Tomonari-Tuggle, 1997a:91-93). There are virtually no land birds represented, such as the presumably highly desirable anatids (ducks, geese). This is, in fact, a common pattern of lowland sites throughout Hawai'i; indisputable archaeological remains indicating human use of land birds are extremely rare (see also Olson and James, 1982;29; Collins, 1995; Moniz, 1997).

7. There is one excellent archaeological case of the bones of two extinct passeriforms occurring in a small pit or depression on the limestone surface that is interpreted as a possible offering (Tuggle and Tomonari-Tuggle, 1997a:92).

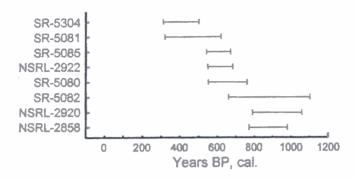


Figure 12. AMS Radiocarbon determinations on *Rattus* exulans bone from sinkhole sites on 'Ewa Plain. All dates depicted at 2 sigma calibrated ranges (from Athens et al., 1999; McDermott et al., 2000). XAD resin protocol (Stafford et al., 19991) used for preparation of all samples.

Upper elevation archaeological deposits in lava tube caves and shelters, however, do contain avian land bird remains (e.g., Athens et al., 1991 for discussion of sites in the saddle area of Hawai'i Island at elevations between 1.500 and 2,000 m), indicating that their scarcity in lowland sites is not a question of archaeological recognition.

The avian extinction problem

Research on the 'Ewa Plain indicates that subfossil avian remains have been accumulating in the sinkholes since the early Holocene and that most of the extinctions occurred around the time of human colonization of Hawai'i or shortly thereafter. The four major possible explanations for avian extinctions are predation by humans, predation by rats, loss of habitat, and disease. There is no evidence to address the question of disease, and predation by rats (*R. exulans*) is unlikely given their food preferences, as discussed below.

Concerning human predation, unlike many other places in the Pacific, early Hawaiian lowland archaeological deposits show no evidence for accumulation of remains of now-extinct or extirpated birds, and avian bones from non-archaeological deposits have no indication of human modification. They also show that marine birds continued to exist and to be utilized throughout the period of prehistoric Hawaiian occupation. Thus, the suggestion of predation as a cause of extinction/extirpation is not supported by the terrestrial avifauna remains of the 'Ewa Plain or anywhere else in the Hawaiian lowlands.

Paleoenvironmental coring demonstrates there was a rapid loss of the lowland forest roughly concurrent with the time of Polynesian colonization of Hawai'i and largely coincident with the avian extinctions. This timing suggests a highly probable causal model of habitat loss leading to extinction. However, the paleontological and archaeological data indicate that this habitat destruction

occurred *prior* to human occupation of the 'Ewa Plain, and certainly prior to any Hawaiian agricultural expansion or forest burning. The absence of evidence for land bird predation in archaeological sites on the 'Ewa Plain and elsewhere in the Hawaiian lowlands thus has an explanation. Most of the land birds were gone before the Hawaiians even had a chance to make use of them for subsistence.

Vegetation and rats

If forest loss is the answer to avian extinction, the problem refocuses on the cause of the forest decline, and we suggest that a good case can be made that the Polynesian rat, *R. exulans*, was a significant destructive agent. The Polynesian rat has been considered as a factor in avian extinction through direct predation (e.g. Kirch, 1985:291), and has been discussed in regard to possible effects on vegetation (e.g. Cuddihy and Stone 1990), but the 'Ewa Plain research provides a set of data that suggests it played a dramatic role in environmental change.

This rat, which was the first non-human land mammal to reach the shores of Hawai'i, was introduced either by the initial Polynesian discoverers/settlers, or soon thereafter by other Polynesian voyagers. There are several points to make regarding the suitability of *R. exulans* as a prime suspect in the demise of the forest. The first concerns the dating evidence.

Following the lead of James et al. (1987), we undertook the radiocarbon dating of three rat bones in our recent project (Athens et al., 1999:347) to use as a proxy indicator for the arrival of humans in the islands, as well as for their history on the 'Ewa Plain. Another series of five bone dates for R. exulans also has been recently reported by McDermott et al. (2000). The results of these dates are listed in Table 6 and also shown in Figure 12.

Although there is no stratigraphic basis for insuring that one is dating the earliest occurrences of *R. exulans* in the sinkhole deposits, the results indicate that *R. exulans* was probably present on the 'Ewa Plan at the time the native forest disappeared and well before human settlement on the Plain. Because of the statistical nature of radiocarbon dating, it may be impossible to narrow the ranges much further. Dye's (2000b) Bayesian calibration of bird bone and rat bone dates obtained by McDermott *et al.* (2000) from sinkholes (see Table 6), shows that there was some likelihood for the overlap of now-extinct anatids with *R. exulans* on the 'Ewa Plain.

The second point is that rat bones are relatively common in the sinkhole deposits (see Fig. 10). This may indicate that *R. exulans* attained relatively high population densities in the past in comparison to the native fauna. It would be valuable to test this model by the radiocarbon dating of a large sample of rat bones randomly selected from sinkhole deposits to develop a population curve for their relative abundance through time.

Third, rats arrived in Hawai'i with no predators except possibly the Hawaiian hawk or the now extinct eagle,

which may have restricted their diets to familiar birds in any case (see Olson and James, 1991:64, 67). Competition for food from other animals (such as folivorous anatids e.g., James and Burney, 1997) may also have been of little consequence. It is also hard to imagine seed eating birds providing very effective competition for the rats since the latter are excellent climbers and can reach almost anywhere the birds can for obtaining seeds. Further, with their teeth, the rats can open even the hardest and thickest seed cases, possibly enabling them to consume some seeds before they might be available to birds when they break open naturally. Although not a competitive factor, it is also interesting to note that seeds, after consumption by rats, presumably would have no chance of viability unlike some seeds that pass through the digestive tract of birds. Thus, given the fact that R. exulans is a very fecund mammal, capable of having four to six litters of just over 4 young each per year on average (Kramer, 1971), it seems likely that their population could have expanded very quickly at an exponential rate. In just a decade or two, rats could have densely covered an entire island like O'ahu up to their elevation maximum.

Fourth, numerous studies show that the primary food preference of R. exulans is plant matter (Mosby et al., 1973; Norman, 1975; Strecker and Jackson, 1982; Temme, 1979; and Wodzicki, 1978/79:442). The argument has been made that rats may have preyed on ground-dwelling birds (Cuddihy and Stone, 1990:34), but a review of relevant case studies indicates that this is rare and occurred only when R. exulans was under severe survival stress in the absence of plant material (Wirtz, 1972; Tomich, 1986), or is occasional and minor (cf. Mosby et al., 1973:808). These rats have been found to rely on plant material as diverse as coconut, sugarcane, pandanus, various fruits, and grasses (summarized in Atkinson and Moller, 1990). In short term studies, Polynesian rats have been shown to affect coastal forest composition during regeneration (Campbell, 1978). That the Hawaiian native flora was particularly attractive to R. exulans is suggested by a statement made by a horticulturalist who specializes in the propagation of endangered native Hawaijan plants: "Let rats near them and they'll be eaten...They're like candy to rats" (TenBruggencate, 1997). The rats could have produced their damage through seed and fruit predation, consumption of seedlings and new leaf production, and girding of softbarked trees, as well as consumption of invertebrates critical to plant pollination and the nutrient cycle (see discussion in Cuddihy and Stone, 1990:34,68-70).

While the above only serves to demonstrate the potential for rats to have been responsible for the demise of the native lowland forest and offers no proof, there is further interesting evidence in Hawai'i suggesting that rats may have played a significant role in this regard. This involves the contrast between two small islands off the north coast of Moloka'i. Huelo Island is a vertically-sided pinnacle rising 60 meters above the sea. The 30 x 60 meter sloping surface of this island is densely covered with both mature and young *Pritchardia hillebrandii*

palms (demonstrating the palms are reproducing) and other native plants (e.g., Diospyros sandwicensis), besides being home to many Wedge-tailed Shearwater chicks in the ground litter. Wildlife surveys have not documented rats on this island. In contrast, nearby Mökapu Island (unoccupied and consisting of steeply sloping — but not vertical — surfaces) has very few Pritchardia palms, including only a single immature plant (suggesting that it is having a difficult time reproducing), but rats have been documented (K.R. Wood, pers. comm., 2000).

The discovery of two Kanaloa kahoolawensis shrubs, a previously unknown plant, on another nearly inaccessible rock spire off the south coast of Kaho'olawe Island in 1992 (Lorence and Wood, 1994) is also relevant to the possible role of rats in the destruction of native vegetation. K. kahoolawensis, representing a genus and species new to Hawaiian botany, is common in the prehuman pollen intervals of lowland cores, but as demonstrated in the Ordy Pond and other cores, it became all but extinct with the arrival of humans and associated rats. With respect to the Kaho'olawe discovery, presumably rats cannot access this extremely difficult location, possibly accounting for the survival of K. kahoolawensis.

Finally, it is of interest that native vegetation in Hawai'i is relatively common above about 1,500 m (although *Pritchardia* palms do not extend to this elevation with the exception of one species on Hawai'i Island, and many other lowland taxa are also absent in the higher elevations — see Gagné and Cuddihy 1990; Wagner et al. 1990). In spite of rare documented instances of its occurrence at higher elevations (Tomich, 1986:42; Cuddihy and Stone, 1990:68), the maximum elevation range for *R. exulans* in Hawai'i is also about 1,500 m. Thus, the persistence of native vegetation at higher elevations (and consequently, the native avifauna), may owe much to the primarily lowland natural habitat range of rats.

Given the cumulative set of data, we thus propose that *R. exulans*, quickly radiating throughout the islands ahead of the human settlers who had brought them, destroyed much of the native Hawaiian lowland forests by consumption of the leafy and reproductive portions of the plants. This may be at least part of the explanation why certain formerly common native woods (e.g., *K. kahoolawensis*) are never found in archaeological contexts despite the examination of over 600 archaeological charcoal samples (containing multiple charcoal fragments) and perhaps 1,000 single specimens of archaeological charcoal (G. Murakami, pers. comm., 2001).

The rapid forest decline in Hawai'i is not matched on other islands where R. exulans seems to have been introduced prehistorically (e.g., Palau and Guam — Athens and Ward, 1999a, 1999b). There is no immediate explanation for this, but one possible factor could relate to the high degree of endemism that characterizes Hawai'i's native vegetation — between 91 and 96+% of the angiosperms (Loope and Mueller-Dombois, 1989; see also Carlquist, 1980). The endemism may also have fos-

tered the development of seed production characteristics that made native plants susceptible to the eating habits of the rats (see Campbell, 1978). If endemic plants of the lowland forest were an ideal food for the rats, the conditions were right for a population explosion of this new species, with the resulting vegetation collapse.

Conclusion

The paleoenvironmental coring data document major and very rapid vegetation change (i.e., disappearance of the dryland forest) prior to the significant presence of humans in the 'Ewa Plain region, and almost certainly before any vegetation clearance by burning. The model proposed here suggests that drastic change of the native plant community led to the relatively rapid extinction or extirpation of some land bird species, particularly passerines and flightless taxa, prior to the advent of humans on the 'Ewa Plain. The model thus explains the absence of early sites of bird hunters, the general absence of bird remains (except for some seabird bones) in most Hawaiian occupational sites of the region, and the general pattern of bird bones underlying cultural deposits in sinkholes (with acknowledgment of the common problem of mixing in the interface zone).

Forest decline as a cause of bird extinction also seems compatible with the limited evidence concerning the pattern of extinction; that is, the survival of procellariids well into the period of human settlement. Presumably the procellariids would have been as susceptible as forest birds (or more so) to population stress from rat or human predation, but less susceptible to stress from forest decline,

To evaluate our model we would like to find and analyze another high resolution laminated wetland deposit like Ordy Pond on perhaps another Hawaiian island. Secondly, we would like to radiocarbon date (using the XAD resin protocol — Stafford et al., 1991) more R. exulans bones not only to determine the date of their earliest occurrence on the 'Ewa Plain with greater precision and assurance than is possible at present, but also to provide a statistically sound means for estimating relative population numbers through time. Finally, we believe that many more subfossil avian bones of the different extinct/extirpated taxa need to be dated using the XAD resin protocol to more firmly establish the date of their disappearance.

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