Land Snail Extinctions at Kalaeloa, O'ahu[1]

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ABSTRACT: A decline over time in the proportion of native land snail taxa believed to be extinct today at Kalaeloa has been interpreted and widely cited as an example of Polynesian influence on the Hawaiian environment. This interpretation is shown to be based on an inappropriate measure of decline and nonstandard calibrations of ^{14}C dates. An analysis of change over time in the diversity of land snail taxa from Kalaeloa sinkholes and recalibration of ^{14}C dates using Bayesian techniques reveals a different pattern, which is interpreted as having two components. There is a long-term, gradual decline in the diversity of native, extinct land snail taxa, explained as the result of desiccation of the sinkhole environment due to a drop in the water table when sea level fell from its mid-Holocene high stand. There is also an abrupt disruption of the land snail fauna late in the stratigraphic sequence. It is argued that this disruption dates to the historic period, when the environment of the 'Ewa plain was drastically altered for sugarcane production and when the vegetation that now dominates the region was introduced. Aside from the appearance of the snail *Lamellaxis gracilis*, which was introduced to the Islands by Polynesians, the land snail assemblages from the Kalaeloa sinkholes yield no evidence for Polynesian influence on the environment.

IN AN INFLUENTIAL PAPER Kirch pointed out the potential for archaeology and ancillary studies of paleoenvironment to provide data on the impact Polynesians might have had on the environment of the Hawaiian Islands. He reviewed preliminary results from several studies of vegetation, fauna, and physical environment that he interpreted as indicating "the endemic biota was drastically affected by ... habitat destruction, with perhaps one-third to one-half of the known non-marine molluskan and bird faunas becoming extinct within the span of prehistoric human tenure" (Kirch 1982:11). He predicted that future studies would confirm that "the prehistoric Polynesian inhabitants of Hawaii seriously transformed and, in many instances, degraded their island ecosystem" (Kirch 1982:11). Since then, evidence for change interpreted as this Polynesian transformation of the environment has appeared in studies of fossil

pollen (Ward 1981, 1990, Athens and Ward 1991, 1993, Athens et al. 1992), avifauna (Olson and James 1982*a,b*, 1984, 1991, James and Olson 1991), and nonmarine mollusks (Christensen and Kirch 1986, Kirch 1989, Cowie 1992, Christensen 1995). In this paper we review and reinterpret the stratigraphic record of nonmarine mollusks (land snails) at Kalaeloa (Barbers Point [The Hawai'i House of Representatives voted in April, 1995, to restore the name Kalaeloa to this region of O'ahu (Honolulu Advertiser 1995).]), O'ahu.

Studies of fossil land snails at Kalaeloa show a decline over time in the relative proportion of taxa believed to be locally or globally extinct today, and an increase in taxa that were "preadapted" (Kirch 1982:9) to disturbed conditions and thus tolerant of the environmental changes inferred to have been wrought by Polynesians. A chronology based on ^{14}C dates has been interpreted as placing these changes "well within the period of Polynesian habitation of the islands..., providing strong circumstantial evidence that

the Hawaiians were the cause of the ecological changes associated with this succession in the land snail fauna" (Christensen 1995:254). [Christensen finished his report in 1985 and did not have the opportunity to make other than minor editorial changes in the 10 yr until the report was published. The differences between his chronology and that of Davis (1995) in the same volume should have been rectified by the author and/or editor of the volume. As a malacologist, Christensen never claimed to be an expert in radiocarbon dating or its interpretation, and his analysis of the snail data might have been different if the chronological framework was changed.] The Kalaeloa land snail data have been used to support the hypothesis that human activities on islands led to the extinction of many small creatures, in contrast to continental areas where the extinctions were primarily among the megafauna, and that "(d)estruction of oceanic island biotas seems to have been more severe in the Holocene than it was historically" (Martin 1986:111). At Kalaeloa, forest clearance and habitat modification by Polynesians are commonly cited as the causes of faunal extinctions (Kirch 1982, Olson and James 1984, Christensen and Kirch 1986).

In this paper we show that the interpretation of Polynesian influence drawn from the stratigraphic record of fossil land snails at Kalaeloa is based on a unique stratigraphic sequence at a single sinkhole. The interpretation was then applied to other land snail sequences, despite their lack of evidence for Polynesian influence. We present a reanalysis of the stratigraphic record to conclude that Polynesians had little, if any, effect on land snail populations in the sinkholes. We show that directional change in the land snail populations was under way before Polynesians colonized the Islands. Decreases in the diversity of snail populations, possibly indicative of environmental stress, do occur near the end of the stratigraphic sequence. Based on the available dating evidence, however, these changes probably took place in the post-contact period when the regional environment was radically altered by sugar cane cultivation.

BACKGROUND

One-hundred twenty-eight land snail assemblages from 18 sites are analyzed here. These were collected during archaeological and paleontological investigations carried out during cultural resources management projects associated with the construction of the Barbers Point harbor and the Ko Olina resort adjacent to the harbor (Figure 1). The investigated sites include 10 sinkholes without cultural modification, four sinkholes that appear to have been modified for use as garden pits by Hawaiians, two habitation sites, and two natural marshes. The minimum number of individuals (MNI) identified in the assemblages is 120,210, with individual assemblages ranging in size from 69 to 21,816 MNI. The number of assemblages that we analyzed at each site ranged from 2 to 16. The sites with relatively few assemblages include the two marsh sites, both habitation sites, and the modified sinkhole sites. Several unmodified sinkholes, including especially sites 1710-1 [Each site is identified here with the last four digits of its State of Hawai'i site number optionally followed by a dash and a feature designation. Each of the four-digit site numbers is preceded by the prefix 50-80-12- (e.g., 50-80-12-1710-1).], 9574 [This site is often referred to in the literature by its Bishop Museum site number, 50-Oa-B6-78. There is some confusion in the records of the State Historic Preservation Division, which assigns site numbers, and Bishop Museum over the correct State of Hawai'i site number for site B6-78. The state site number 50-80-12-9574 is taken from the master list in the Anthropology Department, B. P. Bishop Museum, and refers precisely to the original definition of site 50-Oa-B6-78 (Sinoto 1978).], 9647-2, 9659-1, and 9661-2, yielded nine or more stratigraphically ordered assemblages.

The potential of the Kalaeloa land snail assemblages to contribute to environmental reconstruction was first recognized by Kirch (1978), who identified 11 species of land mollusks in three small assemblages from site 9574. The small sample of identified mollusks and circumstances of their collection precluded detailed interpretation. How-
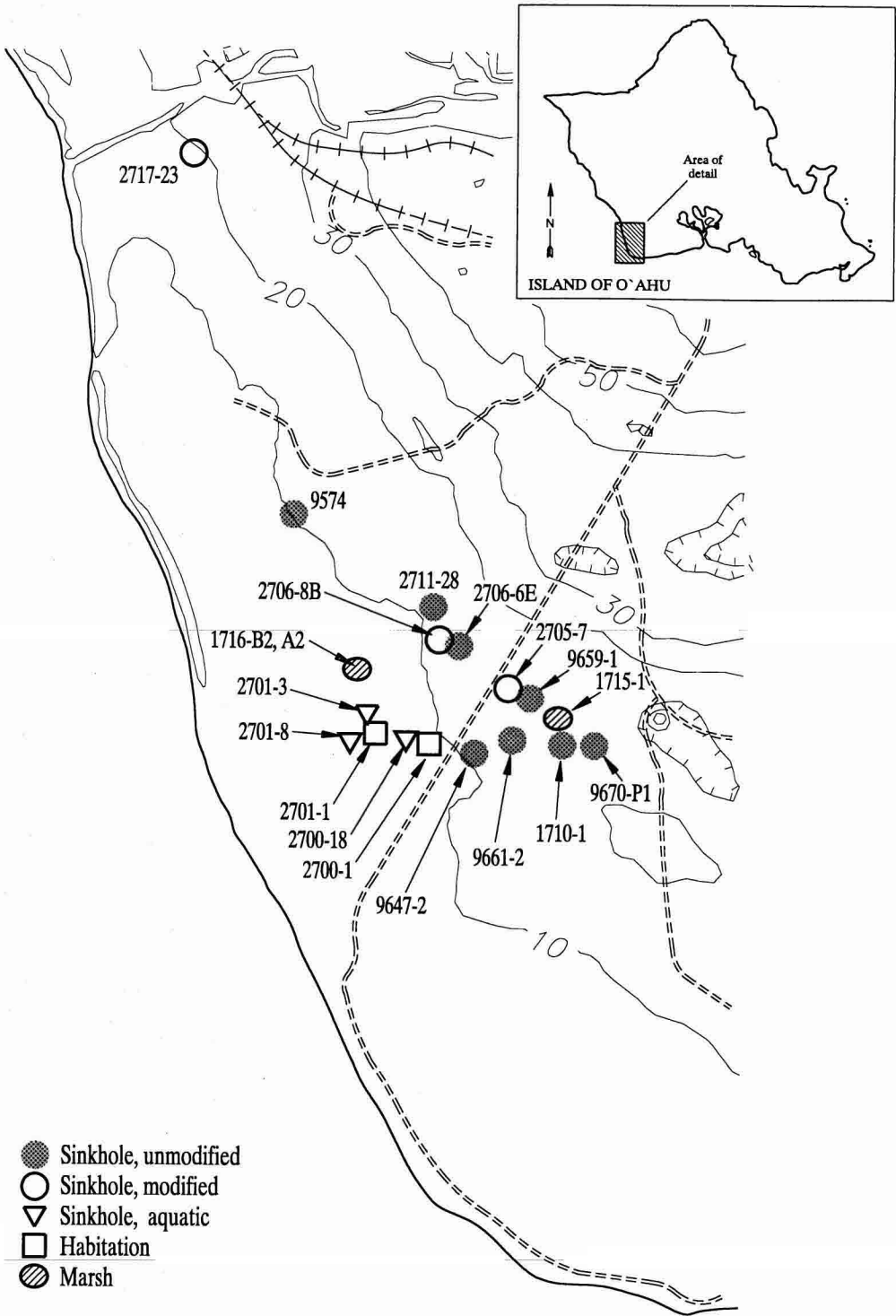
FIGURE 1. Locations of sites mentioned in text.

TABLE 1

LAND SNAIL TAXA AT KALAELOA

TAXON	ECOLOGICAL GROUP
Orobophana uberta (Gould, 1847)	Native, extinct
Assiminea nitida (Pease, 1865)	Aquatic
Melampus sp.	Aquatic
Lamellidea spp.	Native, extant
Pacificella sp.	Native, extinct
Tornatellides spp.	Native, extant
Achatinella mustelina Mighels, 1845	Native, extinct
Leptachatina (Angulidens) cookei Pilsbry, 1914	Native, extinct
Leptachatina (Angulidens) subcylindracea Cooke, 1911	Native, extinct
Leptachatina spp.	Native, extinct
Amastra (Metamastra) cf. *subrostrata* (Pfeiffer, 1859)	Native, extinct
Amastra (Cyclamastra) umbilicata umbilicata (Pfeiffer, 1855)	Native, extinct
Amastra spp.	Native, extinct
Lyropupa sp. (sinistral)	Native, extinct
Lyropupa (Mirapupa) ovatula Cooke & Pilsbry, 1920	Native, extinct
Lyropupa (Mirapupa) perlonga (Pease, 1871)	Native, extant
Lyropupa (Mirapupa) spp.	Native, extant
Nesopupa (Nesopupilla) litoralis Cooke & Pilsbry, 1920	Native, extinct
Nesopupa (Limbatipupa) newcombi (Pfeiffer, 1852)	Native, extinct
Nesopupa (Nesodagys) wesleyana Ancey, 1904	Native, extinct
Nesopupa spp.	Native, extinct
Pupoidopsis hawaiiensis Pilsbry & Cooke, 1921	Native, extinct
Gastrocopta servilis (Gould, 1843)	Introduced, historic
Cookeconcha, undescribed sp.?	Native, extinct
Endodonta kalaeloana Christensen, 1982	Native, extinct
Succinea caduca Mighels, 1845	Native, extant
Lamellaxis gracilis (Hutton, 1834)	Introduced, precontact
Bradybaena similaris (Ferussac, 1821)	Introduced, historic

(From Christensen 1995: table 2.1)

ever, Kirch (1978) was able to set out the field methods that subsequent investigators should follow: samples should be collected from each stratigraphic layer in a site, preferably at 5- to 10-cm intervals; fine-meshed screens should be used to maximize recovery of small individuals; and a survey of the contemporary land snail fauna at Kalaeloa should be made "to serve as a control for interpretation of the subfossil assemblages" (Kirch 1978:4).

The first major application of quantitative snail analysis in Hawai'i was carried out by Christensen and Kirch (1986), who identified a minimum number of 21,376 individual snails in 26 assemblages from five sites, including two unmodified sinkhole sites (9574, 9670-P1), two human habitation sites (2700-1, 2701-1), and one sinkhole site possi-

bly modified for use as a pit garden (2701-3). Their analysis and interpretation of these materials strongly influenced subsequent studies.

Central to the analysis is the division of taxa into various ecological status classes (Table 1). Among the native land snail taxa, "native, extinct" taxa are presumed extinct, either globally or locally, and "native, extant" taxa are found today at Kalaeloa. [Christensen and Kirch (1986) did not note whether "native extinct" taxa were identified on the basis of a field survey, as recommended by Kirch (1978), or by some other means, and there are some differences of opinion among malacologists over which taxa are in fact extinct at Kalaeloa (Cowie 1992, 1997).] In addition to the native land snail taxa, other snails identified in the

Kalaeloa deposits include introduced taxa, the most important of which are the Polynesian introduction *Lamellaxis gracilis* and the ubiquitous postcontact introduction *Gastrocopta servilis,* and various aquatic taxa, of which the most abundant, *Assiminea nitida,* is found in deposits that are dry today and is an important marker of wetter conditions.

Christensen and Kirch's analysis centered on sinkhole site 9574, whose 85-cm-deep, three-layer, stratigraphic sequence suggested that it was "of critical importance in assessing long-term ecological change" (Christensen and Kirch 1986:72). The site showed striking evidence of change over time in the relative proportion of native, extinct taxa. The seven assemblages from the bottom 70 cm of the stratigraphic column yielded between 71% and 85% native, extinct taxa. Native, extinct taxa declined to 67% of the assemblage collected 5–15 cm below surface and fell to 20% in the surface assemblage. None was found in the leaf litter. In the absence of radiometric dates for the stratigraphic sequence, an absence keenly felt (Christensen and Kirch 1986:76), Christensen and Kirch attempted to date the decline of native, extinct taxa through the stratigraphic distribution of temporal index fossils. Taxa introduced to Hawai'i by Polynesians in the first millennium A.D. and found in the sinkhole deposits include the snail *L. gracilis,* scincid and gekkonid lizards, and the Polynesian rat (*Rattus exulans*). Postcontact (A.D. 1778) introductions include the snail *G. servilis,* the house mouse (*Mus musculus*), and rats other than the Polynesian rat. Christensen and Kirch found *L. gracilis,* lizards, and *R. exulans* in the top 25 cm of the stratigraphic column, a distribution that correlates with the decline in relative proportion of native, extinct taxa. The unexpected presence of *G. servilis* throughout the stratigraphic column, often as live or freshly deposited shells, was believed to have resulted from contamination in the period between the site's excavation (Sinoto 1978:21–24) and sampling for the snail assemblages. Thus, it appeared that the decline of the extinct taxa began during the Polynesian period and that Polynesians were responsible for "the extinction of much of the native land snail fauna" (Christensen and Kirch 1986:76).

A decline over time in the relative proportion of native, extinct taxa was found at all other sites (except site 2701-3, which was dominated by the aquatic snail *A. nitida*), but stratigraphic sequences differed from the sequence at site 9574. The variations from the pattern of change documented at site 9574 were not interpreted, however. These include the very gentle relative decline of native, extinct taxa at sinkhole site 9670-P1, their strong presence (>40%) at the end of that sequence, and evidence for mixing of the index fossil *G. servilis* at sites 2700 and 2701.

Subsequent investigations at Kalaeloa greatly augmented the number of land snail assemblages available for analysis, identified six taxa not found previously, and provided the basis for radiometric dating of certain sinkhole sequences. Davis' (1990) excavations at 12 sites, including eight sinkholes (1710-1, 2700-18, 2701-8, 2706-6E, 2711-28, 9647-2, 9659-1, and 9661-2), two modified sinkholes (2705-7 and 2706-8B), and two marshes (1715-1 and 1716), yielded 97 assemblages [At site 1716 seven assemblages were collected, but only two of these assemblages, from Layers II and III, are used for analysis.] and a total of 96,388 identified individuals (Christensen 1995). Six snail taxa not previously identified at Kalaeloa were found in small numbers. These include an amphibious taxon [Christensen (1995) mentioned finding the aquatic snail *Neritina,* but there is no entry for this taxon in the data tables.], one historically introduced taxon, and three native, extinct taxa, including *Pacificella* spp., *Achatinella mustelina,* and *Amastra* (*Metamastra*) cf. *subrostrata,* the latter two of which are generally restricted to moister, forested regions. Their presence, along with the presence of a sinistral *Lyropupa,* well outside their known environmental ranges led Christensen to sound a note of caution about the possible precision of ecological inferences drawn from fossil land snail assemblages. He also recognized that the snails used as index fossils by Christensen and Kirch (1986) were regularly found at depths far too great for their known ages.

Although he provided some general guidelines for distinguishing in situ occurrences of these taxa from secondarily deposited specimens, it is not possible to apply these guidelines to the data as they are reported. In any case, the availability of ^{14}C dates at some of the sites diminished the importance of the index fossils as a basis for chonological inferences.

Davis' dating program focused on the sinkhole sites, whose long stratigraphic sequences provide information on change that is not yielded by the habitation sites, marshes, or modified sinkholes. Davis recognized that the sinkholes showed stratigraphic regularities and that these might be used to posit a regional depositional sequence that would apply generally to sinkholes. These stratigraphic regularities were described by Allen (1995), who defined depositional units based on the formative conditions of the sediments and proposed a three-phase stratigraphic sequence. At the base of the stratigraphic column is a "basal diagenetic deposit characterized by carbonate silts weathering directly off the reefal substrate" (Davis 1990:182). [Davis (1990) and Allen (1995) appear to have used the roman numeral labels for the depositional units (e.g., "Depositional Units III, II, and I") in different ways. Davis (1990) appears to have equated them with the regional deposition regime, and Allen (1995) used them in a site-specific fashion. To minimize the potential for confusion the depositional units are labeled here with descriptive phrases (e.g., "basal diagenetic deposit," "structural collapse deposit," and "transported sediment deposit").] The basal diagenetic deposit was buried by sediments derived from "mass wasting and major episodes of structural collapse of the sinkhole walls" (Davis 1990:182). These structural collapse deposits were buried in turn by a dark-colored, loamy deposit "formed in transported sediments" (Davis 1990:182). Davis hypothesized that "(c)hange in the dominant mode of deposition through the column provides a tentative model of ecological change" (Davis 1990:182) for the region.

Davis concentrated his dating efforts at sites 9659-1 and 1710-1, submitting seven

avian bones (procellariid) for age determinations. The bones came from each of the depositional units, with the structural collapse deposit providing five dates and the transported sediment and basal diagenetic deposits one each. The ^{14}C ages returned by the laboratory (discussed below) are consistent both within and between the two sites, and offer general support for Davis' hypothesis of a regional sinkhole depositional sequence. However, calibration of the ^{14}C ages on procellariid bone is not a straightforward matter. Procellariid birds feed exclusively on sea creatures and thus take in their carbon from the ocean reservoir, which has an apparent ^{14}C age of approximately 400 yr. Calibrating with an atmospheric curve would yield calibrated ages that are too old by several hundred years. Christensen (1995) reported "uncorrected" calendar dates derived by subtracting the conventional ^{14}C age from 1950, a practice roughly equivalent to calibrating with an atmospheric curve. [When Christensen wrote his report in the early 1980s he did not have access to the chronology worked out by Davis (1990).] Davis recognized the problem with dating materials from the ocean reservoir, but instead of following calibration procedures established by the ^{14}C dating community (Stuiver et al. 1986), chose instead to devise his own calibration curve based on ^{14}C dates on paired samples of different materials from his Kalaeloa excavations. Despite the differences in the calendar dates, with those reported by Christensen (1995) averaging about 500 yr older than those reported by Davis (1990), both authors interpreted the ^{14}C dates as supporting the hypothesis that the decline of native, extinct taxa was due to Polynesian influence. Christensen (1995:254) concluded that the first evidence for decline in the land snails dated to A.D. 690, a time believed by many prehistorians to be early in the Polynesian era (Kirch 1985, Hunt and Holsen 1991). Davis (1990:333) dated the period of greatest change in the land snails to A.D. 1200–1500, a period generally regarded as characterized by rapid population growth and expansion of settlements (Kirch 1985).

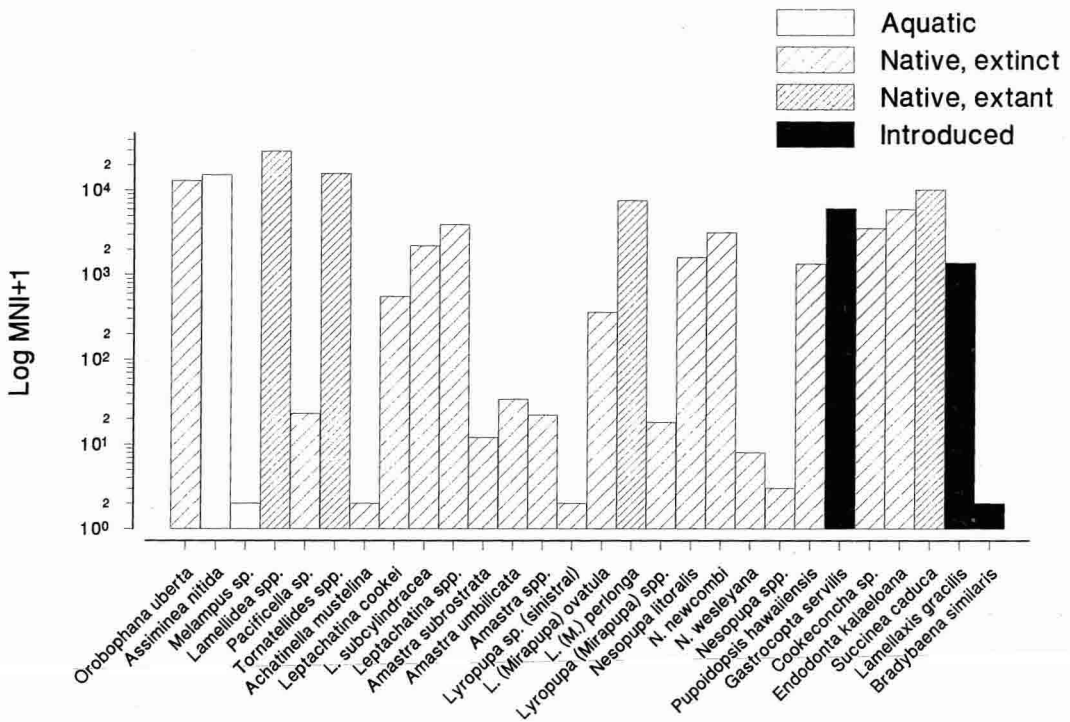Recently, Cowie (1992) identified 1,968

FIGURE 2. Distribution of land snail taxa at 18 Kalaeloa sites. Note the logarithmic y-axis scale.

MNI in six assemblages from the modified sinkhole site 2717-23. These assemblages showed a decline in relative proportion of native, extinct taxa over time, which Cowie, following Christensen and Kirch (1986), interpreted as due to "the decline of native plant communities and the increasing dominance of introduced plants combined with increased human activity" (Cowie 1992: J-4).

THE KALAELOA LAND SNAIL ASSEMBLAGE

The Kalaeloa fossil land snail assemblage is one of the richest and largest faunal assemblages recovered archaeologically in Hawai'i. The large number of identified individuals means that it is likely that most, if not all, land snail taxa that inhabited Kalaeloa over the time covered by the excavated deposits have been identified.

The distribution of identified individuals

among the 28 identified taxa is uneven (Figure 2). Five very abundant taxa each contribute more than 10,000 individuals and together make up 69% of the assemblage. Ten abundant taxa, each with over 1,000 individuals, together make up 30% of the assemblage. Two common taxa, each with more than 100 individuals, make up less than 1% of the assemblage. The remaining 11 rare taxa, each with between 1 and 33 identified individuals, round out the final 0.1% of the assemblage. It is not surprising that three of the five native, extant taxa are very abundant and a fourth is abundant (Table 2). The fifth native, extant taxon, *Lyropupa (Mirapupa)* spp., was not classified by Christensen (1995), but is considered extant here because individuals assigned to this generic taxon might include unidentifiable specimens of the extant *L. (M.) perlonga,* which is identified in greater numbers than the native, extinct taxon *L. (M.) ovatula.* In contrast, only one native, extinct taxon, *Orobophana uberta,* is

TABLE 2

ABUNDANCE OF TAXA BY ECOLOGICAL STATUS

ECOLOGICAL STATUS	VERY ABUNDANT	ABUNDANT	COMMON	RARE
Introduced	0	2	0	1
Native, extant	3	1	0	1
Native, extinct	1	7	2	8
Aquatic	1	0	0	1

very abundant, seven are abundant, and the remaining 10 taxa are either rare or common.

HABITATS OF THE KALAELOA LAND SNAILS

The 'Ewa plain, of which Kalaeloa is part, is often described as featureless, a desolate, barren expanse of limestone. From a land snail's perspective, however, this could be rough and variable terrain. An obvious limiting factor is water; Kalaeloa is the driest corner of O'ahu, with a median annual rainfall of less than 60 cm (Giambelluca et al. 1986) and no running streams. The surface of the land is for most of the year dry, hot, and uninviting. But this is only skin deep. Not far below the surface the water table fills cavities in the limestone, creating subterranean pools. In some places sinkholes are deep enough to reach the water table, and the water standing in them creates a unique habitat. Even where sinkholes do not extend down to the water table the sediment trapped in them provides fertile soil for vegetation, relatively close to a ready supply of water and with a degree of protection from the wind.

The distribution of land snails at Kalaeloa indicates that, for many taxa, this was a patchy habitat. This shows most clearly at the low-lying sinkhole sites 2701-3, 2700-18, and 2701-8 where the aquatic taxon *A. nitida* predominates to the near exclusion of all other taxa. It shows more generally in differences in the ubiquity of taxa among the excavated assemblages. Eleven of the 28 land snail taxa are widely distributed at Kalaeloa, occurring in at least 13 of the 18 site assemblages (Table 3). They include the four abundant native, extant taxa [excluding only

TABLE 3

UBIQUITY OF TAXA BY ECOLOGICAL STATUS AT THE KALAELOA SITES

	NO. OF SITES		
ECOLOGICAL STATUS	18–13	12–7	6–1
Introduced	1	1	1
Native, extant	4	0	1
Native, extinct	6	3	9
Aquatic	0	1	1

Lyropupa (*Mirapupa*) spp. among the native, extant taxa], four of the native, extinct taxa, and the historically introduced *G. servilis*. A good example of the environmental plasticity of these taxa is the native, extant snail *Succinea caduca,* which is often found in "extremely arid conditions" (Christensen and Kirch 1986:60). *Succinea caduca* appears to thrive in wet conditions as well. It composes nearly the entire assemblage recovered from marsh site 1716 and makes up an important component of the assemblage from marsh site 1715-1.

Five taxa have restricted distributions at Kalaeloa, occurring in 7–12 site assemblages. These include three native, extinct taxa; the aquatic snail *A. nitida;* and the Polynesian introduction, *L. gracilis.* In spatial terms, the Kalaeloa invasion of the Polynesian introduction *L. gracilis* appears to have been much more tentative than that of the historic introduction *G. servilis. Lamellaxis gracilis* is absent from the aquatic sinkholes, the marshes, habitation site 2701-1, and sinkhole 1710-1. In contrast, *G. servilis* is found in every site except the marshes, and where it

TABLE 4

OBSERVED AND EXPECTED LAND SNAIL RICHNESS AT THE KALAELOA SITES

SITE	SITE TYPE	RANGE (o–e)	RICHNESS	MNI
1716	Marsh	−13, −10	2	69
2701-3	"Aquatic" sinkhole	−11, −8	9	2,434
2701-1	Habitation	−10, −8	9	877
2701-8	"Aquatic" sinkhole	−9, −6	14	8,232
1715-1	Marsh	−7, −5	10	214
2711-28	Shallow sinkhole	−7, −4	13	1,843
2717-23	Modified sinkhole	−7, −4	13	1,968
2700-18	"Aquatic" sinkhole	−7, −4	13	2,236
2706-8B	Modified? sinkhole	−7, −4	17	14,579
2706-6E	Sinkhole	−7, −4	17	12,750
9574	Sinkhole	−7, −4	17	11,221
1710-1	Sinkhole	−6, −3	19	21,816
9670-P1	Sinkhole	−6, −3	16	6,435
2700-1	Habitation	−5, −3	14	891
9661-2	Sinkhole	−5, −2	18	9,395
9659-1	Sinkhole	−4, −1	19	9,447
2705-7	Modified sinkhole	−3, −1	16	1,440
9647-2	Sinkhole	−2, −1	22	14,363

co-occurs with *L. gracilis* it is always found in greater numbers.

The 12 remaining taxa have very restricted distributions at Kalaeloa, occurring in one to six site assemblages. These are nearly all native, extinct taxa, most of which are rare in the Kalaeloa assemblages, although the common taxon *L. ovatula* is also very restricted in its distribution.

The habitat most favored by land snails at Kalaeloa was the sinkhole. The most diverse assemblages are from the sinkhole sites, with habitation sites, the marshes, and the "aquatic" sinkholes yielding markedly less diverse assemblages (Table 4). Richness (the number of taxa in an assemblage) is the measure of diversity used here. Richness is strongly correlated with sample size (see Grayson 1984), and a straight comparison of richness might be misleading because the sinkhole sites generally yielded the largest assemblages (Table 4). A Monte Carlo method has been proposed for estimating expected richness for an assemblage of a given size drawn from a specified parent population (Kintigh 1989), and this method was applied to each of the sites using all of the land snails identified at Kalaeloa as the par-

ent assemblage. Controlling for the influence of sample size in this way did little to alter the relative diversity of the sites: the sinkhole sites retained their place as the site type that yielded the richest assemblages (Table 4).

Most sites yielded assemblages that are less rich than expected by the Monte Carlo procedure, as indicated by the negative values in the column labeled "Range (o–e)" in Table 4. The small assemblage from marsh site 1716, for example, was expected to yield as many as 15 taxa or as few as 12, but in fact yielded only two, a difference of 10 to 13 taxa. Only sinkhole site 9647-2, with 22 taxa, yielded an assemblage as rich as expected by the Monte Carlo procedure. This result is due to the uneven distribution of taxa among the excavated sites. The parent assemblage in the Monte Carlo procedure included all of the land snails recovered at Kalaeloa, which comprises assemblages collected from the full range of sampled snail habitats. Many of the excavated sites represent habitats that fall outside the environmental ranges of one or more taxa. Thus, the parent assemblage used in the Monte Carlo procedure represents an unrealistically rich population for comparison with individual sites, and the procedure

overestimates the expected number of taxa at most sites. This feature of the procedure does not diminish its utility in a comparative context and it does highlight the degree of land snail habitat variability at Kalaeloa.

The diversity of the land snail assemblages from the sinkhole sites is partially due to the presence of several taxa that are absent from the assemblages collected at other site types. Most of these are rare taxa with very restricted distributions, including *Pacificella* sp., *Achatinella mustelina, Amastra subrostrata, A. umbilicata,* and the sinistral *Lyropupa.* However, it also includes two abundant taxa, *Pupoidopsis hawaiiensis* and *Nesopupa newcombi.* Other taxa, including *Cookeconcha* sp. and *L. gracilis* are only rarely found outside sinkholes. For these taxa, the sinkholes seem to have been islands of suitable habitat in a sea of harsh, forbidding terrain.

This inference that sinkholes were islands of suitable habitat is based on a model that posits primarily local deposition of land snails in sinkholes, with relatively little input from the surrounding landscape. There are two lines of evidence that support this model. The first comes from the two aquatic sinkhole sites 2701-3 and 2701-8, which contain assemblages composed almost exclusively of the aquatic snail *A. nitida.* At site 2701-3, *A. nitida* makes up between 89% and 98% of the assemblages (Christensen and Kirch 1986:70), and at site 2701-8 the proportions range from 78% to 99% (Christensen 1995:219). Clearly, input from the surrounding landscape is minimal in these instances; some terrestrial taxa are expected to live on the walls of the sinkholes and on the vegetation that grows there. A second line of evidence comes from Layer II at habitation site 2700-1 and from the partially mixed Layer II at habitation site 2701-3, which both yielded assemblages of low diversity composed primarily of abundant, widespread taxa. Both of these layers represent prehabitation deposits, and their land snail assemblages presumably reflect the nature of the land snail faunas on the open plain. Although these assemblages are small, and thus stand a good chance of underestimating the diversity of the fauna, they do not contradict the inference that the land

snail fauna of the open plain was not diverse and was composed of taxa that are widely distributed through a range of environments. We believe this evidence supports the plausibility of the hypothesis that land snail assemblages from sinkholes are derived primarily from the fauna of the sinkhole itself, with little input from the surrounding landscape. However, we recognize the possibility of a washed-in component and point to the continued desirability of detailed study of the depositional processes at work in sinkholes.

LAND SNAIL POPULATIONS IN THE SINKHOLES

Variability in the distribution of land snail taxa among habitats has implications for the interpretation of change over time. The history of land snail populations in sinkholes, to which we now turn, is to a certain extent a collection of individual histories where chance local events might have great effects on the character of the small land snail populations in the sinkholes. Where local events resulted in extirpation of rare taxa, with no well-established populations nearby, purely local changes might permanently alter the character of the land snail population in a sinkhole through the failure of extirpated taxa to recolonize. Alternatively, the diversity in snail habitats through the region opens the possibility that regional environmental change might have different effects on land snail faunas from different habitats. Despite the difficulty of interpreting change in this context, it is worth examining in detail the stratigraphic records of the sinkhole sites. The large size of most sinkhole assemblages and their division into many stratigraphic units yield a record of change that is unparalleled at other site types in the region.

Previous analyses were unable to establish control over the chronology of sediment deposition in the sinkholes. Two recent developments make it worthwhile to reestablish an absolute chronology for the land snail sequences. The first is a model of the marine carbon reservoir (Stuiver et al. 1986, Stuiver and Braziunas 1993) and its local variations (Dye 1994a), which together provide the the-

oretical and empirical justification for calibration of the ^{14}C dates on seabird bones. The second is development of statistical techniques for calibration that make it possible to combine archaeological information, in this case the stratigraphic positions of the dated samples relative to the depositional units defined by Allen (1995), with the information provided by ^{14}C dates (Buck et al. 1991, 1992, 1996). The addition of archaeological information to an analysis generally improves the results of calibration relative to an analysis of the ^{14}C dates alone and yields a result that is archaeologically interpretable.

Another problem is that land snail sequences have been characterized almost exclusively in terms of changes in the relative proportion of native, extinct taxa in the assemblages. The problem with this analysis is that there is not necessarily a relationship between a change in the relative proportion of a taxon in an excavated assemblage and a change in the absolute abundance of that taxon in the environment. (Another problem is the unresolved issue of how many taxa listed as native, extinct are, in fact, locally extinct. This issue is critical for an analysis that relies on changes in the relative proportion of native, extinct taxa.) This is referred to as the problem of "closed arrays" (Grayson 1984:19). The absolute abundance of a taxon whose relative proportion is declining need not be declining; it can be static or even growing. In these latter two instances, all that is required is that the absolute abundance of other taxa in the assemblages increase more

quickly, either through an increase in the population of extant taxa or through the introduction of new taxa that are able to colonize and exploit unoccupied niches.

Diversity is an alternative measure useful in tracking changes over time in fossil assemblages. Diversity has two dimensions: richness refers to the number of taxa in the assemblage; evenness to the distribution of individuals among the taxa. Paleontologists investigate the extinction of a taxonomic class by tracking a decline over time in the richness of some lower-order class. Typically, extinction of a family of organisms is illustrated by the declining number of species in the family. Evenness can be used to the same effect and is potentially more sensitive to stress in a population than is richness; changes in population structure that don't involve extirpation of a taxon will affect evenness measures but not richness. Here we investigate changes in the richness and evenness of native, extinct taxa over time, comparing and contrasting patterns of stasis and change in these measures with changes in the relative proportion of these taxa in the assemblages.

A ^{14}C Chronology

Seven ^{14}C dates on procellariid bone from sinkhole sites 1710-1 and 9659-1 (Table 5) provide the data needed to construct an absolute chronology for the stratigraphic sequences of the Kalaeloa sinkholes. (The ^{14}C age determinations are listed fully here because, to the best of our knowledge, all pre-

TABLE 5

^{14}C DATES ON PROCELLARIID BONE

LAB. NO.	SITE	DEPTH cm below surface	DEPOSITIONAL UNIT	CONVENTIONAL RADIOCARBON AGE	$\delta^{13}C^a$ ‰	EVENT
Beta-11192	9659-1	10–20	Transported	920 ± 100	−17.6	θ_1
Beta-11193	9659-1	20–30	Collapse	1,130 ± 100	−17.5	θ_2
Beta-11194	9659-1	30–40	Collapse	1,370 ± 100	−19.0	θ_3
Beta-11188	1710-1	16–26	Collapse	1,090 ± 100	−23.2	θ_4
Beta-11189	1710-1	26–36	Collapse	1,260 ± 100	−13.8	θ_5
Beta-11190	1710-1	36–46	Collapse	1,730 ± 100	−19.8	θ_6
Beta-11191	1710-1	56–65	Basal	2,320 ± 100	−24.7	θ_7

^{a} Stable carbon isotope ratio.

vious listings are either incomplete or contain errors. The information in Table 5 is from records kept at the Beta Analytic dating laboratory.) Davis designed the dating project carefully, selecting bone samples for dating from each of the three depositional units present at the two sites. Because of this, the dating calibration can integrate the relative stratigraphic information by use of a Bayesian statistical framework (Buck et al. 1991, 1992, 1996). In this framework, information on the relative ages of dated events is used to constrain the calibrated ages of dated samples; the calibrated age of a sample will always be younger than the calibrated age of a sample recovered from a stratigraphically older deposit, regardless of the relative ^{14}C ages of the two samples. Thus, samples that yield inverted ^{14}C ages are restored to their correct relative ages, as this relationship is defined stratigraphically. In addition, adoption of a Bayesian framework provides a way to obtain age estimates for events that were not directly dated, which is useful in this case because it is possible to estimate the ages of depositional unit boundaries. Under the assumption that changes in depositional modes were penecontemporaneous across the region, age estimates for depositional unit boundaries derived from sites 1710-1 and 9659-1 can be extrapolated to the depositional sequences of sinkhole sites that were not dated. A primary objective of the Bayesian ^{14}C calibration reported here was to estimate the calendar ages of the transitions from one depositional unit to the next.

The analysis requires three assumptions: (1) sediment deposition in sinkholes is continuous—there are no hiatuses between or within depositional units; (2) there is no significant hiatus between the death of the bird whose bone was dated and deposition of the bone in the sinkhole; and (3) postdepositional movement of the dated bones through the stratigraphic column was not sufficient to change their positions relative to depositional unit boundaries. We believe that these assumptions are reasonable at this stage of the analysis, but do not believe that they are universally valid. In our view, further study of the dynamics of sediment deposition in sinkholes is clearly warranted.

Given the stratigraphic and ^{14}C information, and the assumptions listed above, it is possible to formulate a model of the relationships among the depositional units and the unknown calendar ages of the events represented by the seven ^{14}C dates. Following standard practice, we indicate the lower boundary of depositional unit i ($i = $ I, II, III) as β_i and the upper boundary as α_i. Let θ_j denote the unknown calendar date B.P. of event j ($j = 1..7$). Then the archaeological and ^{14}C information from the two Kalaeloa sinkholes can be expressed in the form of the following inequalities.

$$\beta_{III} > \theta_7 > \alpha_{III} = \beta_{II} > \theta_6 > \theta_5 > \theta_4 > \alpha_{II} \quad (1)$$

$$\beta_{II} > \theta_3 > \theta_2 > \alpha_{II} = \beta_I > \theta_1 > \alpha_I \quad (2)$$

This model was implemented using the OxCal software package (Ramsey 1995). The seven ^{14}C determinations associated with the θ_i (Table 6) were calibrated with a marine curve (Stuiver and Braziunas 1993) using a Δr value of 110 ± 80 established for the ocean waters surrounding the Hawaiian Islands (Dye 1994a).

Estimates of the calendar ages of the dated events are listed in Table 6 as 2σ highest posterior density regions, along with the calendar ages reported by Davis (1990) and Christensen (1995). The estimates yielded by the Bayesian analysis are younger by 200–700 yr than the age estimates reported by Christensen (1995), as expected. They are, however, very close to the results yielded by Davis' calibration procedure, with two important exceptions. The two exceptions are θ_7, at the early end of the sequence, and θ_1 at the late end of the sequence. The Bayesian estimate for the age of θ_7 is 400–600 yr earlier than Davis' estimate, and the estimate for θ_1 is 200–400 yr later. These differences have the effect of doubling the estimated duration of the interval between the earliest and latest events in the sequence, transforming the 400- to 1,000-yr sequence posited by Davis to one that spans 1,000–2,000 yr.

The 95.4% highest posterior density region yielded by the Bayesian calibration for the estimated age of the boundary of the basal diagenetic and structural collapse deposits is

TABLE 6

ESTIMATED AGES OF THE DATED EVENTS

EVENT	DAVIS	CHRISTENSEN	DYE AND TUGGLE 95.4% HIGHEST POSTERIOR DENSITY REGION
θ_1	A.D. 1265–1490	A.D. 1030	A.D. 1420–1880
θ_2	A.D. 1215–1410	A.D. 820	A.D. 1150–1510
θ_3	A.D. 1030–1325	A.D. 580	A.D. 830–1340
θ_4	A.D. 1255–1415	A.D. 860	A.D. 1200–1540
θ_5	A.D. 1055–1350	A.D. 690	A.D. 1010–1410
θ_6	A.D. 790–1215	A.D. 200	A.D. 580–1060
θ_7	A.D. 445–855	370 B.C.	200 B.C.–A.D. 450

(From Davis [1990], Christensen [1995])
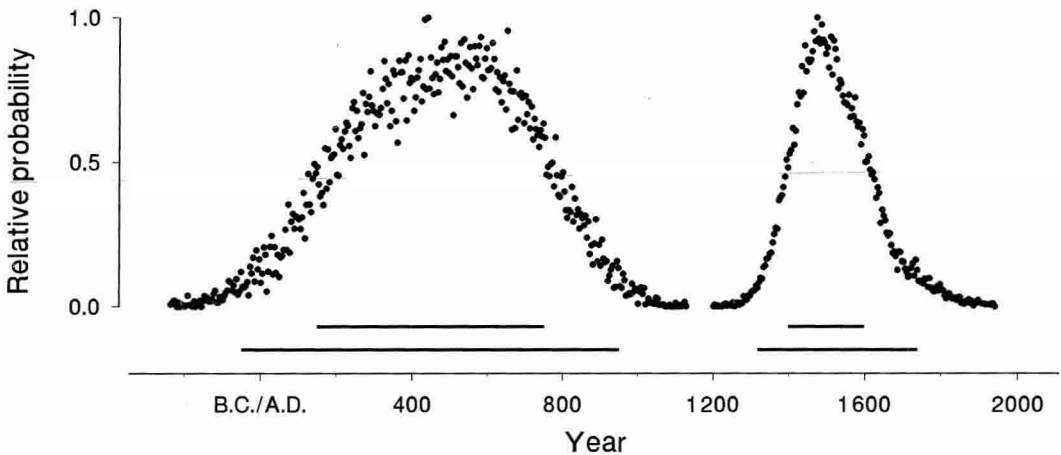
FIGURE 3. Estimated ages of the depositional unit boundaries. *Left*, boundary of the basal diagenetic and structural collapse deposits; *right*, boundary of the structural collapse and transported sediment deposits. Solid lines above the x-axis indicate 67% and 95.4% highest posterior density regions.

50 B.C.–A.D. 950 (Figure 3), an interval that spans current estimates of the date of initial Polynesian colonization of the Islands. The date of colonization has become a point of contention, over which roughly two schools of thought have formed. There is an argument for "early" colonization dating to the A.D. 100–400 range (e.g., Kirch 1985, Hunt and Holsen 1991) and an argument for a "late" colonization, as late as A.D. 600–1000 or even A.D. 800–900 (e.g., Spriggs and Anderson 1993, Athens et al. 1997). Events in the basal diagenetic deposit, exemplified by θ_7, are likely to have occurred either very early in the Polynesian era or before Polynesian colonization of the Islands. Although the early colonization estimate is coeval with the boundary of the basal diagenetic and structural collapse deposits, it is unlikely that Polynesians would have settled or farmed this marginal region soon after colonization (Tuggle 1997), and it is safe to say that events in the basal diagenetic deposits predate significant Polynesian activities at Kalaeloa. It is not possible with the data at hand to estimate with confidence when basal diagenetic sediments were first deposited. That event predates event θ_7, however, and a reasonable

inference is that deposition of the basal dia-genetic deposits began more than 2,000 yr ago.

The 95.4% highest posterior density region for the estimated age of the boundary of the structural collapse and transported sediment deposits is A.D. 1320–1740, an interval that encompasses the last four centuries of the precontact era (Figure 3). The structural col-lapse deposits represent at least the first half of the Polynesian era, but because of uncer-tainties in the date of Polynesian coloniza-tion and in the age estimate of the depositional unit boundary, these deposits might encom-pass nearly the whole of the era. Events in the transported sediment deposits took place either late in the precontact era or in the period after contact. The bone dated for event θ_1, whose estimated age falls late in the Polynesian period, was collected from the bottom half of the transported sediment de-posit at site 9659-1 and is consistent with this assessment.

Changes in Populations of Native, Extinct Taxa

The primary datum in the argument for the extinction and extirpation by Polynesians of land snails at Kalaeloa is a decline over time in the relative proportion of 18 native taxa in excavated archaeological and pale-ontological assemblages. This pattern was first noted by Christensen and Kirch (1986) at site 9574, where native, extinct taxa are absent in the leaf litter on the surface of the sinkhole. Subsequent excavations and analy-ses failed to yield another site where the decline of native, extinct snails was complete. At several sites this decline is pronounced (e.g., 9647-2, 9661-2,), but at others the de-cline is more moderate (e.g., 1710-1, 9659-1, 9670-P1). At most sites the relative propor-tion of the native, extinct taxa never declines to nil. Native, extinct taxa are absent only in the cultural layer (II) at site 2701-1 and in the leaf litter of sinkhole site 9574.

Because of the interpretive difficulties in-herent in the use of relative proportions, we analyzed change over time in the diversity of the land snail assemblages, using measures of richness and evenness to characterize diver-sity. Richness is a straightforward measure that can take on integer values between 0 and the maximum number of taxa in the assem-blage. Evenness is more difficult to quantify and several different measures have been proposed (Bobrowsky and Ball 1989). The measure used here, called H/H_{max} by Kintigh (1989:29), can take on real values between 0.0 and a maximum that depends on the richness of the assemblage, but usually is between 2.0 and 3.0. In an extinction event, both richness and evenness decline to 0.

The richness and evenness measures on the Kalaeloa snail assemblages estimate the diversity of the land snail faunas that existed within the catchments of the sites where they were deposited. Like richness measures, evenness measures are sensitive to sample size, and both measures can yield poor esti-mates of faunal diversity if sample sizes are small (Grayson 1984:158 ff.). The Monte Carlo technique used to estimate expected richness, discussed above, can also estimate expected evenness (Kintigh 1989), and esti-mates of expected richness and evenness were calculated for each of the land snail assem-blages, using the site assemblage as the parent population from which samples were drawn. Use of the site assemblage, rather than the Kalaeloa assemblage, as the parent popula-tion helps to control for differences in the diversity of land snail faunas among different habitats.

Figures 4–9 show comparisons of the rela-tive proportions of native, extinct taxa over time with their expected richness and even-ness at six sinkhole sites. These include the two sinkhole sites analyzed by Christensen and Kirch (1986) and four of the eight sink-holes excavated by Davis (1990) for which land snails were identified (Christensen 1995); the sediments of these four sinkholes were analyzed by Allen (1995), and it is possible to assign estimated ages to their depositional unit boundaries. Error bars for relative pro-portions are based on one standard deviation counting errors, calculated as the square root of sample size. Richness and evenness are expressed on the figures as the difference be-tween the observed values and the expected

values generated by the Monte Carlo method. The error bars for richness and evenness represent 80% confidence intervals. It is rare at Kalaeloa to find an assemblage that is as diverse as expected by the Monte Carlo method, and most of the plotted differences between observed and expected diversity measures are negative. This is because most sinkhole sites show evidence for change over time in the land snail fauna, including episodes of colonization and extirpation of taxa, which affect richness, and changes in relative proportions of taxa, which affect evenness. Because any single assemblage contains material from only a portion of the time that materials were deposited in the sinkhole, use of the site assemblage as the parent population in the Monte Carlo method often overestimates the diversity of individual assemblages.

The distributions of the introduced taxa *L. gracilis* and *G. servilis* are illustrated in the bottom panel of the figures because of their use by Christensen and Kirch (1986) as index fossils, as discussed above. They are plotted on a logarithmic scale as MNI + 1, to compensate for the wide variation in counts from one assemblage to the next, many of which include nil values.

SITE 9574. Sinkhole site 9574 is the type site for a decline in native, extinct land snails at Kalaeloa. Christensen and Kirch (1986) divided the 85-cm-deep stratigraphic column into three layers and collected 10 samples for land snail identification. Layer I, a thin, black, relatively loose A_0 and A_1 horizon, yielded a single sediment sample for land snail identification; Layer II, a 30-cm-deep, brown, silt and sand deposit with angular fragments of limestone, yielded three samples; and Layer III, a 50-cm-deep, reddish yellow deposit of limestone breccia in a matrix of silt and sand, yielded five samples. A single sample collected from the leaf litter above Layer I represents the modern land snail fauna of the sinkhole.

Christensen and Kirch (1986) argued for a period of increased change and decline in the relative proportion of native, extinct taxa beginning in Layer II and continuing through

to their extirpation. This argument is based on the following data (Figure 4, *top*). Native, extinct taxa make up 71 ± 3% of the land snail assemblage in the bottom sample from Layer III at the base of the stratigraphic column and rise to a maximum of 85 ± 6% in the top two samples from this layer. This high level is maintained through the bottom two samples in Layer II, but it declines in the top sample to 67 ± 2%. The error bars indicate that this proportion is not different from the proportion at the base of the stratigraphic column, and the relative proportion of native, extinct taxa in Layers II and III can be characterized as fluctuating slightly between about 65% and 91% of the total assemblage. The relative proportion of native, extinct taxa does decline in Layer I, where they make up only 20 ± 1% of the assemblage. There are no native, extinct taxa in the leaf litter.

The diversity measures for the native, extinct taxa at site 9574 show no sign of a decline through the three layers of the stratigraphic column, and it is not until the leaf litter, when both measures decline to 0, that the diversity measures indicate any stress in the native, extinct land snail fauna.

It is not possible to correlate the stratigraphic layers with Allen's (1995) depositional units and there are no ^{14}C dates from the site, so absolute dates cannot be assigned to changes in the land snail assemblages. Christensen and Kirch (1986) believed that Layer II was deposited, at least in part, during the Polynesian period, based on the occurrence of small numbers of *L. gracilis* shells in the top two samples from the layer. This inference is by no means secure, however, as discussed below. The only layer that is securely dated is Layer I, whose rich assemblage of Polynesian and historically introduced land snail shells indicates that it was laid down after Polynesian colonization and into the postcontact period.

Christensen and Kirch (1986) correlated the onset of the decline in relative proportion of native, extinct taxa with Polynesian influence. This inference was based on the stratigraphic distribution of various animals introduced by Polynesians, including the land
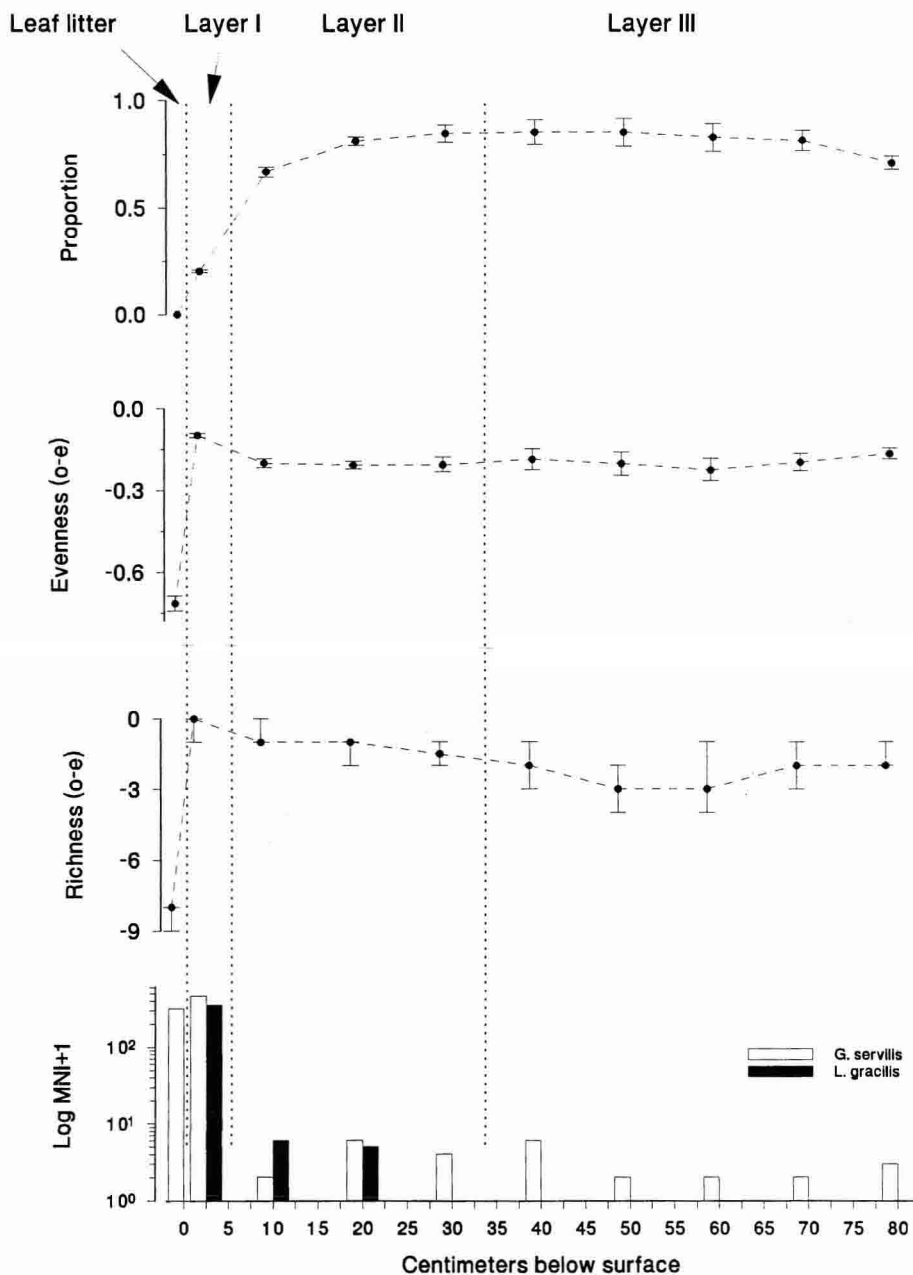
FIGURE 4. Native, extinct land snail taxa at sinkhole site 9574. *Top,* relative proportion with 1σ errors; *second from top,* difference of observed and expected evenness with 80% confidence intervals; *third from top,* difference of observed and expected richness with 80% confidence intervals; *bottom,* frequency of introduced taxa (note the logarithmic scale).

snail *L. gracilis.* As the bottom panel in Figure 4 shows, however, the correlation of the decline with the introduction of *L. gracilis* is not particularly clear. *Lamellaxis gracilis* is first present in Layer II, but it occurs as five or fewer individuals in the two Layer II assemblages in which it appears, and is not well represented until Layer I, when the historically introduced taxon *G. servilis* is also first present in large numbers. Because of the pervasive mixing of small numbers of land snails down through the stratigraphic column at sites excavated subsequently (Christensen 1995), the presence of a few shells of *L. gracilis* in Layer II does not necessarily indicate this snail's colonization of the sinkhole at the time the Layer II sediments were deposited. The distribution of *G. servilis* down to the base of the stratigraphic column is apparently not due to mixing and was explained as contamination of the sampled sediments by living snails that colonized the excavated portion of the sinkhole before the land snail samples were collected (Christensen and Kirch 1986:63). (Curiously, *L. gracilis* is absent in the leaf litter along with the native, extinct taxa. The other introduced taxon, *G. servilis,* is the dominant component of the leaf litter assemblage.)

The history of the native, extinct land snail fauna that emerges from this analysis is much different than the history posited by Christensen and Kirch (1986) based on a consideration of relative proportion. The population of native, extinct land snails at site 9574 is stable until the loose sediments of Layer I were deposited, at which time the relative proportion of native, extinct taxa falls to levels not experienced previously. This is stratigraphically coeval with colonization of the sinkhole by the historically introduced *G. servilis,* and possibly by the Polynesian introduction *L. gracilis,* as well. The diversity of the native, extinct land snail population shows no stress in the population at this time, but declines suddenly after Layer I was deposited. This indicates that a drastic change leading to extirpation of native, extinct taxa at the site belongs either to the late precontact period or more likely to the postcontact period. There are no data here that indicate that changes in the native, extinct land snail population were caused by Polynesian settlement, rather than by the major environmental changes in the region documented historically.

SITE 9670-P1. Sinkhole site 9670-P1 was also analyzed by Christensen and Kirch (1986). The deposits at site 9670-P1 are much shallower than at site 9574, reaching a maximum depth of 27 cm. The stratigraphic sequence at the site is divided into three layers. One sediment sample for land snail identification was collected from Layer I and five samples were collected from Layer II. No samples were taken from Layer III.

Christensen and Kirch (1986) hypothesized, on the basis of the distribution of *L. gracilis* to the base of the stratigraphic column, that the stratigraphic sequence correlated with the upper portion of the sequence at site 9574 (Christensen and Kirch 1986:72). The land snail sequence at site 9670-P1 differs from the upper portion of the sequence at site 9574, however, in that the relative proportion of native, extinct taxa declines moderately up through the stratigraphic column and native, extinct taxa never disappear from the assemblages. Instead, they represent $40 \pm 3\%$ of the total land snail assemblage in Layer I. There is a slight decline in richness between the sample from the base of the stratigraphic column and the two samples from the top of the column, but there is no change in evenness.

As was the case with site 9574, it is not possible to correlate the layers at site 9670-P1 with the depositional units of Allen (1995). The distribution of the introduced taxa *L. gracilis* and *G. servilis* through the stratigraphic column is consistent with the relative timing of their introductions and supports the inference that Layer II was laid down from the Polynesian period through to the early postcontact era, although the small number of *L. gracilis* shells in the assemblages from the bottom half of Layer II suggests some interpretive caution (*pace* Christensen and Kirch 1986:64). A plausible argument could be made for deposition of the bottom half of Layer II during pre-
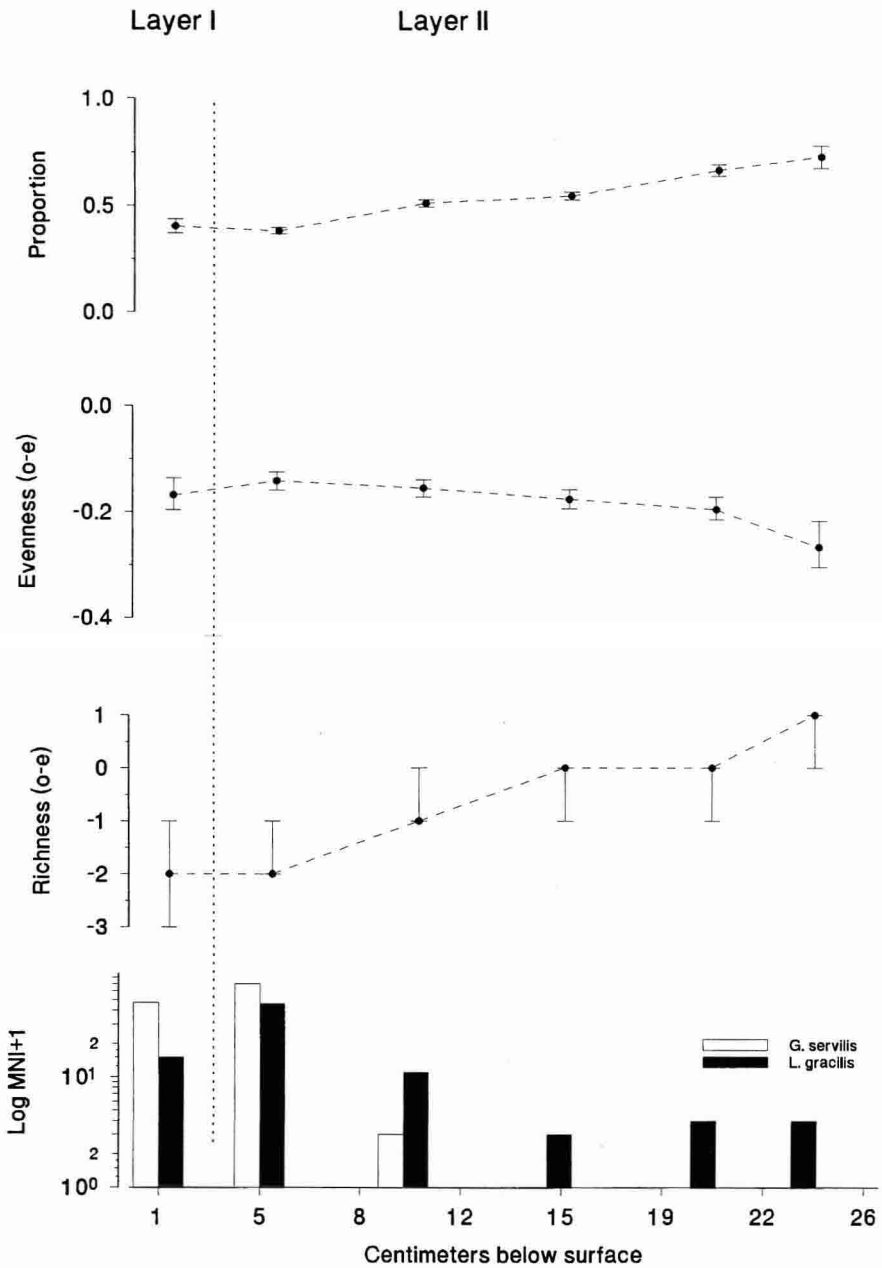
FIGURE 5. Native, extinct land snail taxa at sinkhole site 9670-P1. *Top*, relative proportion with 1σ errors; *second from top*, difference of observed and expected evenness with 80% confidence intervals; *third from top*, difference of observed and expected richness with 80% confidence intervals; *bottom*, frequency of introduced taxa (note the logarithmic scale).

Polynesian times, with subsequent downward mixing of a few *L. gracilis* shells. Lacking ^{14}C dates, it is not possible to discriminate between these alternative hypotheses.

It is difficult to see in these data any effect on the native, extinct taxa that can be attributed to Polynesian influence. Christensen and Kirch (1986) chose to focus their analysis on the decline in the relative proportion of just two native, extinct taxa *(O. uberta* and *E. kalaeloana)* and increases in three native, extant taxa *(Lamellidea* spp., *Tornatellides* spp., and *S. caduca),* citing these trends as supporting evidence for the decline in native, extinct taxa documented at site 9574. The implication of this choice is that differences in the depositional histories of land snails at sites 9574 and 9670-P1 reflect a deviation at site 9670-P1 from a widespread pattern, rather than simply an expression of general variability in land snail faunas among the Kalaeloa sinkholes.

SITE 9659-1. Site 9659-1 was excavated by Davis (1990). His analysis indicated that all of the sinkholes he excavated at Kalaeloa "yielded similar patterns of change in the snail assemblage" (Davis 1990:197) and that this change was that described by Christensen and Kirch (1986) at the land snail "type site," sinkhole site 9574. Davis (1990) illustrated the pattern of change with the land snail sequence from an excavation under the overhang at sinkhole site 9659-1, which he believed showed the pattern most clearly. The ~50-cm-thick sediment deposit was excavated in seven arbitrary 5-cm and 10-cm levels that were later assigned to four layers (Davis 1990:182). Allen (1995) recognized three depositional units in the four layers. A total of 10 sediment samples (Christensen 1995:245) was collected for land snail identification. [The bar graphs in Davis (1995:199) and Davis (1990:438) indicate 15 and 13 samples, respectively, but there is no published record of samples identified in addition to the 10 identified by Christensen (1995).] The ~21-cm-thick gravelly loam of the transported sediment deposit (Layers I and II) yielded three sediment samples for snail identification; four samples were taken from the

15–20 cm of very gravelly, coarse sandy loam of the structural collapse deposit (Layer III); and three samples were collected from the 5–10 cm of gravelly, very coarse sandy loam of the basal diagenetic deposit (Layer IV and Layer V from Square 4 in the exposed portion of the sinkhole).

There are two periods of marked decline in the relative proportion of native, extinct taxa in the assemblages (Figure 6), although the sequence itself is characterized by a first-order decrease in relative proportion over time. The first period of decline occurs at the base of the stratigraphic column, where the proportion drops from 100-11% to 76 ± 4%. The second begins at the top of the structural collapse deposit, where the relative proportion is 65 ± 3%, and continues through to the base of the transported sediment deposit, where the relative proportion drops to 22 ± 1%. Native, extinct taxa are well represented at the top of the stratigraphic column, making up 19 ± 2% of the assemblage there. [Davis described this assemblage as consisting "entirely of native survivors and more recently introduced snails" (Davis 1990:198). The use of the term "survivors" is potentially confusing here, because it seems to indicate that only native, extant taxa remain. In fact, both native, extinct taxa and native, extant taxa are present in the assemblage.]

In contrast to the moderate first-order decline in the relative proportion of native, extinct taxa, richness and evenness measures indicate an increase in diversity through to the base of the transported sediment deposit. Richness declines in the transported sediment deposit and evenness dips deeply in the middle of the deposit because of a sudden peak in *N. newcombi* shells, which make up 25.5% of the assemblage (Christensen 1995:246). These data indicate that there was some stress in the population of native, extinct taxa by the middle of the transported sediment deposit.

This sinkhole was dated by Davis, and age estimates can be assigned directly to depositional unit boundaries, as discussed above. The distributions of introduced taxa appear to substantiate the chronology derived from ^{14}C dates. *Gastrocopta servilis* is found only
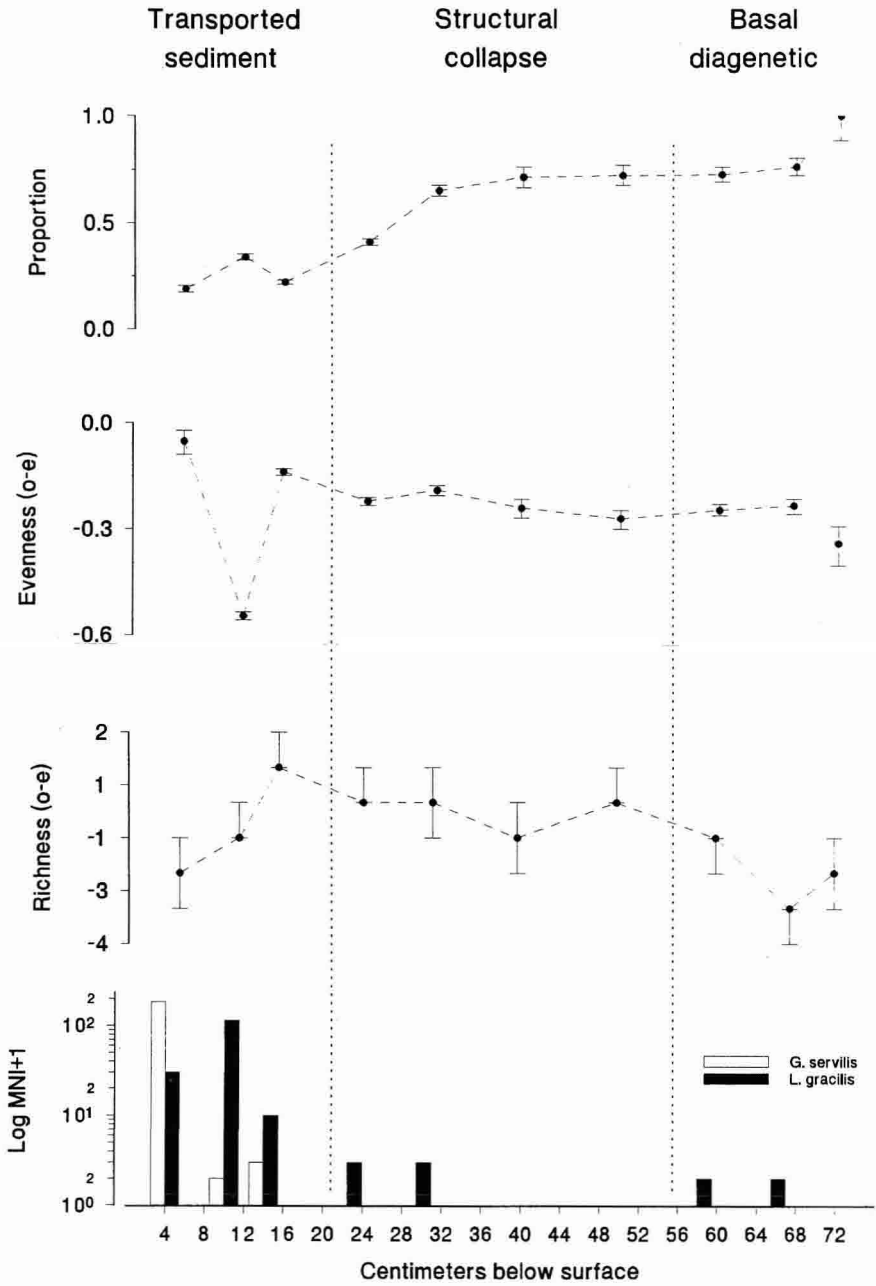
FIGURE 6. Native, extinct land snail taxa at sinkhole site 9659-1. *Top,* relative proportion with 1σ errors; *second from top,* difference of observed and expected evenness with 80% confidence intervals; *third from top,* difference of observed and expected richness with 80% confidence intervals; *bottom,* frequency of introduced taxa (note the logarithmic scale).

in the transported sediment deposit and in large quantities only in the top-most assemblage, so the lower boundary of the unit appears to be late precontact in age. *Lamellaxis gracilis* also occurs most frequently in the transported sediment deposit, but is found in scant numbers in the structural collapse and basal diagenetic deposits as well. The presence of this taxon in deposits laid down in the era before Polynesian colonization and its discontinuous distribution through the stratigraphic column suggest that the few shells in the basal diagenetic deposit are intrusive. [Christensen (1995:245) reported nonapical fragments of *L. gracilis* from the lower two samples in the structural collapse deposit.] Although the four MNI of *L. gracilis* at the top of the structural collapse deposit might indicate when the snail colonized sinkhole 9659-1, it is also possible that these few shells, like the few shells in the basal diagenetic deposit, are intrusive. If this latter is the case, then *L. gracilis* was first deposited in the transported sediments, either late in the precontact era or early in the postcontact period.

The timing of changes in the land snail assemblages at site 9659-1 casts doubt on the proposition that Polynesian activities were responsible for the decline of native, extinct taxa. First, the relative proportion of these taxa declines over the entire stratigraphic sequence. The onset of this first-order decline is likely to predate the fifth century A.D. (Figure 3). Second, the diversity of the native, extinct land snail population does not decline until after deposition of the transported sediments began. This depositional unit began either very late in the precontact era or in the postcontact period (Figure 3). Finally, regardless of when the population of native, extinct taxa began to decline, either late in the precontact era or in the postcontact period, the cause of the decline was insufficient to extirpate them at the site. At the top of the stratigraphic column, the population of native, extinct taxa is as diverse as it was in assemblages from both the Polynesian and pre-Polynesian periods.

SITE 1710-1. Sinkhole site 1710-1 was excavated in four layers to a maximum depth of 76 cm, a depth comparable with the deep deposit in site 9574 (Davis 1995). Land snails were identified in 16 sediment samples from the site. The transported sediment deposit (Layers I and II), a dark, organic loam, yielded four samples; the structural collapse deposit (Layers IIIa and IIIb) yielded nine samples; and the basal diagenetic deposit yielded three samples. Avian bones from the site were dated, and boundaries between the three depositional units can be assigned absolute dates as discussed above.

Assemblages from the basal diagenetic deposit are characterized by an abundance of the aquatic snail *A. nitida*, and this accounts for the low relative proportion of native, extinct taxa in these assemblages (Figure 7, *top*). Davis believed that the sinkhole was at least partially flooded throughout the period represented by this unit (Davis 1990:200), and the basal diagenetic deposit assemblages strongly resemble assemblages from the low-lying, "aquatic" sinkholes. The structural collapse deposit marks the beginning of terrestrial land snail dominance in the deposits, but native, extinct taxa never dominate the assemblages here as they do in the older assemblages of other sinkholes. Native, extinct taxa make up between $35 \pm 2\%$ and $51 \pm 2\%$ of the structural collapse deposit assemblages, with a small dip in the top two assemblages. The population of native, extinct taxa does undergo a change at the boundary of the transported sediments, where their relative proportion drops to approximately 22% of the assemblage. It remains at this level to the top of the stratigraphic column.

Diversity measures indicate that the native, extinct taxa were not under stress during the period represented by the basal diagenetic and structural collapse deposits. Both diversity measures rise slightly over this time. The transition to transported sediments saw a marked decline in diversity, with both measures showing a drop from previous levels.

The decline in diversity occurs in either the late precontact or postcontact periods; ^{14}C dating does not distinguish between these possibilities (Figure 3). The distributions of the introduced snails are also little help in this regard. The Polynesian introduction *L.*
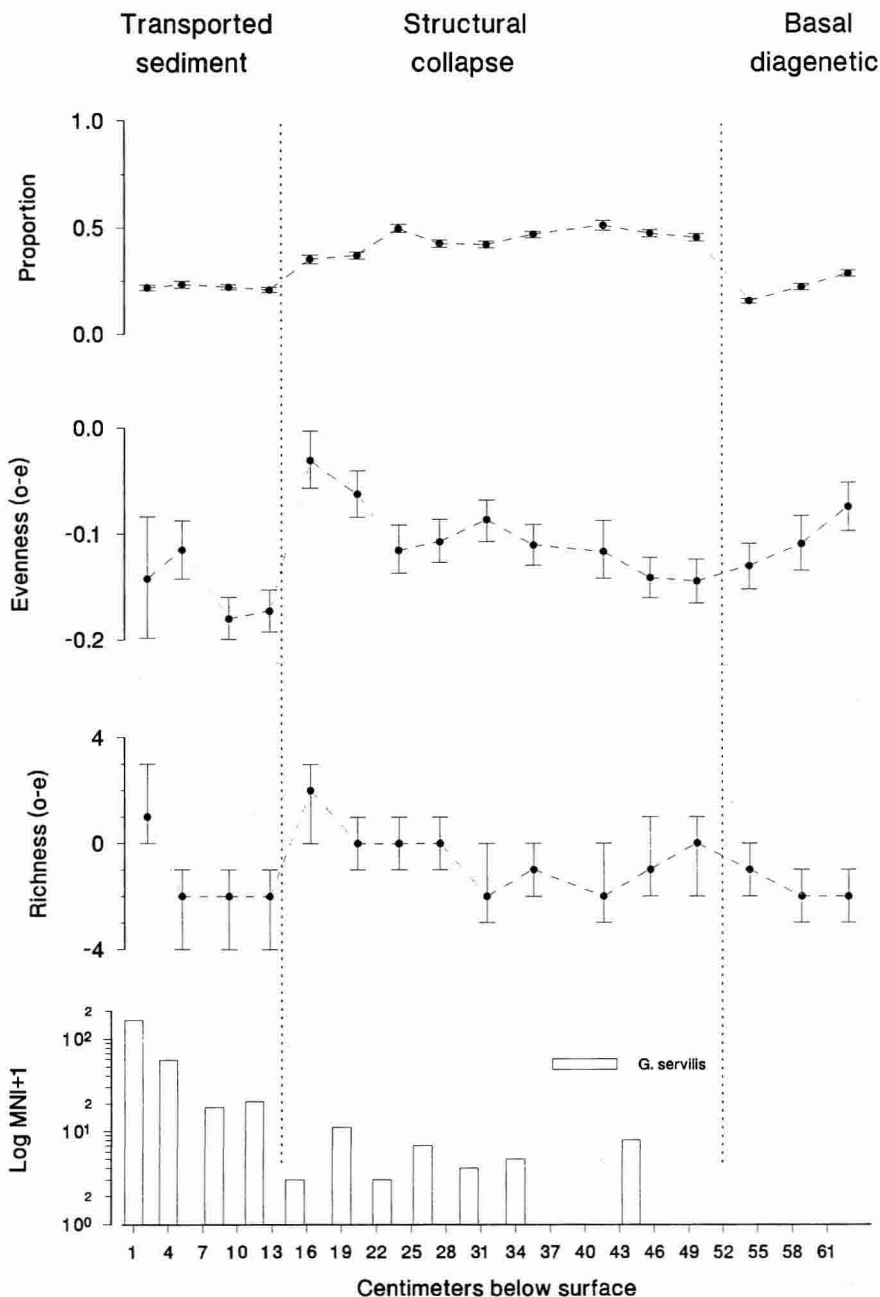
FIGURE 7. Native, extinct land snail taxa at site 1710-1. *Top*, relative proportion with 1σ errors; *second from top*, difference of observed and expected evenness with 80% confidence intervals; *third from top*, difference of observed and expected richness with 80% confidence intervals; *bottom*, frequency of *G. servilis* (note the logarithmic scale). *Lamellaxis gracilis* was not recovered from this site.

gracilis is absent from the site. The occurrence in small numbers of the historically introduced *G. servilis* in most of the structural collapse deposit assemblages is almost certainly the result of mixing and gives some indication of the potential magnitude of this problem. The taxon is present throughout the transported sediment deposit, and this might be interpreted as an indication that these deposits are postcontact in age. Although the absolute numbers of this taxon rise a bit in the lower two assemblages from the transported sediment deposit, their relative proportion does not increase until the top two assemblages. Thus, an argument could also be made that all of the *G. servilis* shells found below the top two assemblages of the transported sediment deposit are intrusive.

SITE 9647-2. Excavations at site 9647-2 revealed 65 cm of deposit in four layers beneath a cobble fill (Davis 1995). The transported sediment deposits (Layers II, III, IVa, and a portion of Layer IVb [The layer designations used here are those reported by Davis (1995) and by Allen (1995). They designated the rock fill at the site as Layer I; the first sediment deposit is Layer II. The layer designations used by Christensen (1995) ignored the rock fill and began with Layer I at the top of the sediment deposit.]) yielded nine sediment samples for land snail identification; four samples were taken from the structural collapse deposits (Layer IVc and a portion of Layer IVb) [The Layer IVb sample was taken adjacent to the sample column (Christensen 1995: 243)]; and a single sample was collected from the basal diagenetic deposit (Layer V) [This sample was taken adjacent to the sample column (Christensen 1995:243)]. A sample was also taken from the leaf litter at the surface of the deposit.

The assemblages from site 9647-2 reveal two periods of rapid decline in the relative proportion of native, extinct taxa. At the base of the stratigraphic column, native, extinct taxa make up $96 \pm 4\%$ of the assemblage from the basal diagenetic deposit (Figure 8). This is followed by a large drop to $50 \pm 3\%$ at the base of the structural collapse deposit. The structural collapse deposit is charac-

terized by increases in the relative proportion of native, extinct taxa, which reach $97 \pm 6\%$ at the top of the unit. Relative proportions decline slowly through the bottom three assemblages in the transported sediment deposits. The assemblage from 22 to 24 cm below surface yielded $59 \pm 3\%$ native, extinct taxa, a proportion slightly greater than that of the assemblage from the base of the structural collapse deposit. The second period of rapid decline brings the proportion to $14 \pm 1\%$, and it remains in the range of 7–17% through to the top of the stratigraphic column and into the leaf litter.

The first period of rapid decline in relative proportion of native, extinct taxa is mirrored by a decline in diversity. The assemblage of native, extinct taxa from the basal diagenetic deposit is the most diverse from the site. Richness and evenness both decline through the transition from basal diagenetic to structural collapse deposits. The second period of rapid decline in relative proportion of native, extinct taxa is accompanied by a slight drop in richness, but this is barely detectable with the materials and techniques at hand. Both diversity indices indicate little change through the transported sediment deposit, which yields values of the indices that are within the ranges seen previously in the structural collapse deposits.

Under the assumption that depositional units are penecontemporaneous among sinkholes, the first period of decline in the population of native, extinct taxa at site 9647-2 took place in the early centuries of the first millennium A.D. and the second in the late precontact or postcontact period. The stratigraphic distribution of the Polynesian introduction *L. gracilis* appears to contradict the estimated age of the second period of decline, however. The interpretation of the stratigraphic distribution of introduced snails is not straightforward, and the assemblages yield evidence for disturbance down to the base of the stratigraphic column. A single *L. gracilis* individual is present in the assemblage from the basal diagenetic deposit [Nonapical fragments of *G. servilis* were also found in this assemblage (Christensen 1995:240)], and it is found with *G. servilis*
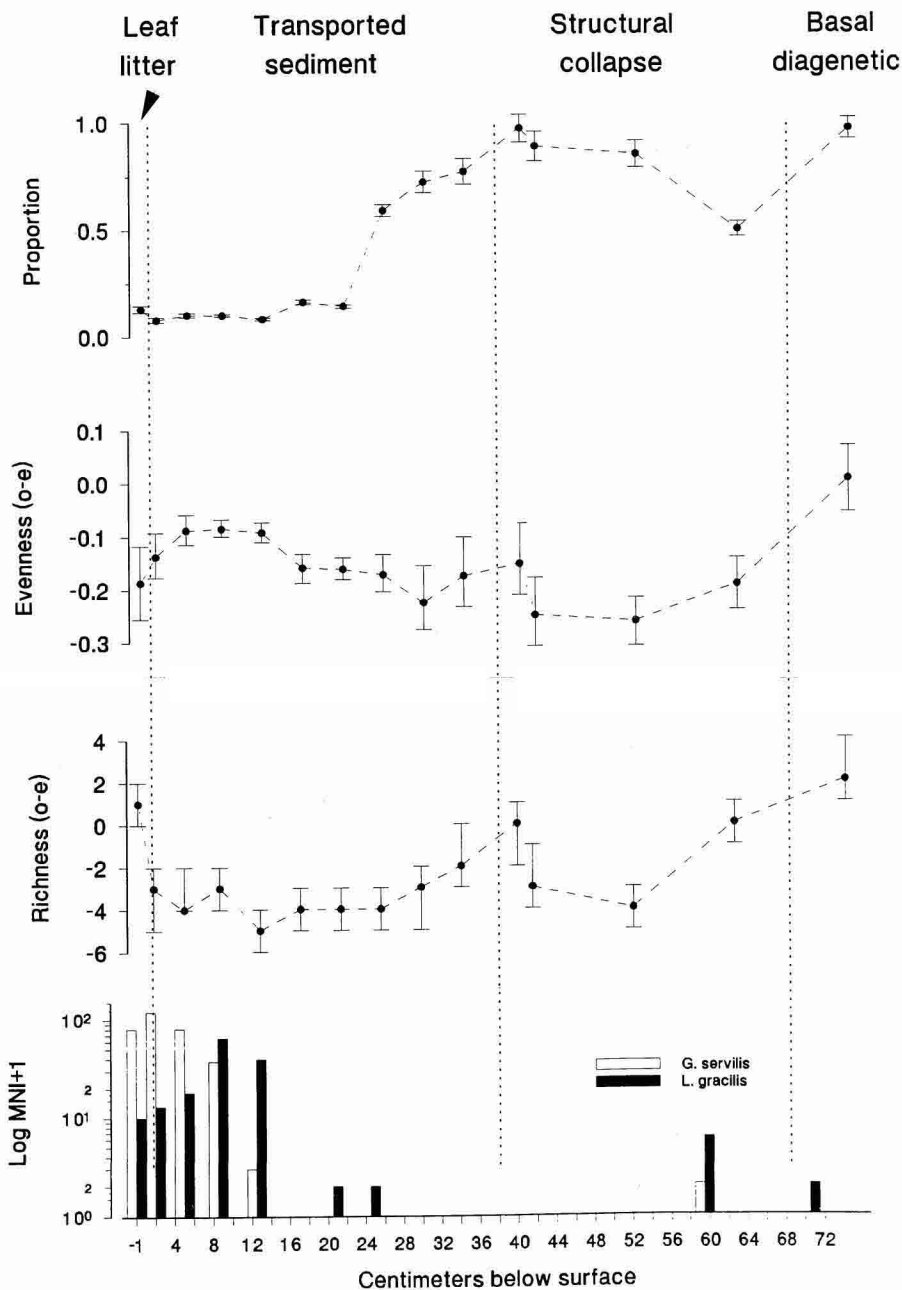
FIGURE 8. Native, extinct land snail taxa at sinkhole site 9647-2. *Top,* relative proportion with 1σ errors; *second from top,* difference of observed and expected evenness with 80% confidence intervals; *third from top,* difference of observed and expected richness with 80% confidence intervals; *bottom,* frequency of introduced taxa (note the logarithmic scale). The sample from the basal diagenetic deposit was taken adjacent to the sampling column at a depth of 45–60 cm below surface. This sample has been given an arbitary depth of 70 cm below surface to keep the deposits in their correct stratigraphic order.

deep in the structural collapse deposits. These contexts are stratigraphically inferior to four assemblages in which both taxa are absent. Single individuals of *L. gracilis* are found midway through the transported sediment deposits, but it is not until the top of the stratigraphic column that either introduced taxon is found in large numbers. The mode of the *L. gracilis* distribution is earlier than that of *G. servilis,* but both modes are later than the second period of decline in relative proportion of native, extinct taxa at the site. If the assumption of penecontemporaneity in the depositional unit boundaries holds, then *L. gracilis* was not established at site 9647-2 until very late in the precontact period or more likely the postcontact period. [Allen suggested that the formation of the site 9647-2 sinkhole might have been later than other sinkholes in the region, based on the low density of bird bones and the apparent on-going structural collapse at the site (Allen 1995:43). One or two ^{14}C dates from the base of the stratigraphic column would likely provide the evidence needed to discriminate between this hypothesis and the hypothesis that depositional regimes were penecontemporaneous throughout the region.] If the penecontemporaneity assumption is violated at site 9647-2, then all that can be said is that the second period of decline predated establishment of an *L. gracilis* population at the site.

SITE 9661-2. The sediment deposits of site 9661-2 were excavated in six arbitrary 6-cm and 10-cm levels (Davis 1995:331). [The sediment deposits at site 9661-2 were capped by limestone rubble that was excavated as Level 1 and assigned to Layer I.] The six sediment levels were later assigned to four natural layers and grouped into two depositional units. Basal diagenetic and structural collapse deposits are present at the site, but transported sediment deposits are absent. Seven samples for land snail identification were recovered from the structural collapse deposit, and a single sample was taken from the basal diagenetic deposit. A sample was also collected from the leaf litter at the surface of the sediment deposit.

The relative proportion of native, extinct

taxa declines steadily from the base of the stratigraphic column, where they make up 76 ± 5% of the assemblage, to its top, where the proportion is reduced to 9 ± 1% (Figure 9). The assemblage from the leaf litter shows a slight increase in relative proportion to 20 ± 4%.

Richness and evenness measures indicate a decline in the diversity of the native, extinct land snail population near the top of the structural collapse deposit. The population of native, extinct taxa never regains its richness, but evenness recovers to previous levels by the top of the deposit and maintains this level into the leaf litter. Fluctuations in diversity in the early portion of the sequence are within the range of estimation error.

Both of the introduced land snails are found throughout the structural collapse deposit, and a few individuals of *G. servilis* were recovered from the basal diagenetic deposit. If the depositional units at this site were correctly identified, then the presence of large numbers of *G. servilis* in the structural collapse deposit indicates substantial mixing of the stratigraphic column (cf. Christensen 1995:252–253). Otherwise, the presence of *G. servilis* through most of the structural collapse deposit indicates a postcontact age for the upper boundary of the depositional unit and a very recent age for the decline in richness of native, extinct taxa at the site.

Although the timing of events at site 9661-2 is problematic, the site shows a common pattern of change in native, extinct land snails. Against a background of steady decline in their relative proportion beginning in the basal diagenetic deposit, diversity indices remain stable until the recent end of the sequence. The decline in diversity at site 9661-2 takes place at a date that is likely to fall in the postcontact period, if the large numbers of *G. servilis* are any indication, but the decline cannot be dated with sufficient precision to rule out a date in the precontact era.

DISCUSSION AND CONCLUSIONS

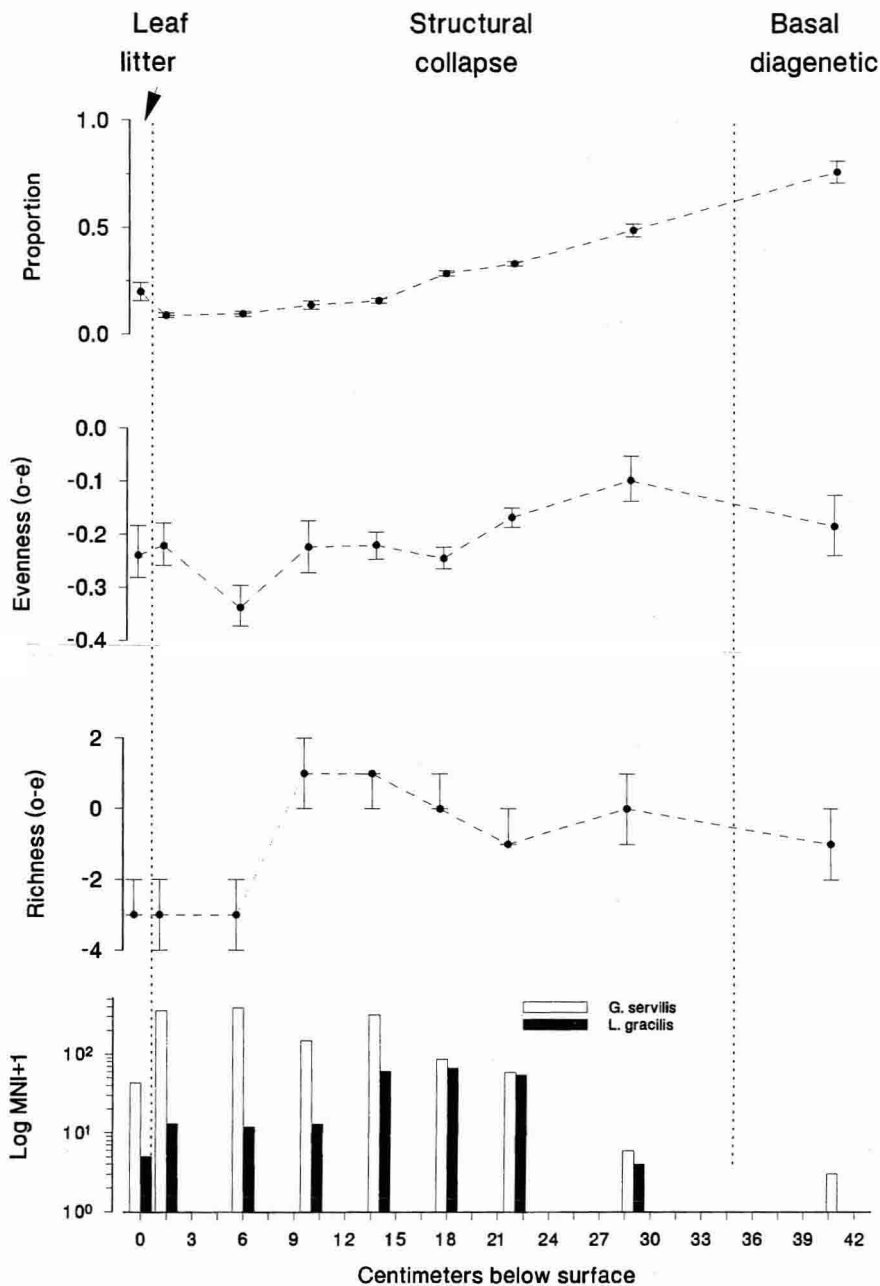Sinkhole site 9574 is the type site for the hypothesis that Polynesian activities led to

FIGURE 9. Native, extinct land snail taxa at site 9661-2. *Top*, relative proportion with 1σ errors; *second from top*, difference of observed and expected evenness with 80% confidence intervals; *third from top*, difference of observed and expected richness with 80% confidence intervals; *bottom*, frequency of introduced taxa (note the logarithmic scale). The site lacks a transported sediment deposit.

the extirpation of native, extinct land snail taxa at Kalaeloa. There is a decline in the relative proportion of native, extinct taxa observed at site 9574 and this proves to be a regional phenomenon, which is present at all sites. The decline at site 9574 appears suddenly and relatively late in the sequence after a long period of relative stasis, and it led to the extirpation of native, extinct taxa from the sinkhole. In this regard site 9574 is unique. The pattern of sudden, late change leading to extirpation discovered there is unlike that of any of the region's sinkholes excavated subsequently. These features of the site's land snail sequence, which are crucial for the argument that Polynesians were responsible for extirpation of native, extinct taxa, are not found elsewhere.

Our analyses indicate a regional pattern of long-term decline in the relative proportion of native, extinct taxa. [At site 9574, where this long-term trend in relative proportions is not evidenced, an analysis by proportional similarity matrix of the entire assemblage clearly indicates a gradual, directional change beginning at the base of the stratigraphic column (Christensen and Kirch 1986: fig. 3).] At all other sinkhole sites, except site 1710-1, whose basal deposits were laid down in a flooded environment, this decline begins at the base of the stratigraphic column and continues, as a first-order trend, through to the top of the column. Dating the onset of this long-term, first-order decline is critical to understanding its causes. On the basis of the available ^{14}C dating of the sinkhole deposits, the decline began before the structural collapse deposits began to form, sometime before 50 B.C.–A.D. 950. This is perhaps 1,000 yr before human settlement of the 'Ewa Plain, which is argued to be the fourteenth century A.D. at the earliest (Davis 1990, Athens et al. 1997, Tuggle 1997), although temporary base shelters for fishing expeditions might have been established somewhat earlier. The archaeological community is divided over the date Polynesians colonized Hawai'i, but if the estimate for a "late" colonization at the end of the first millennium A.D. proves correct, then the long-term decline probably began before humans set foot on the island. In

either case, any human role in this decline is extremely unlikely.

We propose that lowering of the water table, probably caused by a drop in local sea level from its mid-Holocene high stand, is the explanation for the long-term decline in the relative proportion of native, extinct taxa in the Kalaeloa sinkholes. [Lowering of the water table frequently has been mentioned in regard to environmental change on the 'Ewa Plain (Davis 1990, Allen 1995, Christensen 1995), although this is usually attributed to causes other than sea level change.] The mid-Holocene high sea stand on O'ahu is believed to have culminated 6,000–4,000 yr ago at a height of 1.6 ± 0.45 m, with a drop to present levels about 2,000 yr ago (Athens and Ward 1991, 1993, Fletcher and Jones 1996), a period that overlaps deposition of basal diagenetic sediments in the sinkholes. The effects of this process show most clearly in the land snail sequence at sinkhole site 1710-1, in which the basal diagenetic deposits are dominated by the aquatic taxon *A. nitida*. These deposits today stand a bit higher than 1.5 m above mean sea level and only 1 m above the modern high water table (Davis 1995:355) and would have been underwater during most of the mid-Holocene high stand. The proportion of *A. nitida* declines markedly in the succeeding structural collapse and transported sediment deposits, as the water table dropped and the sinkhole environment became drier. Wetter conditions early in the regional sequence are also indicated by the wet forest snail taxa recovered from the basal diagenetic deposits at site 9647-2. Similar effects would have been felt at sinkholes throughout the region. Thus, one component of the decline in relative proportion of native, extinct taxa does not indicate drastic ecological disturbance, and we interpret this trend as indicative of ecological succession in the context of natural environmental change. [Sea-level decline is unlikely to have been the only environmental change under way in the region. Other evidence indicates a pattern of increased rainfall, and possibly onset of El Niño–southern oscillation (ENSO) conditions (Athens et al. 1997). If this were the case, it might have mitigated the effect of the

decline of the water table on the land snail taxa, producing a more gradual change than would otherwise have been the case.]

The relatively great diversity of land snail assemblages from the Kalaeloa sinkholes, compared with other site types, leads us to characterize the 'Ewa plain as a patchy environment for land snails, where moist conditions inside the sinkholes provided relatively congenial habitat compared with the harsh, dry conditions on the surface of the plain. Our analysis of change over time in the diversity of native, extinct land snail taxa indicates that stability, rather than population stress, characterizes most of the stratigraphic sequence. The sinkhole habitats might have provided a buffer against changes on the surface of the plain. Recent evidence from coring in a wetland at Kalaeloa is interpreted as indicating a drastic change in the dry forest cover of the region around A.D. 1000 unrelated to Hawaiian farming or settlement of the region (Athens et al. 1997). If this change did, in fact, occur, it had no measurable effect on the land snail faunas in the sinkholes. Similarly, our analysis indicates that the environmental consequences of Polynesian settlement at Kalaeloa, with the exception of the introduction of *L. gracilis,* were not felt by the land snail populations of the sinkholes. This does not necessarily indicate that Polynesian settlement was without environmental consequence, however. It does indicate that Polynesian use of this environmentally marginal corner of O'ahu did not result in ecological disturbance sufficient to extinguish land snail populations in the sinkholes.

Diversity indices indicate a complex pattern of decline near the top of several stratigraphic columns, and we interpret this as indicating some stress in the population of native, extinct land snails in the sinkholes. In the two dated sinkhole sites, the decline in diversity is associated with the transported sediment deposits, and thus might date either to the end of the precontact period or to the postcontact period. We prefer the latter alternative because the massive environmental changes to the region brought on by sugarcane cultivation in the nineteenth century and

by the introduction of plants and animals that now dominate the flora and fauna of the region should have had an observable effect on the sinkhole land snail faunas. If we are right about the importance of the water table to the sinkhole habitat, then the water wells drilled to irrigate sugarcane fields after 1880, which lowered the water table (Macdonald and Abbott 1970:247), might have had an appreciable effect on the land snail faunas of the sinkholes.

The apparent simplicity of the karst setting of the 'Ewa Plain belies a complex environmental and human history. There have been a series of changes associated with sea level, rainfall patterns, Polynesian introductions and activities, and postcontact land uses. We conclude that land snail extinctions at Kalaeloa resulted from the first and last of these factors, and that the activities of Polynesians before the advent of European influence in A.D. 1778 contributed little, if anything, to the extinction process.

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