



Prodromus of the Fossil Avifauna
of the Hawaiian Islands

STORRS L. OLSON
and
HELEN F. JAMES

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ABSTRACT

Olson, Storrs L., and Helen F. James. Prodrum of the Fossil Avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, number 365, 59 pages, 12 figures, 1982.—In the past decade, fossil deposits from five of the main Hawaiian Islands have yielded thousands of bones of extinct and living species of birds. Through these specimens, the number of endemic species of land birds in the avifauna of the main islands has been more than doubled. There are 40 extinct species known only from bones, including 1 petrel (Procellariidae), 2 ibises (Plataleidae), 7 geese (Anatidae), 1 small hawk and 1 eagle (Accipitridae), 7 rails (Rallidae), 3 species of a new genus of owl (Strigidae), 2 large crows (Corvidae), 1 honeyeater (Meliphagidae), and at least 15 species of Hawaiian finches (Fringillidae, Drepanidini). The present report discusses the fossil deposits and the physical and biological features of the islands in order to provide background information for our future systematic publications on the fossil and modern avifauna of the Hawaiian Islands. An informal listing of the species found as fossils permits preliminary analyses of extinction and biogeography. The major fossil localities are on the islands of Kauai, Oahu, and Molokai, from each of which there are diverse collections of small passerines, as well as many specimens of nonpasserine land birds, shorebirds, and seabirds. Fossils of a few additional extinct species have been found incidentally on Maui and Hawaii. Bones of extinct birds have been found in situations as diverse as sand dunes, sinkholes, and a flooded cavern in a raised coral reef, lava tubes, loess deposits, an ash deposit under a lava flow, and in archeological sites. Although some of the fossil deposits may be from the late Pleistocene epoch, most of the more important ones are probably Holocene, ranging from about 6700 years B.P. to much younger. Evidence is presented to show that the extinct species of birds survived into the period of Polynesian colonization. We believe that the extinction of half or more of the land birds of the Hawaiian Islands prior to European discovery resulted mainly from the destruction of lowland forest by Polynesians, augmented by predation by man and introduced mammals. This has altered the distribution of species within the archipelago as well as the species composition of individual islands in such a drastic manner as to suggest that the data used in traditional and modern ecological studies of island biogeography may be too incomplete to permit generalizations about any islands that were settled by prehistoric man.

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Preface

When fossil birds began to be discovered in the Hawaiian Islands with some frequency in the early 1970s, they quite naturally found their way into the hands of Alexander Wetmore, then the dean of avian paleontologists and the describer of the only fossil bird known from the islands at that time. Although Wetmore had a very active interest in these specimens, he was unable to devote much time to them because of his commitment to his magnum opus on the birds of Panama. After Wetmore's death at the age of 92 in 1978, S. Dillon Ripley, Secretary of the Smithsonian Institution, suggested that it would be appropriate to see to completion a number of Wetmore's unfinished research projects, among which were the Hawaiian fossils. When we first conducted some preliminary field work in Hawaii to recover a few more fossils of small passerines, there was little indication of the enormity of the final undertaking. Ultimately we made six trips to the islands and studied some tens of thousands of fossil specimens. Throughout this long period of investigation, our research was generously supported by trust funds from the Smithsonian Institution allocated for completing Wetmore's unfinished projects. This is the eleventh in a series of papers dedicated to that end. We are especially grateful to S. Dillon Ripley for his generous encouragement in a project that has taken much longer than ever anticipated and that is still far from completion.

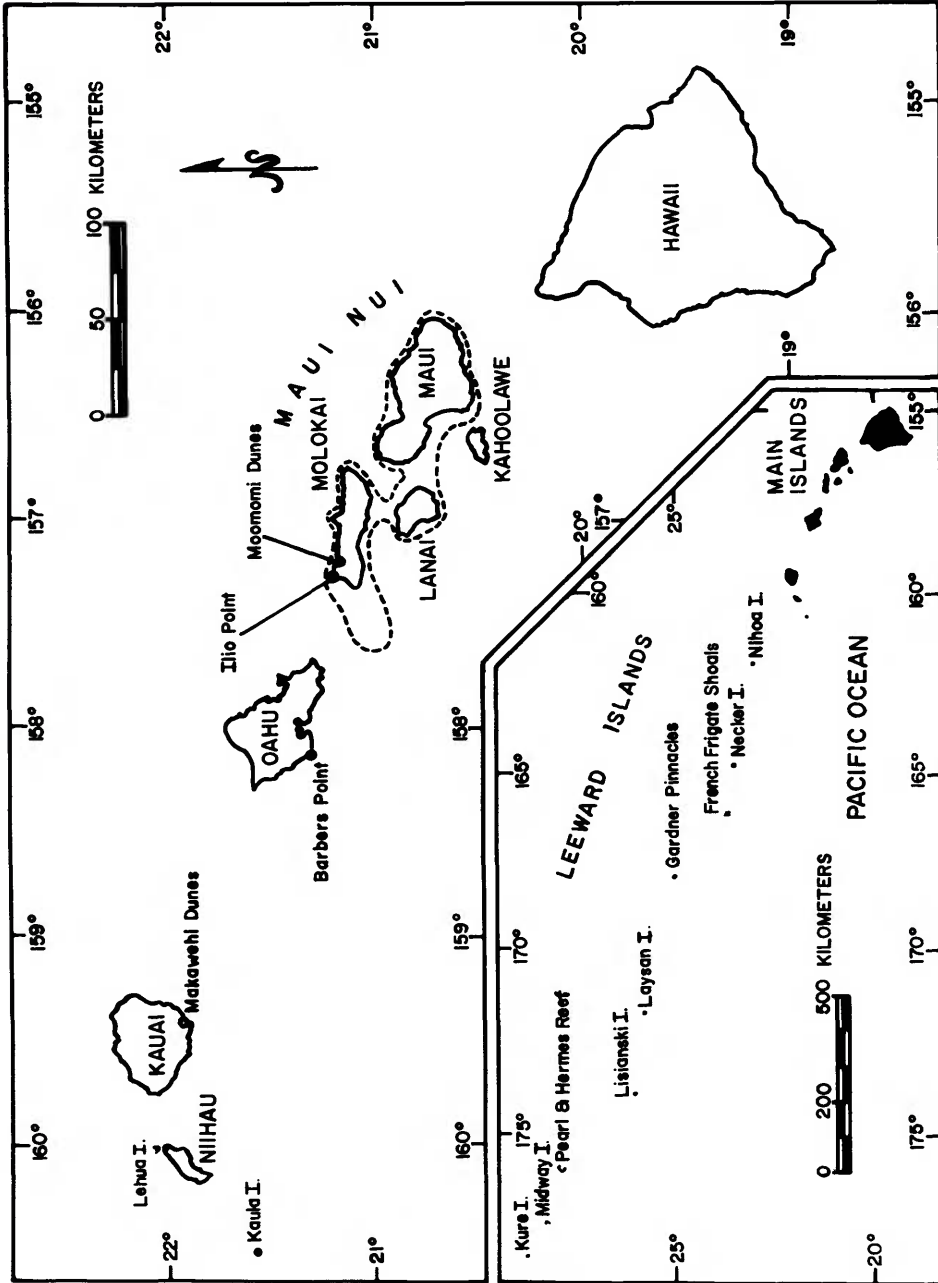


FIGURE 1.—Outline map of the main Hawaiian islands showing the location of major fossil sites and relationship to the Leeward Islands (inset). Dashed line shows the configuration of the Pleistocene island of Maui Nui, as it probably appeared at the height of the Wisconsinan glacial period of maximum lowering of sea level.

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Introduction

In the past 10 years, great quantities of bird remains have been collected in the Hawaiian Islands. We now have significant fossil material from five of the eight main islands in the chain. From three of these islands the collections are sufficiently comprehensive to provide a reasonable indication of the former diversity of each island's avifauna, with specimens numbering in the thousands. Not only are remains of large birds such as geese and eagles preserved, but those of small passerines, particularly drepanidines (*Drepanididae* auct.), are likewise well represented. The majority of extant and recently extirpated species occur as fossils, as well as an almost bewildering array of extinct taxa of which there had previously been no clue. Through the fossil discoveries made since 1971, the number of species of endemic land birds known from the Hawaiian Islands has already been doubled. As a consequence, all previous concepts of the diversity and distribution of Hawaiian birds must be extensively revised.

The ramifications of this immense body of new data go well beyond the systematic revisions necessitated by the fossil discoveries. The fossil record, along with other evidence, provides a strong

indication that before European contact the lowland habitats of the Hawaiian Islands suffered extensive destruction and alteration, which in turn caused massive extinction. This took place after Polynesians colonized the archipelago, perhaps as early as A.D. 400 (Kirch, 1974). There is no reason to assume that the Hawaiian Islands are exceptional in this regard. Undoubtedly, prehistoric human interference has had an impact on island ecosystems elsewhere in the world. If destruction in other places was comparable to that observed in the Hawaiian Islands, then the data used in many studies of island biogeography are almost certainly unreliable.

The sheer magnitude of the Hawaiian collections amassed so far creates the problem of how best to elucidate this extensive fossil avifauna. We anticipate that at least seven monographs will be required for a proper analysis of the systematics of the various taxonomic groups involved. These revisions cannot be effected rapidly, however. Naturally, the new fossil discoveries have excited much attention in Hawaii and elsewhere, and some information has already been circulating by word-of-mouth and in the popular press. We therefore felt the need to produce a preliminary report dealing with the entire fossil avifauna as we presently understand it, along with descriptions of the geological contexts and ages of the fossil sites, analyses of the biogeographical signif-

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icance of the fossil avifauna, and conclusions relating to the effects of human alterations of habitats on extinction. We hope that the present paper will obviate the necessity of repeating or scattering these data in our proposed systematic treatments. We have also included brief synopses of the geology, physiography, climate, and vegetation of the islands. Although some of this information may not pertain directly to our paleontological studies, it is not readily available elsewhere in a single source, and we feel that its inclusion provides a necessary background against which the history of avian evolution in the archipelago may be better understood and assessed.

The Hawaiian archipelago is unusual in being far removed from potential sources of colonization, yet it possesses numerous large islands with greatly varied habitats, thus providing abundant opportunities for isolation and allopatric speciation among organisms able to reach the islands. The native flora contains only four orchids and no gymnosperms, bromeliads, oaks, elms, willows, maples, figs, or mangroves (Zimmerman, 1970). Two-thirds of the world's orders of insects have no native representatives in the archipelago (Zimmerman, 1948). No primary fresh-water fishes occur naturally (Zimmerman, 1970), and the native terrestrial vertebrates consist entirely of a single species of bat (Tomich, 1969) and a variety of birds.

The estimated proportion of endemic species among the major taxonomic categories of the native Hawaiian biota is 96 or 97 percent for the modern species of flowering plants and terrestrial vertebrates (St. John, 1973; Juvik and Austrig, 1979), and nearly 100 percent for insects (Zimmerman, 1948). Endemism would probably be closer to 100 percent for all groups if the many taxa that have been extirpated by man were known (Degener and Degener, 1974). With the addition of the fossil species of birds, nearly 99 percent of the terrestrial vertebrates are now seen to be endemic. The endemics include over 1394 species of plants (St. John, 1973), about 6500 species of insects (Zimmerman, 1970), over 1000

forms of terrestrial mollusks (Zimmerman, 1948; Kondo, 1972), and, according to our current estimate, roughly 80 species of land birds.

Although relatively few organisms have successfully colonized these islands, the paucity of immigrant species has been compensated for by unparalleled examples of adaptive radiations within the archipelago. Among plants, the lobelioids have evolved six endemic genera with about 150 species and varieties in the archipelago, whereas only three other Pacific islands possess lobelioids, and these have only one or two species each (Rock, 1919). Over 600 species of Drosophilidae have evolved in the Hawaiian Islands from a small number of original colonists (Carson et al., 1970). Other excellent examples of "explosive" evolution include the moth genus *Hyposmocoma* (over 500 endemic species), the beetle genus *Proterhinus* (about 250 endemic species), and the wasp genus *Odynerus* (over 100 endemic species) (Zimmerman, 1970). That insect speciation may be extremely rapid in the Hawaiian Islands is illustrated by the five or more species of moths of the endemic genus *Hydylepta* that apparently evolved in the 1500 years or so since bananas were introduced by Polynesians (Zimmerman, 1960).

For breadth of adaptive radiation from a single ancestral species, the Hawaiian finches (the so-called honeycreepers or Drepanididae of previous authors) surpass any other group of birds. This diverse assemblage, which we treat as a tribe (Drepanidini), evolved from a fringillid belonging to the subfamily Carduelinae. About 13 genera and 27 species of Hawaiian finches with extremely diverse feeding adaptations survived to historic times.

The fossil record now shows not only that the radiation of Hawaiian finches was greater than previously suspected, but that the entire avifauna was much more varied before the arrival of Polynesians. From the percentage of extinctions of birds that is now evident, we may begin to deduce something of the losses that must have occurred among other groups of organisms. Authors describing the Hawaiian terrestrial biota

often understandably succumb to such rapturous modifiers as “spectacular,” “astounding,” “unparalleled,” “magnificent,” and “truly wonderful.” One wonders what superlatives would have been applied to the Hawaiian biota had its true diversity been known.

We emphasize the fact that our systematic studies are not yet completed and that we fully expect the total number of species ultimately recognized in the avifauna to differ from that discussed here. A great many of the birds mentioned herein are new and still undescribed. We have therefore identified these taxa only in an informal manner, so as to establish their existence and distribution. We have made considerable progress on a revision of the Drepanidini and expect to publish our systematic conclusions on this group following the present paper. Other proposed monographs will treat the remaining passerines, the raptors, the geese, the ibises, the rails, and seabirds and shorebirds.

In this paper, the noun “Hawaii” refers to the island itself, whereas we use the adjectival form “Hawaiian” to refer to the archipelago as a whole. We use the term “prehistoric” to refer to the period of human occupancy prior to the arrival of James Cook in 1778, which marked the beginning of the “historic” period. We have used the term “fossil” in its broadest sense, as an object dug up, thus including bones that might be considered “subfossil” or even “recent,” and encompassing archeological material as well. We have attempted to use “land bird” to exclude not only marine birds, but also such aquatic birds as ducks, coots, gallinules, and stilts.

ACKNOWLEDGMENTS.—In the Hawaiian Islands we have always been received with enthusiasm and interest and we have been assisted in diverse ways by scores of generous people to whom we shall continue to be indebted. The response of museum curators, who have lent many specimens, often of an extremely rare nature, has likewise been most gratifying. Any success our studies may achieve will be in large part due to the cooperation we have received from these quarters.

The new era of Hawaiian ornithology that was

ushered in by the discovery of extensive fossil deposits is directly attributable to Joan Aidem, an ardent amateur collector who made the first significant fossil finds on the island of Molokai early in the 1970s. Since then, she has carefully and systematically collected great numbers of fossil bird bones on Molokai, and on Kauai as well, all of which she has donated to the Bernice P. Bishop Museum, Honolulu, with full data. In addition, she and her husband Louis have most generously met all of our needs for transportation, accommodations, and assistance in the field during our several collecting trips to Molokai. To Joan Aidem we are especially grateful. Access to fossil localities on Molokai was kindly granted by Aka Hodgins, manager of the Molokai Ranch Company.

At the Bishop Museum (BBM), Alan C. Ziegler has helped us in more ways than we can possibly enumerate or even remember. He has supplied information, many valuable contacts, and material for preparing and packing specimens, and has allowed us to use his office as a base of operations. His assiduous curation of the fossil specimens deposited with the Bishop Museum, and his generosity in lending them, has greatly facilitated our efforts. Our thanks are truly inadequate recompense for all the services he has performed for us, or for all the pleasant afternoons of work and conversation we have spent in his office. The Bishop Museum in general has extended every courtesy to us; in this regard we particularly thank former acting director Frank J. Radovsky.

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prepared the typescript. Museum curators and technicians who lent specimens and provided other services will be acknowledged in our forthcoming monograph on the Hawaiian finches. Photographs of specimens are by Victor E. Krantz, Smithsonian Institution, and the maps are by Jaquin B. Schulz.

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Geology and Physiography

The Hawaiian Archipelago is the subaerial portion of a chain of giant shield volcanoes that form the Hawaiian Ridge, a roughly linear southeast-trending topographic high on the Pacific Ocean floor. Situated in the middle of the North Pacific, over 3800 km (2375 miles) from North America, the nearest continent, and an approximately equal distance to the south from the nearest high islands (the Marquesas), no other major group of islands is more isolated. Its 132 islands, reefs, and shoals extend for a distance of 2450 km (1531 miles) from the young and growing island of Hawaii (154°41'W, 18°54'N) to Kure Atoll (178°20'W, 28°25'N). As a general rule, the islands that lie to the northwest are older and more eroded, and thus much lower and smaller, than those in the southeast (Dana, 1890; McDougall, 1964, 1979). The eight larger islands of the main Hawaiian chain occupy the southeastern portion of the archipelago, from the young eastern island of Hawaii, with its two active volcanoes, to the old and deeply eroded western islands of Kauai and Niihau (Figure 1). These eight islands make up over 99 percent of the land area of the archipelago.

The islands beyond Kauai and Niihau to the northwest, from Nihoa to Midway and Kure, are mere erosional remnants of what may formerly have been high volcanic peaks. This segment of the archipelago, the Leeward or Northwest Hawaiian Islands, consists of a string of 10 small islands and atolls, and over a dozen reefs and shoals, spread over a distance of about 1648 km (1030 miles). Only the four islands nearest the main chain still have volcanic rock exposed; the subaerial portions of the rest are now entirely limestone and sand. Nevertheless, all of the islands, reefs, and shoals of the Leeward group are perched on shallow platforms supported by submerged volcanic mountains (Macdonald and Abbott, 1970).

The Hawaiian Ridge, formed of submerged volcanoes, extends northwestward beyond the Leeward Islands to about 32°N, 172°E. Here it meets the Emperor Chain of seamounts, which in turn extends northward to Meiji Guyot near the Aleutian trench. There is evidence that these two volcanic mountain chains have a related origin (Morgan, 1972; Dalrymple et al., 1973). Although the Hawaiian Islands were once thought to have formed along a fracture zone opening in a southeasterly direction (Stearns, 1946; Carlquist, 1970), the currently accepted theory is that all of the shield volcanoes of the Hawaiian-Emperor chain formed over a fixed "melting spot" in the mantle, centered near the island of Hawaii, and were carried to their present positions by the motion of the Pacific plate (J.T. Wilson, 1963; Grommé and Vine, 1972; Jackson et al., 1972). This theory suggests that land could have existed in the vicinity of the present main Hawaiian islands for over 70 million years, the apparent age of Meiji Guyot (Scholl and Creager, 1973; Worsley, 1973). Whether such land has existed continuously since this time is an important but unanswered question for Hawaiian biogeography, but there is a possibility that some parts of the Hawaiian biota could be older than the archipelago itself, as it now exists (page 52).

The subaerial portion of a Hawaiian volcano is built by copious eruptions of fluid basalts at

the summit and along one or more major rift zones, creating a mountain with the shape of a broad dome or shield. Mauna Loa volcano on Hawaii is presently in the shield-building phase of volcanism, and has this shape. The shield-building phase is typically followed by extinction or a long period of quiescence. Marine and stream erosion, aided by subsidence, eventually obliterate the original smooth shield shape. The mass and height of the volcano are reduced, great canyons and valleys are cut into the shield, and fluctuating sea levels produce a complex shoreline with drowned valleys, sea cliffs, terraces, reefs, and dunes along the periphery of the island. Some Hawaiian volcanoes enter a rejuvenated phase after a long period of rest, replacing part of the mass that has been stripped away by erosion. The islands of Oahu and Kauai are examples of large but deeply eroded high islands that have passed through a phase of posterosional eruptions. In time, the volcanic mountains are reduced to small, low volcanic islands, such as Nihoa. These later may persist above sea level as limestone atolls, such as Midway, or submerge completely and become guyots.

The shield-building phase of Hawaiian volcanism occurs so rapidly that radiometric potassium-argon ages of the oldest exposed lavas are probably good approximations of the age of the island (McDougall, 1964; Jackson et al., 1972). Our discussion of the times of emergence of the main islands relies on the accuracy of the potassium-argon ages listed in Table 1. In some cases the ages quoted in the table differ from those quoted in other summary papers. We have given the oldest age considered reliable by the original authors; thus some are ages of samples and others are means. Most ages would be an average of 2.67 percent older if recalculated using recently revised decay constants for potassium (Steiger and Jäger, 1977; McDougall, 1979). Although published potassium-argon ages are subject to emendation and revision (e.g., Dalrymple et al., 1977; McDougall, 1979), it is unlikely that the error is greater than half a million years for any

TABLE 1.—Potassium-argon ages of Hawaiian lavas (sources: 1 = Bonhommet et al., 1977; 2 = Clague et al., 1975; 3 = Dalrymple, 1971; 4 = Dalrymple, unpublished data in Jackson et al., 1972; 5 = Dalrymple et al., 1974; 6 = Dalrymple et al., 1977; 7 = Doell and Dalrymple, 1973; 8 = Jackson et al., 1972; 9 = McDougall, 1964; 10 = McDougall, 1979; 11 = Porter et al., 1977)

Island/Volcano	K-Ar age (my)	Source
MAIN ISLANDS		
Hawaii		
Mauna Kea	0.375 ± 0.05 ^b	11
Kohala	0.7 ± 0.15 ^a	3
Maui		
Haleakala	0.84 ± 0.03 ^b	8,9
West Maui	1.30 ± 0.04	8,9
Molokai		
East Molokai	1.48 ± 0.04	8,9
West Molokai	1.84 ± 0.06 ^b	8,9
Lanai	1.25 ± 0.04	1
Oahu		
Koolau	2.6 ± 0.2	7
Waianae	3.6 ± 0.1	7
Kauai	5.00 ± 0.17	10
Niihau	3.0 ± 0.2 ^c	4
LEEWARD ISLANDS		
Nihoa	7.0 ± 0.3 ^d	5
Necker	10.0 ± 0.4	5
La Perouse Pinnacles	11.7 ± 0.4	5
Pearl and Hermes Reef	20.1 ± 0.5 ^b	2
Midway	27.0 ± 0.6 ^b	6

^a Possibly too old; see McDougall and Swanson (1972).

^b Probably too young.

^c Tentative, based on unpublished data.

^d Unreliable because of sampling problems.

of the ages that are not specifically noted as being dubious.

Formation of the main Hawaiian islands began when Waialeale volcano emerged from the sea and began to build the island of Kauai over five million years ago. Subaerial shield-building on Kauai apparently persisted for 1.5 million years (McDougall, 1979). The configuration of the remainder of the archipelago during most of this period is unknown. As Kauai was forming, its nearest neighbor was probably Nihoa, 274 km

(170 miles) to the northwest, an island then only two or three million years old. It is reasonable to assume that during the early subaerial history of the main islands, Nihoa and some of the other Leeward Islands were larger and supported a more diverse biota than at present. It is not definitely known whether Niihau, the large island southwest of Kauai, emerged before, during, or after the shield-building phase of Waialeale on Kauai.

Disregarding Niihau, the next volcano to emerge above water was Waianae, about 120 km (75 miles) to the southeast. This occurred approximately four million years ago. Approximately another million years elapsed before Koolau volcano emerged as a separate island, eventually to coalesce with Waianae and form the present-day island of Oahu.

Thus, during the first three million years in the history of the main islands, new volcanic mountains emerged at a rate of slightly more than one per million years. The succeeding million years, however, saw the emergence of six volcanoes, beginning with West Molokai about two million years ago, followed by East Molokai, West Maui, Lanai, Kahoolawe, and Haleakala. These six volcanoes are so close to each other that their lavas form a single mass below sea level. At the present sea level, they are separated into four islands—Molokai (composed of East and West Molokai), Maui (composed of West Maui and Haleakala) and Lanai and Kahoolawe (composed of one shield each).

The remaining island, Hawaii, constitutes over 60 percent of the present dry land area of the archipelago. Kohala, the oldest and northernmost of the seven shield volcanoes forming the island, probably emerged less than one million years ago. Near the southern end of the present island of Hawaii, another volcanic mountain, Ninole, emerged and achieved a height of about 2440 m (8000 feet) above present sea level, probably in the interval between 500,000 and 100,000 years ago. Ninole had reached the erosional stage before it was nearly buried by the lavas of Mauna Loa, incorporating Ninole and a younger volcano to

the northeast, Kulani, into the island of Hawaii (Macdonald and Abbott, 1970). In the meantime, two additional volcanic mountains, Mauna Kea and Hualalai, were forming farther north, creating the connection between Kohala and the volcanoes to the south. The sequence of emergence from the sea of these six shield volcanoes is not definitely known. The seventh volcano, Kilauea, emerged less than half a million years ago, not from the sea, but from the eastern slope of Mauna Loa.

Of the volcanoes that built the main Hawaiian islands, only Mauna Loa and Kilauea are actively producing fresh lava at present. Haleakala and Hualalai have each erupted once between 150 and 200 years ago, Mauna Kea has been dormant for at least 2000 years, and the rest of the Hawaiian volcanoes are apparently extinct (Macdonald and Abbott, 1970).

As we have already described, volcanic activity has produced tremendous changes in the configuration of the archipelago during the past five million years. Changing sea level and isostatic movements of the islands have also had a large impact. Certain areas of the older main islands that are presently emergent were once below sea level. Stearns (1966) has postulated that during one period of extreme submergence of the islands, sea levels were high enough to drown the lowlands now connecting East and West Molokai, and also West Maui and Haleakala, creating four islands where there are now two. Conversely, in periods of relative emergence, several of the central main islands were connected by land bridges (see below).

For biogeographic purposes, it would be useful to determine the form of each island during various periods in the development of the archipelago. Yet despite several admirable attempts to reconstruct the geologic history of individual islands (see Stearns, 1966; Macdonald and Abbott, 1970), reliable comparisons between islands at various ages are hindered by lack of precise information on the amount and timing of eustatic and isostatic changes in sea level and their relation to other processes that have altered the islands. The

islands show abundant evidence of former stands of the sea (Stearns, 1978), but the literature on Hawaiian shorelines is rife with disputes over the interpretation of this evidence and its value for correlation (e.g., McDougall and Swanson, 1972, 1973; Easton, 1973, 1977; Stearns, 1973b, 1974, 1977; Ward, 1973, 1974; Easton and Olson, 1976; Bonhommet et al., 1977). Hawaiian volcanoes experience an initial period of isostatic subsidence, probably due to the great uncompensated mass extruded onto the crust during the shield-building phase of volcanism (Hamilton, 1957; Furumoto and Woolard, 1965; Strange et al., 1965; Moore and Fiske, 1969; Watts, 1978). That isostatic subsidence continues long after upward growth of the volcano ceases is demonstrated by bathymetric and seismic refraction studies, revealing deep canyons apparently cut by stream erosion into the islands of Kauai, Oahu, and Molokai, now drowned by as much as 1800 m (5905 feet) of sea (Shepard and Dill, 1966; Mathewson, 1970; Andrews and Bainbridge, 1972; Coulbourn et al., 1974). Moreover, the direction of isostatic movement of the islands may not always be consistently downward. Based on an analysis of tide-gauge records, after correcting for the current eustatic rise of sea level, Moore (1970) concluded that Hawaii and Maui are presently sinking, that Oahu is isostatically stable, and that Kauai and Midway appear to be emerging. Stearns (1978) believes that some catastrophic magmatic or tectonic event has caused Lanai to emerge rapidly 365 m (1197 feet) or more, though the evidence for this seems equivocal. In any case, Stearns's (1978) contention that the main Hawaiian islands have been isostatically stable for the past 600,000 years seems improbable; the correlations he has made on the basis of this assumption are subject to doubt. We concur with Coulbourn et al. (1974:232) that, for the Hawaiian archipelago, it would "appear premature, without great improvement in radiometric, fossil, or paleomagnetic dating, to correlate subsurface rock units of one area with terraces several kilometers away; or to correlate any but the very

youngest stands of the sea with those elsewhere in the world.”

Although current knowledge of Hawaiian geology does not permit the reconstruction of the exact number and form of the islands in the archipelago at specific times in the past, at least one major change that resulted from Pleistocene climatic fluctuations is well established. During the Wisconsin glacial period, a maximum glacioeustatic lowering of sea level of approximately 120 m (394 feet) was reached approximately 17,000 years ago (Gascoyne et al., 1979). The shallow channels that now separate Molokai, Maui, and Lanai were then dry land, joining what are presently three islands into a single large island, “Maui Nui” (Big Maui). The Penguin Bank, a submerged shelf extending west-southwest from West Molokai, was also emergent during the last glaciation, so that Maui Nui was much closer to Oahu than Molokai presently is (see Figure 1, and Stearns, 1966). The present island of Kahoolawe, near Maui, was probably not a part of the larger island of Maui Nui during the last glacial epoch, though it may have been connected to Maui at an earlier stage of the growth of the islands (Stearns, 1966). The history of land connections between Maui, Molokai, Lanai, and Kahoolawe probably began long before the last glacioeustatic drop in sea level. Because the long-term trend in isostatic movement of the islands is downward, some or all of these central main islands may have been joined and separated at least twice in the past (Stearns, 1966).

Climate

The following summary is mainly from Armstrong (1973) and the National Climatic Center (1978), with additional information from Voorhees (1933), Ripperton and Hosaka (1942), Leopold and Stidd (1949), and Taliaferro (1959).

The major factors affecting the climate of the eight main islands are their position within the tropics and far from continental land masses, their topography, and the patterns of air circu-

lation over the Pacific Ocean. Temperatures are equable over most of the land area, with seasonal variation in mean monthly temperatures less than 5°C (9°F) at most localities. Coastal diurnal temperatures are typically between 21° and 29.5°C (70° and 85°F). Mean monthly temperatures decrease by about 1.6°C (3°F) with every 300 m elevation, so that at 3049 m (10,000 ft) elevation the mean annual temperature is 4.4°C (40°F). The summits of Mauna Loa and Mauna Kea on Hawaii are often snowcapped in winter.

Despite the generally equable temperatures, local climatic contrasts within the main islands are among the most extreme in the world. This is best illustrated by average annual precipitation. The main Hawaiian islands boast one of the wettest spots in the world (Mount Waialeale, Kauai, averaging 1230 cm [484 in] annually), as well as some very dry areas (less than 25 cm [9.8 in] annually on some leeward coasts). Usually the spatial gradient of change is very abrupt. Annual rainfall gradients of 40 cm per km (25 in per mile) are not uncommon in the islands, and in one area of Kauai the gradient reaches 188 cm per km (118 in per mile).

On all but the highest mountains, average annual precipitation increases with elevation. The exceptions are the volcanoes of Mauna Kea and Mauna Loa on Hawaii, and Haleakala volcano on Maui, whose summits rise above the inversion layer that usually exists in the tradewinds between 1500 and 2100 m (4920 and 6890 ft). These mountains have a belt of maximum precipitation between 610 and 1100 m (2000 and 3600 ft) on the windward (northeast) slopes, above which average annual precipitation has an inverse relation to elevation. The greatest annual precipitation in the islands, over 1016 cm (400 in), falls on the summits of the two mountains with a maximum elevation near the usual inversion layer, and deep V-shaped valleys on their windward slopes funneling the moist tradewinds to the summit regions. These mountains are Waialeale, Kauai (1653 m, 5423 ft) and West Maui (1761 m, 5777 ft). Mountains of lesser elevation have the same pattern of increasing precipitation

toward their summits, but have lower maxima. Thus the median annual precipitation in the wettest part of the Koolau range (960 m, 3150 ft) on Oahu is slightly less than 762 cm (300 in).

The islands derive most of their precipitation from the humid northeasterly tradewinds, and the most general climatic division is between land that is exposed to the tradewinds and land that is not. The tradewinds lose much of their moisture as they pass over and around windward slopes and summit regions. The zone of maximum precipitation spills over the summits of mountains that are lower than the usual inversion layer, creating a climate on leeward slopes at high elevations that is scarcely different from comparable windward regions. Below this zone, clouds disperse and precipitation decreases more rapidly on leeward than on windward slopes. Local convective winds and eddies often replace the tradewinds in protected leeward regions, but only in the western part of the island of Hawaii do these winds produce a significant portion of the annual rainfall.

Certain areas other than the summit regions of the highest mountains and the leeward regions receive relatively little tradewind precipitation or cloud cover. The climate of these areas is generally similar to that of leeward slopes. For instance, all of the low-lying parts of West Molokai are fairly arid, despite exposure to tradewinds. The islands of Niihau, Lanai, and Kahoolawe have low precipitation partly because of low elevation and partly because they lie in the leeward rainshadows of high mountains. Of the two mountainous regions on Oahu, the Waianae range in the west is higher in elevation than the Koolau range in the east but receives much less precipitation because it lies in the rainshadow of the latter.

Windward regions are not only wetter than leeward regions at equivalent elevations, but their climates are less variable in nearly every respect. Because of their exposure to trade winds and more frequent cloud cover, the difference between average daily maximum and minimum temperature in such regions is less. For instance, the

difference is 4.4° C (8° F) at Kaneohe on the windward coast of Oahu, and 10.5° C (19° F) on the leeward Ewa Plain. Precipitation on windward exposures is more evenly distributed throughout the year, and is usually much less variable from one year to the next than for comparable leeward areas.

There are two seasons in the Hawaiian Islands—winter and summer. In summer months (May to September), the northeasterly tradewinds blow almost uninterruptedly from the Pacific anticyclone, bringing frequent, consistent rains to windward slopes. The leeward lowlands are often virtually rainless during this season. In winter (October to April), as the Pacific anticyclone weakens and moves south, the tradewinds are more frequently interrupted by other weather systems, usually southerly “Kona” winds or cold fronts from the north. Kona weather sometimes results in heavy rains that may be spotty and often locally intense, but which fall more randomly over the islands than rains generated by tradewinds. Cold fronts also distribute rains more generally over the islands, but they affect the islands that lie to the northwest more than those to the southeast. Nearly twice as many cold fronts reach Kauai as reach Hawaii.

The drier leeward areas depend on Kona storms, and to a lesser extent on cold fronts and other cyclonic storms, for most of their precipitation. In some years, localities in the leeward lowlands receive over half of their annual precipitation from a single storm; in other years the Kona storms do not materialize.

Although the general distribution of climates over the Hawaiian Islands is known, the great differences that occur within very circumscribed areas have been little studied. That such contrasts exist is immediately evident to the most casual observer, who is struck by abrupt changes from mesic to xeric vegetation on many adjoining ridges and valleys. These differences are often caused by the influence of local topography on wind patterns and the distribution of tradewind rains.

Vegetation

The vegetation of the Hawaiian Islands is as varied as the climate, and over the years several different schemes for defining vegetation zones or regions have been proposed (Hillebrand, 1888; Rock, 1913; Robyns and Lamb, 1939; Ripperton and Hosaka, 1942; Selling, 1948; Carlquist, 1970; Fosberg, 1972). Most authors have not attempted to relate their systems directly to those proposed previously. We have constructed the following brief summary from these sources but we have not chosen one system over the others, nor do we discuss the introduced vegetation that has usurped much of the Hawaiian landscape.

Two vegetation zones occur only on mountains that rise above the inversion layer. Above 3050 m (10,000 ft) on the summit regions of Mauna Kea and Mauna Loa, Hawaii, where rainfall is less than 50 cm (20 in) per annum, is a desolate, sparsely vegetated region of alpine stone desert (Ripperton and Hosaka, 1942). Alpine vegetation also occurs at the summit of Haleakala, Maui. Below the alpine desert on the island of Hawaii, and near the summit of Haleakala, is a mountain parkland region, the dominant trees of which are *Sophora chrysophylla* (mamane) and *Myoporum sandwicense* (naio), and at lower elevations, *Acacia koa* (koa), and occasionally *Metrosideros collina* (ohia lehua) (Rock, 1913; Robyns and Lamb, 1939). This region is typified by scattered clumps of scrubby trees and rather sparse ground cover of native grasses and some subalpine shrubs, although growth forms and density of vegetation vary considerably with local climate, soil development, and elevation (Fosberg, 1972). Before introduced feral herbivores invaded these parklands, the flora of native shrubs and herbs was probably much richer (Fosberg, 1972; Warner, 1960).

All of the larger, higher islands have regions of high precipitation between about 610 and 1830 m (2000 and 3000 ft), and extending as low as 100 m in places. Within the belt of high precipitation, variation in climatic and topographic conditions, as well as the various complements of

species occurring on each island, favor the development of a variety of vegetation types. Some endemic plant groups, such as the arborescent lobelioids, reach their greatest diversity in the rain forests (Rock, 1913, 1919). *Metrosideros collina* is by far the most common tree, and though this species seems to thrive in virtually all conditions from sea level to timberline, its finest development at present is in the montane rain forest, where it may grow in pure stands, although it often occurs in association with other native trees (Fosberg, 1972; Rock, 1917). *Cheirodendron* (olapa) and the tree fern *Cibotium* (hapuu) are prominent as understory trees. Under favorable conditions, usually above the rain forests, cloud forests develop with stunted trees and dense epiphytic growth. Montane bogs also occur on the five highest islands, usually between 1200 and 1765 m (3940 to 5790 ft), though these are limited in extent (Selling, 1948).

It is the vegetation of regions below the rain forest or *Metrosideros* belt that is of primary interest here. These are the regions that are most amenable to human settlement and agriculture, and as a consequence relatively little is known of the original composition and extent of this part of the flora (see page 46).

The first botanist to make a concerted effort to investigate leeward lowland habitats, J.F. Rock, was surprised to find a much greater diversity of species of trees than in wet montane forests. He reported (1913:15) that "not less than 60% of all the species of indigenous trees growing in these islands can be found in and are peculiar to the dry regions or lava fields of the lower forest zone." This astonishing diversity of trees occurred primarily in what Rock termed the "mixed lowland forests." At the time he collected, these forests were very limited in extent, each locality "being only perhaps two to four miles [3.2–6.4 km] long at the most and much less wide." Areas with vestiges of mixed lowland forest persisting at that time included the heads of some leeward valleys on Kauai, the Waianae Range on Oahu, the West Molokai shield, the leeward slopes of Mount Haleakala on Maui, and several spots on Hawaii.

More recently, Hatheway (1952) described remnants of Rock's "mixed lowland forest" growing on steep slopes, inaccessible to grazing mammals, in the northern part of the Waianae Range on Oahu. The forest patches occurred in fairly high, mesic areas that are subject to the summer droughts typical of leeward locations. Accordingly, Hatheway called them "seasonally dry forests," but Fosberg (1972) has renamed them "mixed mesophytic forests." The composition of these patches of forest varied greatly between nearby slopes, and no one species or group of species was consistently dominant (Hatheway, 1952).

Not all forests of semi-mesic slopes and lowlands are as diverse botanically as those described by Rock and Hatheway. Below the rain forests, under climatic conditions that resemble those found in the mixed mesophytic forests, *Acacia koa* is often the dominant tree, although it may be associated with a large variety of native species of trees and shrubs. The *Acacia* forests usually occur on relatively young soils and may represent a long successional stage leading to mixed forests (Fosberg, 1972). Both mixed mesophytic and *Acacia koa* forests were undoubtedly much more extensive, particularly at lower elevations, before the coming of man (page 46). What now remains of these forests is largely restricted to rugged or higher mountain slopes.

A second category of the mixed lowland forests originally described by Rock is termed by Fosberg (1972) "dryland sclerophyll forest." Because this forest type will have a prominent role in our discussion of extinction in the Hawaiian avifauna, it is useful to quote Fosberg's description of it (1972:32-33).

Large areas of dry coastal slopes and higher rain shadows, probably most of the relatively dry areas below 1500 m, were originally covered by an open scrub forest, principally of broad-sclerophyll trees. A few scraps and traces of this remain, mostly on rough lava flows, on the two largest islands, and even these are mostly in a sad state of degradation from overgrazing.

The simplest of these forests are almost pure stands of *Metrosideros collina* or *Diospyros ferrea* var. *pubescens*. More generally they include mixtures of several species and

some have a considerable number, including many of the rarest Hawaiian plants. . . .

In its best development this is a low closed forest, the trees with rounded crowns. More commonly it is open, the trees not touching. What occupied the spaces between them, originally, is not certain, but some of the native shrubs, such as *Abutilon*, *Gossypium*, *Euphorbia*, *Nototrichium*, *Chenopodium*, *Dodonaea*, *Wikstroemia*, and *Sida* occur in this sort of habitat, but usually now with *Prosopis* [keawe, an introduced plant related to mesquite].

This is one of the most important of the original forests types of the Hawaiian Islands. It is the one that has suffered most from the activities of man, and is now almost gone.

Although in this paper we will emphasize the effects of Polynesian activities on native Hawaiian ecosystems, the tremendous reduction that the Hawaiian biota has suffered since the islands were made known to the western world by Cook in 1778 should also be borne in mind. The historic period of interference was initiated by Cook and Vancouver, whose introductions of herbivorous ungulates in the late eighteenth century were to have dire consequences for all of the main islands. Subsequent introductions of exotic plants and animals, both accidental and deliberate, and the encroachment of modern civilization, have effectively restricted the native ecosystems to the mountainous regions of the higher islands today.

How many native organisms were extinguished between the time of Cook's discovery and the initiation of relatively thorough scientific collecting will never be known. An inkling of the magnitude of the losses, however, is provided by St. John's (1976a, b, 1978) dogged search through the herbarium of the British Museum for the botanical specimens collected by David Nelson on Cook's second visit to the islands. Nelson obtained specimens during a four-day trek up the slopes of Mauna Loa in the Kona district of western Hawaii. In this collection, St. John found and described 15 endemic species that were new to science, and that have never been found subsequent to Nelson's collecting trip. Hence these must have vanished before other botanists visited the Kona District. These 15 new species constitute more than 1 percent of the total of endemic

species of flowering and seed plants currently recognized for the entire archipelago (St. John, 1973). Degener and Degener (1974) believe that even greater extinction of endemic plants through human interference took place in the prehistoric Polynesian period, a conclusion that seems quite likely in light of the evidence presented here for widespread prehistoric extinctions of birds. It is probable that many populations of organisms that became extinct after the arrival of Europeans had already been diminished in number because of habitat alteration by Polynesians.

Climate and Vegetation at the Major Fossil Sites

The four major fossil localities thus far discovered in the Hawaiian Islands (Moomomi Dunes and Ilio Point, Molokai; Barber's Point, Oahu; Makawehi Dunes, Kauai) share one important feature—they are situated in the lowlands, usually within 1 km of the ocean (Figure 1). Little or no native vegetation exists in these regions today. Except for the strand plants on dunes, virtually all of the vegetation surrounding the fossil sites is introduced. It is possible, however, to make an educated guess at what the vegetation was like before man inhabited the island, based on modern climate, topography, and what little is known of the original lowland vegetation.

Ilio Point and the Moomomi dunes lie less than 8 km (5 miles) apart on the north coast of West Molokai. Southwest of the two fossil localities, the West Molokai shield rises gently to a maximum elevation of 420 m (1378 ft), not high enough to extract great amounts of precipitation from the tradewinds. Only about 76 cm (30 in) of rain falls annually on the wettest part of West Molokai, which is roughly 8 km (5 miles) inland from the fossil localities. Near the fossil localities, the average annual precipitation is 38 cm (15 in) or less.

Rock (1913) mentions West Molokai as one of the places he collected plants belonging to the "mixed lowland forest." Fosberg (1972) observes that in 1932 there were still traces of "dryland sclerophyll forest" in the most mesic part of the

shield, and he believes that such forest covered the western half of Molokai before human intervention.

Barber's Point, Oahu, lies at the southwest end of the leeward Ewa Plain, most of which receives about 50 cm (20 in) of precipitation annually. Although the Barber's Point sites lie on the leeward part of Oahu, the climate in the area is basically similar to that of the Molokai sites, which are on the windward part of that island. North of the Ewa Plain, precipitation increases as the Waianae Range is ascended, but the increase is gradual relative to that usual for the Hawaiian Islands. The closest approach of the 30 in (76 cm) isohyet of annual precipitation is about 11 km (7 miles) north of Barber's Point. Although the natural vegetation of the Ewa Plain and the southern Waianae Range has been destroyed, it was probably similar to the mixed dryland sclerophyll forest that once covered West Molokai.

Char and Balakrishnan (1979:60) have attempted to reconstruct the vegetation of the Ewa Plain as it was before human settlement by using the results of a recent botanical survey, combined with a search of literature and herbarium specimens. They conclude that "the vegetation of the coralline plains may have consisted of an open savannah with scattered trees." Kirch and Christensen (1981) reached a similar conclusion on the basis of the land snail shells from the Barber's Point deposits, in which species characteristic of moist forest are totally lacking. The species of land snails that are present suggest arid vegetation.

Near the Makawehi dunes on Kauai, the median annual rainfall is 84 cm (33 in) (Taliaferro, 1959), or over twice the average annual precipitation at Ilio Point or the Moomomi dunes, Molokai. Inland from the Makawehi dunes, the rainfall gradient is fairly steep, increasing to a maximum of 190 cm (75 inches) annually in a distance of only about 4.8 km (3 miles). The relatively high precipitation of the region surrounding the fossil deposits on Kauai contrasts with the dry climates of the other major collecting localities, but the marked seasonality of precipitation that

characterizes the region, with more precipitation in winter (October to April), is shared with the localities on Molokai and Oahu. The exact composition of the original vegetation of this region is difficult to reconstruct, but the climate suggests that the "seasonally dry forest" described by Hatheway (1952) and Fosberg (1972) may have been present. The climate may also have been favorable for forests of *Acacia koa*.

The Fossil Deposits

Macdonald and Abbot (1970:6) remarked that "a book on geology of the Hawaiian Islands comes close to being one on geological processes in general. . . . Only paleontology . . . is conspicuously lacking." This statement is no longer true. Not only are birds now represented in the Hawaiian Islands by an extensive paleontological record, but their fossils have been found in the most diverse variety of geological settings imaginable. These include lava tubes, limestone sinkholes, a flooded subterranean cavern, sand dunes, loess deposits, and an ash bed under a lava flow.

The first major advance in avian paleontology in the Hawaiian Islands came with Joan Aidem's discovery of fossils in the dunes of Molokai in 1971. Subsequently, Olson found bones in similar deposits on Kauai. Very shortly thereafter, archeological reconnaissance on Oahu led to the discovery of numerous fossil sites in the sinkholes at Barber's Point. We collected fossils in the Hawaiian Islands in 1976, 1977, 1978, 1980, and 1981. In the course of our studies we made four collecting trips to Kauai, seven to Molokai, and collected at Barber's Point, Oahu, in three different years. We searched for fossils twice on Maui and once each on Lanai and Hawaii. In addition, Joan Aidem has collected fossils on Molokai at intervals since 1971, and on Kauai on several occasions. Archeological survey work at Barber's Point, Oahu, contributed many days of fossil collecting in addition to our own efforts in conjunction with these archeologists.

The three islands of Molokai, Oahu, and Kauai have yielded the only extensive fossil faunas found

to date. Incidental finds of fossils have been made on Maui and Hawaii, but only a few species are represented. Lanai has been searched briefly for fossils, without results. The small and heavily eroded island of Kahoolawe has not been explored paleontologically. The same is true of the island of Niihau, which has great paleontological potential, as the entire southern end consists of extensive sand dunes (Stearns, 1947, pl. 2*b*). The island is entirely in private ownership, however, and we have been unable to obtain access to it.

Note added in proof: Robert Michael Severns recently found on East Maui two lava tubes that contain abundant remains of extinct birds. We have examined a sample of specimens from one of these tubes, and it documents the former presence on Maui of *Branta* cf. *sandvicensis*, a new species of *Thambetochen* different from either *T. chauliodous* or the Oahu species, and what is possibly a third species of goose. Further collecting at these sites will doubtless render obsolete much of what we have said about Maui in the present paper.

HAWAII

Hawaii is the largest and also the youngest island of the chain. Because most of the surface of the island consists of recent volcanics, there are few opportunities for bird remains to be preserved. Nevertheless, a few bones have been found that are of interest.

The first fossil bird found in the Hawaiian Islands was uncovered in the course of digging an irrigation tunnel near Pahala, on the southern side of Hawaii. This consisted of fragments of the hind limb and pelvis of a large goose that Wetmore (1943) described as a new genus and species, *Geochen rhuax*. The bones were found in a pocket at or near the top of a bed of Pahala Ash which was covered by 23–25 m (75–80 ft) of prehistoric lava flows that were densely forested at the time of discovery. Obviously this was an extremely fortuitous find that is not likely to be repeated. The bones bear swollen, longitudinally-oriented cracks such as can be duplicated by placing a

chicken bone in hot coals until all the organic matter is driven from it.

Bones of birds are regularly found in lava tubes in almost all parts of the island. Most of the remains recovered so far in these situations are referable to extant species, with *Pterodroma phaeopygia* being the most common. We have not listed each of these localities. A lava tube of particular interest yielded a few bones of a goose larger than *Branta sandvicensis*, almost surely belonging to *Geochen rhuax*. This lava tube is located in the Kona District about 8.8 km (5.5 miles) east-southeast of Kailua (Puu Lehua Quadrangle 19°37'N, 155°52'W) at an elevation of 1353 m (4440 ft). The remains of two individuals of *Asio flammeus* were also found in this tube. The bones were picked up from the surface of the floor at the north end of the tube at distances of 18, 30, and 45 m from the entrance. The specimens were collected in June 1978 by John J. Jeffrey and Philip R. Ashman.

Another lava tube on the Kona coast yielded a few fragments, including a partial cranium, of an extinct goose much larger than *Branta* or *Geochen*. This lava tube (Bishop Museum Site 50-Ha-D8-33) is situated 1 km east-northeast of Kailua Bay and had experienced considerable prehistoric modification to provide a refuge for warring Polynesians. Although the few goose bones from a test pit in this site were in a level containing cultural materials, much more extensive excavation failed to turn up any additional specimens, and it is possible that the bones were carried by water from higher portions of the tube after the site was settled.

In the vicinity of South Point, the southernmost tip of Hawaii, are deposits of yellow loess, presumably derived from the Pahala Ash. Olson and C.J. Ralph explored this area in July 1976 and found numerous remains of *Puffinus pacificus* from 1.2 to 4.5 m (4–15 ft) from the top of the loess cliffs in the southwest corner of the bay at Green Sands Beach, 4.8 km (3 miles) northeast by jeep trail from South Point. No other species was found here, however.

We have also included mention of remains

from one of Hawaii's more interesting archeological sites, the adz quarry on Mauna Kea (McCoy, 1977; McCoy and Gould, 1977). This quarry is situated mostly above the present tree line between 3355 and 3780 m (11,000–12,400 ft), with most of the individual quarrying areas being concentrated in an area of 1.5 square miles. Within this area are numerous rock shelters from which faunal remains were recovered. Because the environment at this altitude is cold and windy and vegetation is practically absent, virtually all vertebrate remains were probably brought here from lower elevations as provisions for quarry workers. Radiocarbon ages indicate that the site was worked between approximately A.D. 1264 and 1657. Not all of the bones from this site have been identified as yet, but extinct taxa are discussed, including two species of flightless rails (Rallidae), only one of which is known historically from the island.

Another archeological site on Hawaii (Bishop Museum Site 50-Ha-D24-22), a shelter about 18 km west-southwest of Pohakuloa Ranger Station at about 1540 m elevation, yielded mostly remains of petrels, but also a few bones of a small rail.

MAUI

We have not yet found good fossil deposits on Maui. This is most unfortunate because a number of species of native forest birds are absent today from Maui for no apparent reason. The fossil record could potentially fill in these gaps, but so far it is too meager to be faunistically significant. Although there are extensive areas of calcareous sand on the isthmus between East and West Maui, and also along the northeast coast of West Maui (Stearns and Macdonald, 1942, pl. 1), most of these are now either developed for industrial or residential use, or are well vegetated. In 1976, Olson and Aidem investigated exposures of this sand at Waiehu (now a housing development) but found only a few shafts of procellariid bones and a fragment of eggshell, possibly of the extinct goose *Thambetochen*. An exposure of sand in down-



FIGURE 2.—Betsy H. Gagné collecting land snail shells near the site of recovery of bones of flightless rails from the bare rock floor of a lava tube in the lower Waihoi Valley, Maui. (Photograph by F.G. Howarth.)

town Wailuku produced an isolated distal end of a small passerine femur.

The only fossil locality on Maui that has yielded identifiable remains thus far is a lava tube at the eastern end of East Maui, at an elevation of about 425 m (1400 ft) in the lower Waihoi Valley about 4.8 km (3 miles) south of Hana. In 1972 and 1974, F.G. Howarth, W.C. Gagné, and B.H. Gagné collected bones of several individuals of two species of flightless rails and much of the skeleton of a flightless ibis (*Apteribis* sp.) at this location (Figure 2). The specimens are quite friable and deteriorated. They are probably of late Holocene age, as in the humid environment of a lava tube such as this one, exposed bone eventually disintegrates completely.

MOLOKAI

Fossiliferous deposits of calcareous sand occur at two separate localities on the northwest part of Molokai: the so-called Desert Strip or Dune Strip near Moomomi Beach, and Ilio Point on the northwesternmost tip of the island. Within each of these major areas are numerous individual fossil sites. These were designated by number by Joan Aidem in the order in which they were discovered, with sites at Moomomi and Ilio Point

being numbered in the same series. For the sake of convenience in associating specimens from a particular site, we used the same numbering system in all of our own collecting. The location of each of these sites is indicated on the maps in Figures 3 and 6, and we briefly discuss them individually below. Additional locality information is kept on file at the B.P. Bishop Museum, Division of Vertebrate Zoology, and in the Division of Birds at the National Museum of Natural History.

MOOMOMI DUNES.—This locality takes its name from Moomomi Beach, although most of the fossiliferous deposits lie to the west of this feature (Figure 3), where there is an extensive area of dunes composed of calcareous sand formed of fragments of coral, coralline algae, and mollusk shells. These dunes were described briefly by Stearns and Macdonald (1947) and in more detail by Wentworth (1925) and Stearns (1973a). Unconsolidated dune deposits extend inland from the beach to a distance of 8.8 km (5.5 miles) in a southwesterly direction. The orientation of these eolian deposits indicates that they were formed by northeasterly winds such as prevail in the islands today. The great extent of dunes probably indicates that the sand was carried inland when these winds were more forceful than at present. Trade winds were evidently considerably stronger during glacial periods than during interglacials (Hays and Perruzza, 1972; Parkin, 1974; Parkin and Padgham, 1975; Thiede, 1979). We did not encounter fossil deposits of any significance far inland, almost all of the sites being within a few hundred meters of the present coast line. This is due at least in part to the inland dunes now being stabilized by dense vegetation.

The first fossil bird from the Moomomi dunes, the holotype of the flightless goose *Thambetochen chauliodous* (Olson and Wetmore, 1976), was exceptional in being preserved as a nearly complete articulated skeleton (Figure 4) in a weakly cemented dune, rather than as scattered bones in unconsolidated sand, as is the case for the majority of bird remains recovered here. The geology of this site (Site 1) was treated in some detail by

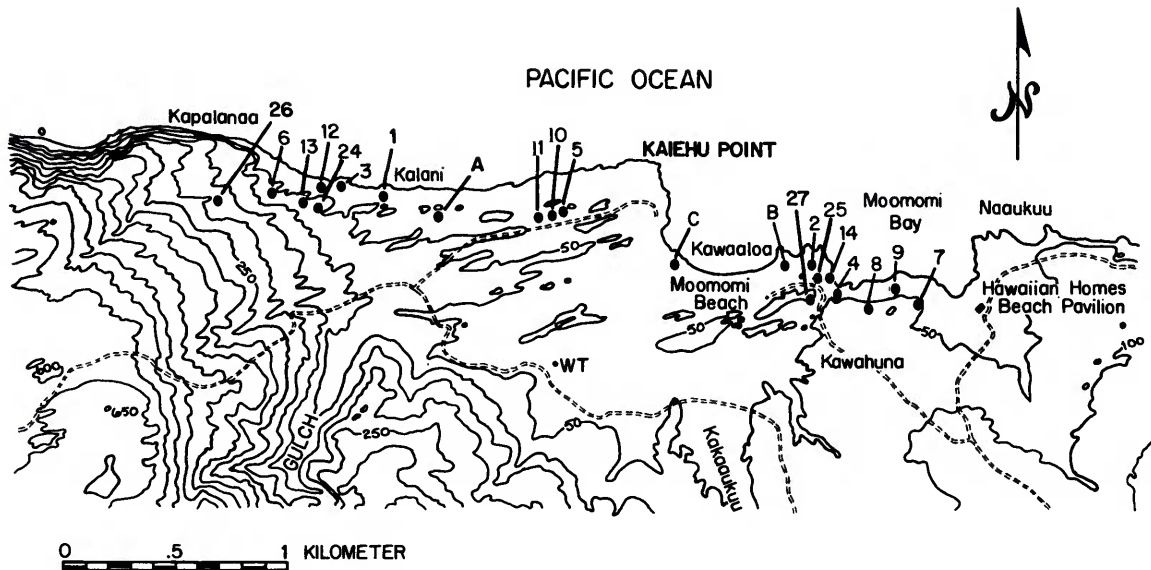


FIGURE 3.—Map showing locations of principal fossil sites in the Moomomi dunes, Molokai. (Modified from Molokai Airport Quadrangle, U.S. Geological Survey topographic map 7.5 minute series, 1968.)



FIGURE 4.—Partially exposed skeleton of the holotype of the flightless goose *Thambetothen chauliodous* from Site 1, Moomomi dunes, Molokai. The skull and some cervical vertebrae had been collected prior to jacketing the remainder of the skeleton. Partial associated skeletons are rare in the Molokai dunes and this is the only complete skeleton yet found in articulation. (Photograph by Victor E. Krantz.)

Stearns (1973a). The fossil goose occurred in the “upper lithified dune” described by Stearns (1973a:161), who considered most of the loose sands at Moomomi, including those extending far inland, to be of the same “epoch.” Underlying the “upper lithified dune” in the vicinity of Site 1 is an indurated bed of reddish sediment containing calcareous root molds and abundant land snail shells, described by Stearns (1973a:160):

The soil is windblown dust derived from a weathered basaltic terrane but . . . it contains abundant calcareous grains and the [land snail] shells appear to have been transported to the site by wind or water, or both. The soil can be traced in one place below sea level and, in another place, at least 100 feet above sea level. (Emphasis added.)

That part of the red sediment layer extended below sea level indicates that it must have formed at a lower stand of the sea, and for this reason Stearns tentatively correlated it with the Kawela low stand on Oahu, where a similar “soil” layer extends below sea level (Stearns, 1978). This

stand is thought to be of Wisconsinan age. Despite his reference to the land snail shells having possibly been water-borne, Stearns (1973a:161) nevertheless regarded the red layer as being eolian in nature and hypothesized that it had to have been blown from farther inland, "indicating that antitrades prevailed during its deposition."

This explanation is unlikely. Instead, the red layers in the Molokai dunes are more probably fluvial and deltaic in origin, not eolian, being deposited by temporary streams. We have observed the formation of such layers taking place on the Moomomi dunes today, where streams bearing heavily silted runoff flow out onto the active dunes immediately above the beach. Wave action on the sand here generally forms a dam, causing the freshwater runoff to spread out over a fairly wide area in which the red alluvium quickly settles. Although this sediment was probably of eolian origin, it is not transported to the dune area by wind. With very heavy rains or rough surf, the dam of sand may be breached, draining the lake behind it, although percolation through the underlying sand probably accomplishes this nearly as quickly. Sand rapidly blows back over the moist red mud and thus another layer of red sediment is formed. A repeated sequence of this sort is particularly well illustrated by an erosional remnant of sediment in the vicinity of Site 13. This tongue is exposed to a depth of 1–2 m and consists of reddish silty sand. Interspersed at intervals of about 0.3 m are several layers of nearly pure silt about 1–3 cm thick containing abundant snail shells. These layers appear to have formed in temporary pools. The red layers in the Moomomi dunes are therefore probably extremely localized features that have no correlative value, even within this dune system.

The red layer at Site 1 "is crisscrossed with calcareous root casts indicating it was once covered with dense vegetation" (Stearns, 1973a:160). This interpretation requires some amplification. Molds of plant parts (stems or roots) are common, sometimes extremely so, not only on the Moo-

momomi dunes, but also at Ilio Point and on the Kauai dunes as well (Figure 5). Those at Moomomi were described in some detail by Wentworth (1925:48–49). All of the molds that we have seen bear a strong resemblance in size and habitus to the thick, procumbent stems of the naupaka (*Scaevola sericea*), the dominant component of Hawaiian dune vegetation. There is thus no satisfactory evidence that the dunes themselves ever harbored any vegetation other than is typical of similar habitats today, although nearby areas doubtless had a fairly diverse lowland vegetation.

Beneath the soil layer at Site 1 is the "lower lithified dune" of Stearns (1973a), which extends below sea level and therefore also had to have formed at a low stand of the sea. It was tentatively correlated by Stearns with the Bellows Field Formation, supposedly of Illinoian age. At Moomomi, the sand itself, whether consolidated or not, is thought to have been "derived from the former marginal sea floor when it was bared during the Waipio low stand of the sea" (Stearns and Macdonald, 1947), which according to Stearns (1978) is of Illinoian age. At this time, sea level was evidently about 107 m (350 feet) lower than at present (Gascoyne et al., 1979). Most of the fossil sites at Moomomi are at elevations higher than Site 1.

There are eight numbered fossil sites (Sites 2, 4, 7, 8, 9, 14, 25, and 27) east of Kawaaloa Bay (Figure 3). Most of the fossils from these sites were collected by Joan Aidem prior to 1976; since then, relatively little has been found in this area, the dunes here being evidently more stable than those to the west.

Site 2 lies along the pathway to the beach about 50 m inland from the sea and 15 m above sea level. The sand here is considerably mixed with reddish sediment and fossils are noticeably stained. The site has produced mainly bones of the large flightless goose, *Thambetothen chauliodous*, single elements of a few other extinct species, *Branta*, and few seabirds.

Sites 14 and 25 lie about 50 m south of Site 2, site 25 being an eroded bank by a path near the



FIGURE 5.—Growth form of the naupaka, *Scaevola sericea*, and calcareous molds as found in situ on the Makawehi dunes on Kauai. These molds appear to form around the stems of *Scaevola* and do not indicate the former presence of any vegetation other than that characteristic of dunes today. (Photograph by C.J. Ralph.)

adjacent road. These sites have produced only a few bones of seabirds and shorebirds. Site 7, located 50 m from the sea at about 23 m elevation, produced only a few bones of *Thambetochen* and a pedal phalanx of an extinct owl.

Site 8 is in a large exposure of loose, shifting sand about 200 m from the sea and at about 30 m elevation. It was originally a very productive site, yielding many bones of larger birds, some of which were associated: the extinct long-legged owl (particularly well represented), *Thambetochen chauliodous*, *Branta*, *Corvus*, the flightless ibis *Apteryx glenos*, rails, seabirds, and a few small passerines, including a fossil owl pellet containing remains of an extinct species of *Ciridops*. Fragments

of heavy egg shell, most likely of *Thambetochen*, were quite common here.

Site 9 lies about 30 m north and 100 m east of site 8. It produced little other than a few seabirds, although a sand quarry just inland from here yielded fragments of *Thambetochen* and a skull and mandible of a large species of *Corvus*. The diagnostic fused pedal phalanges of an extinct eagle of the genus *Haliaeetus* were found just beyond the west end of this quarry in 1980.

Site 27 is a steep bank of sand that was formed at least partially as the result of quarrying operations. In 1981, it yielded several well-preserved elements of an individual of *Thambetochen chauliodous*, as well as bones of *Numenius tahitiensis*, and *Pterodroma hypoleuca*.

The sites west of Kawaaloo Bay have generally produced bones more continuously than those east of the bay. The most fossiliferous area is a large east-west oriented depression (blowout) about 100 m long, situated 100 m from the ocean at 7 m elevation, behind the first ridge of dunes. Sites 5, 10, and 11 are merely subdivisions of this larger feature, which has yielded numerous bones of *Thambetothen chauliodous*, *Apteribis glenos*, *Corvus*, the extinct long-legged owl, *Branta*, rails, seabirds, shorebirds, and a few bones of the extinct eagle and small passerines. Fish bones, shells of edible limpets (opihī), the gastropod *Nerita* (pipipi), other mollusks, and crab claws are also concentrated here, probably as human refuse. Bird bones were usually found individually as they weathered out, although at times it seemed probable that certain lots came from a single individual. In 1976, Olson and Aidem found a sternum and a pelvis with articulated femora of the extinct long-legged owl, lying in association at the surface near the middle of the blowout. Further digging revealed much of the rest of the skeleton of this individual, including the complete skull with parts of the sclerotic rings and most of the palate in place, the mandible, both tarsometatarsi, wing elements, and the articulated toes. The various parts were scattered, however, over a distance of more than 3 m and at depths ranging from surface level to nearly a meter. The matrix was loose sand, and no bones of other species were encountered while digging out the owl. Much of a crow skeleton was found under similar circumstances toward the west end of the blowout, although the bones here were more nearly in a single level and the sand was slightly cemented with a white, powdery matrix. The circumstances of preservation at these sites suggest that bird remains were scattered about somewhat before burial. Certain parts, however, must still have been held together by skin or ligaments, as they remained in articulation. Burial by shifting sand must have been rather rapid, as these particular bones are in perfect condition, being unweathered by sun, wind, or rain, all of which cause very

rapid deterioration of exposed fresh bone in Hawaiian dunes.

Site 1, the type-locality of *Thambetothen chauliodous*, has been discussed in the preceding section and by Stearns (1973a).

Site 3, located 50 m from the ocean, yielded only a tarsometatarsus of *T. chauliodous*.

Site 12 represents a concentration of land snail shells in cemented dune and has produced few other fossils.

Sites 13 and 24 are about 50 m apart in a large, rather flat area of exposed sand behind the third ridge of dunes about 150 m from the ocean. Although less productive than sites 5, 10, and 11, this area has yielded associated partial skeletons of *T. chauliodous*, and disassociated elements of *Apteribis glenos*, *Corvus*, *Branta*, extinct long-legged owl, small rails, shorebirds, seabirds, and a few small passerines.

Site 6 is a steeply sloping blowout about 50 m from the sea that extends through about 15 m of elevation. Bones occur at the surface and in sufficient quantity below the surface to have rewarded random digging over a fairly large area. This appears to be a geologically active site and the sands here have probably been turned over repeatedly. Bones were never found in association and most of those that were dug out from below the surface bore signs of weathering. There is a complete admixture of bones of extinct birds with human cultural evidence such as opihī (edible limpet) and pipipi (*Nerita*) shells, other mollusks, crab claws, fish and chicken (*Gallus gallus*) bones, and even human bones. *Thambetothen* is well represented, as is *Apteribis glenos*, this being the type-locality of the species. *Corvus*, *Branta*, the extinct long-legged owl, and shorebirds have also been found here, as have three bones of the Hawaiian Hawk (*Buteo solitarius*), the only fossils of this species encountered on Molokai. Remains of petrels are particularly abundant at Site 6, which is dominated by hundreds of bones, including nestlings, of the Bonin Petrel, *Pterodroma hypoleuca*, a species now extinct in the main Hawaiian chain. Nowhere else in the Hawaiian islands have we found remains of this species in such abundance.

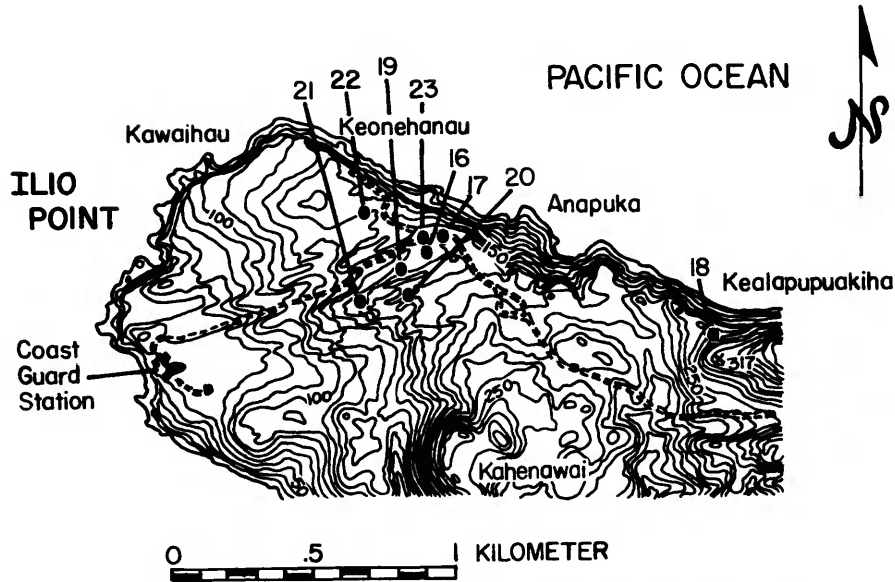


FIGURE 6.—Map showing location of principal fossil sites in the dunes at Ilio Point, Molokai. (Modified from Ilio Point Quadrangle, U.S. Geological Survey topographic map 7.5 minute series, 1968.)

Bones from Site 6 are almost never encrusted with sand, in contrast to most other fossil sites on Molokai. There is a possibility that many of the bones here, including those of extinct birds, were accumulated as human refuse.

Although extensive areas of dunes occur inland from Site 6, these have produced only bones of *Puffinus pacificus*, except for a partial skeleton of what appears to be a single individual of *Thambetochen* from a point about 300 m west (uphill) from Site 6, at an elevation of about 60 m (Site 26).

Three archeological sites are designated on the map of the Moomomi area (Figure 3) by the letters A, B, and C. Of these, only Site C has any ornithological significance. This is a cultural deposit exposed in a wave-cut wall at the west end of Kawaaloo Bay. It contained evidence of fire, burnt sea turtle bone, mollusk shells, fish bones and at least one discrete layer of fish scales, and portions of a skeleton of a goose (*Branta* sp.).

ILIO POINT.—Large outcrops of eolian calcareous sand occur on Ilio Point, at the northwestern

tip of Molokai, about 11 km (6 miles) west of Moomomi Beach. The dunes are consolidated in places. At one point they extend below sea level (Stearns and Macdonald, 1947), indicating that they were formed at a lower stand of the sea. Most of the dunes are presently situated above rather steep sea cliffs on both the windward and leeward sides. The marine erosion that formed these cliffs “occurred before the minus-60-foot [18 m] stand of the sea” and the dune rock is notched by 5- and 25-foot [1.5 and 7.6 m] stands of the sea (Stearns and Macdonald, 1947:28). Although there are exposures of loose sand over an area more than 1.6 km wide, the productive fossil sites at Ilio Point are largely restricted to a small area 1 km east-northeast of the abandoned Coast Guard station located on the southwest coast of the point (Figure 6). Most of these sites are at elevations between 49 and 55 m (160–180 ft).

Two of the sites at Ilio Point (16 and 20) are of outstanding importance in having produced quantities of bones of small passerines. Site 20 is located near the southwestern end of a long (250

m) valley or blowout in the dunes. In the floor of this blowout is an area roughly 5×15 m in which occurred numerous fossils. At the north end of this area the sand was somewhat consolidated in a white powdery matrix, where there was also a notable abundance of land snail shells. We screened intensively at this site on several occasions and obtained thousands of bones of small passerines, dominated by those of finch-billed drepanidines, but also including a diversity of other species of Drepanidini. We assume that this great accumulation of bones of small birds indicates this was the site of a roost of the extinct owl, bones of which were also recovered here, along with those of *Thambetochen*, *Corvus*, *Branta*, seabirds, shorebirds, and a species of small, flightless rail. In 1980 at a point about 200 m north of Site 20, we found much of an articulated skeleton of *Corvus* in a somewhat indurated lump of sand in place on an eroded portion of dune.

Sites 16, 17, 19, and 23 are part of one large blowout system located north of a ridge separating this area from the valley containing Site 20. The majority of the specimens here come from Site 16, a bank of shifting, pure calcareous sand in which fossils regularly weather out. Bones of small passerines could at times be found lying in place here, but seldom appeared to be directly associated. That these were originally accumulated by owls was confirmed by the discovery of a relatively intact pellet cemented by calcareous sand (Figure 7). Parts of the skeleton of *Apteribis glenos*, probably from a single individual, were found several years in succession scattered over a fairly wide area. We were never able to locate a single source containing a major portion of a skeleton, suggesting that most of the carcass had been disassociated before burial. In 1980, however, we did succeed in finding the pelvis of this ibis associated with a femur, radius, and carpometacarpus. Bones of *Thambetochen*, *Branta*, *Corvus*, the extinct owl, rails, shorebirds, and seabirds also occurred here in good numbers. Site 23 is a small pocket of sand that has produced bones of *Thambetochen*, *Corvus*, and *Branta*, as well as seabirds. Site 19, at the southeast end of the blowout,



FIGURE 7.—Remains of a fossil owl pellet from Site 16, Ilio Point, Molokai, containing bones of small passerines (Drepanidini). (Scale in mm; photograph by Victor E. Krantz.)

yielded a few associated bones of the extinct owl. Site 22 is situated about 250 m northwest of Site 16, where there is a barren extent of sandy soil with numerous bones of procellariids exposed. Two bones of *Thambetochen* were found here and in 1980 we took out much of an associated skeleton of *Branta* from a bank of blackish sandy sediment about 0.5 m below the top of the bank.

Site 18 consists of a considerable exposure of sand about 1 km east of the more productive areas. Only bones of *Puffinus pacificus* were found here, however.

KALAUAPAPA PENINSULA.—The low, flat Kalauapapa peninsula, projecting out from the cliffs on the north-central coast of Molokai, is the site of the most recent volcanic activity on the island (Macdonald and Abbott, 1970). In 1974, W.C. Gagné and F.G. Howarth explored the crater in the center of the peninsula and in a cave there they collected two bird bones. These are of interest in that both belong to species that are extinct on Molokai. One is the distal end of an ulna of *Apteribis* and the other is a coracoid of *Pterodroma hypoleuca*.

KAUAI

The first fossil birds from Kauai were found by Olson in 1976 in dunes on the southeast coast of

the island. We collected here in subsequent years, and Joan Aidem also conducted independent explorations. The main fossil-bearing sites (Figure 8) were in the expanse of dunes about 2 km (1.25 miles) east of Poipu, immediately northeast of Keoniloa [=Keonelo] Bay at a point designated "Makawehi." These dunes are briefly discussed by Macdonald et al. (1960). In places they are perched above sea-cliffs 10–15 m high, whereas in others they extend below sea level, indicating that parts of them formed during a lower stand of the sea.

Olson found concentrations of fossils in loose sand at three sites at Makawehi, all within about 100 m of one another (designated Sites K-1, K-2, and K-3). There were no lithological or physio-

graphic features that distinguished these localities from surrounding areas of dune. Joan Aidem also found lesser amounts of bones at three sites in these dunes (designated Sites 300, 301, and 302). Some of these sites are certainly different from, and none can be definitely identified with, any of the K series.

Site K-1 was notable for producing parts of a skeleton, including a very peculiar rostrum and mandible, of a large flightless goose. Unfortunately this site lay partly in a jeep trail, and the bones had been considerably scattered and broken. Bones of *Branta* sp., seabirds, a few passerines, and of an extinct owl were also found here.

Site K-2 (Figure 9) was discovered through encountering a partial skeleton of an albatross

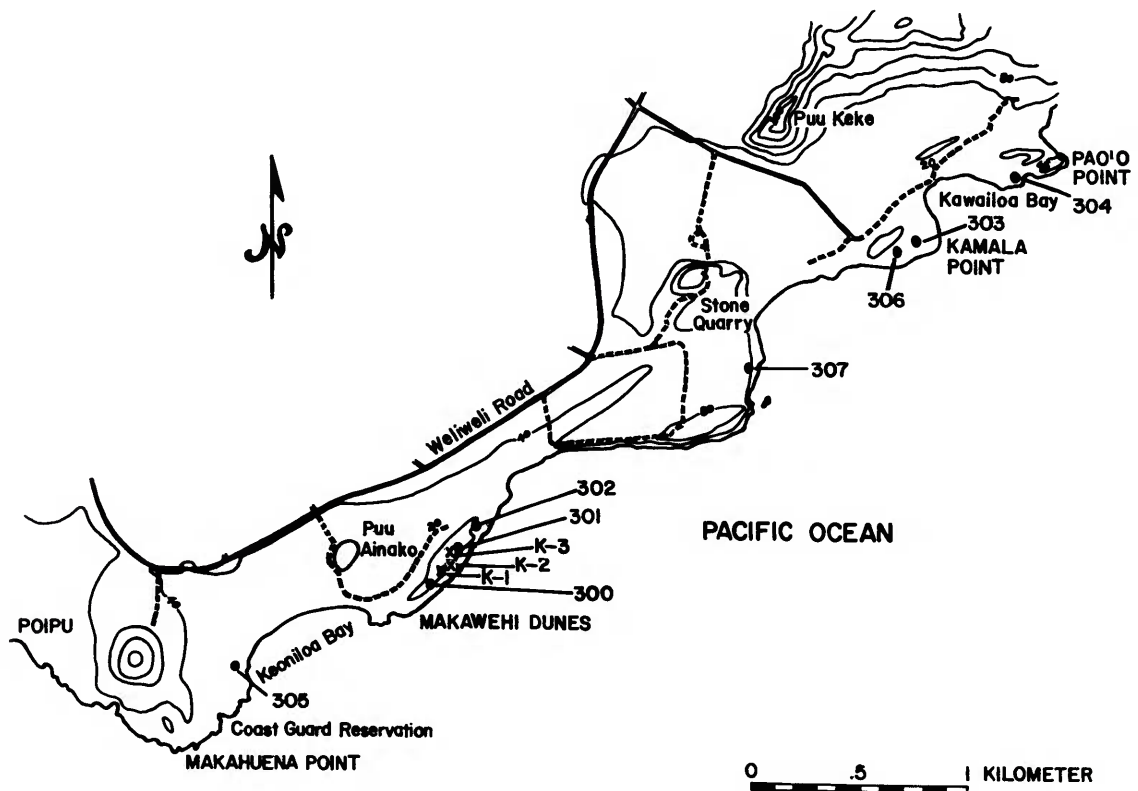


FIGURE 8.—Map showing location of principal fossil sites in and near the Makawehi dunes, Kauai. (Modified from Koloa Quadrangle, U.S. Geological Survey topographic map 7.5 minute series, 1963.)



FIGURE 9.—Fossil collecting operations at Site K-2, Makawehi dunes, Kauai. *Top view*, facing west; Site K-1 is indicated by an arrow. *Bottom view*, facing east; note the sea-cliffs over which these dunes are perched. (Photographs by Carol Pearson Ralph.)

(*Diomedea*) weathering out of the sand. In the process of removing this, most of the skeleton of a *Branta* was also uncovered, along with bones of small passerines. Intensive screening of the sand here yielded hundreds of bones of drepanidines and the meliphagid *Moho braccatus*, as well as a few bones of other passerines, a small rail, and seabirds. As with some of the Molokai deposits, the presence of small passerines is certainly due to predation by owls, and a particularly fine fossil owl pellet was found at Site K-2 (Figure 10).

Site K-3 was discovered in a similar fashion; the large bird that led to more extensive digging in this case was a third species of goose. Screening at this site also produced quantities of bones of small passerines, shorebirds, and seabirds. Although only about 75 m from K-2, the preservation at Site K-3 was different, the sand here being mixed with a white or gray powdery matrix that adhered to the bones, whereas at K-2 the sand was pure and bones were, for the most part, clean. Despite the fact that fewer passerine bones were collected at Site K-3, at least one species from this site did not occur in the more productive deposits at K-2.



FIGURE 10.—A fossil owl pellet from Site K-2, Makawehi dunes, Kauai. This pellet contained bones of one individual each of three species of drepanidines (*Loxops virens stejnegeri*, *L. parva*, and an extinct species of *Ciridops*). (Scale in mm; photograph by Victor E. Krantz.)

Additional fossils were found by Joan Aidem in dune deposits about 2.5 km (1.6 miles) north-east of Makawehi at Kamala Point (Lihue Quadrangle, U.S. Geological Survey 7.5 minute series topographic map, 1963). The major site (Site 303), discovered by John Maciolek and Quentin Tomich, was in and around a sand quarry (not the rock quarry 1 km to the west that is indicated on the Koloa Quadrangle map). This sand quarry produced a partial skeleton of the extinct owl, bones of *Branta* and the large flightless goose, a number of small passerines, seabirds and shorebirds. Site 304, about 0.5 km northeast of Site 303 in the vicinity of Pao Point, yielded bones of *Branta*, a carpometacarpus of the extinct owl, three passerine bones, and several bones of procellariids.

Olson found a few bones in the sandy area west of Keoneloa Bay near Keneaukai Point, as did Aidem, who designated this as Site 305. Only seabirds and shorebirds occurred here, most notably *Numenius tahitiensis*. Bones from this site are usually not encrusted with sand and appear fairly recent.

OAHU

Although Oahu has a number of large areas of dunes, no vertebrate fossils have as yet been found in them. Instead, fossil birds have been obtained in great numbers from sinkholes and other karstic features on the Ewa Plain in the southwestern part of the island at Barber's Point. These occur in an extensive area of raised coral-algal reef that is considered to be late Pleistocene in age. "Much of the exposed reef surface is close to 25 feet [7.6 m] above present sea level and, therefore, it probably grew during the plus-25-foot (Waimanolo) stand of the sea" (Macdonald and Abbott, 1970:355).

Normal solution weathering has produced hundreds of sinkholes and caverns in the limestone of this raised reef. These are not only conducive to deposition of fossils, but many of the larger sinks were modified and used in various ways by Polynesians, so the area has considerable

archeological significance as well. Barber's Point is the site of a proposed deep-draft harbor and warehouse complex, and consequently the area has been extensively explored, mapped, and described for the purpose of archeological reconnaissance and salvage prior to dredging and construction. Each of the fossil localities has received a permanent site number, either in the Bishop Museum or State of Hawaii archeological series of formal site designations (see Sinoto, 1976, 1978, 1979; Hammatt and Folk, 1981). As there is abundant documentation available for the fossil sites, we have not attempted to map or describe each of them here; instead we shall deal only with some of the more important localities.

In most instances we do not know precisely how bird bones were deposited at Barber's Point. The species composition and preservation in these sinkhole deposits does not indicate deposition only in owl pellets or only by entrapment, although both of these processes may have been involved. Many of the species are of a size compatible with having been prey of the extinct long-legged owl, but many are too large. Of these, a good number seem unlikely to have been subject to entrapment (crows, eagles, the large meliphagid, the owl itself). In some instances, accumulations of bird bones have resulted from prehistoric human activity.

The sinkholes and caverns at Barber's Point have yielded fossils in different types of depositional environments. The most common is in the floor of exposed sinkholes where sediments have accumulated, presumably as the result of rain and wind carrying in material from the surface above. At one site (Bishop Museum No. 50-Oa-B6-22), perfectly preserved fossils occur in a sheltered portion of a very large sink in the nearly pure, whitish dust formed by the disintegration of the surrounding limestone. Another site (50-Oa-B6-139) is a large flooded cavern that was exposed during quarrying operations. Associated skeletons of extinct birds were found here lying exposed on rocks and crevices under 4–5 m (13–16 ft) of fresh water.

This unique site is briefly described by Sinoto

(1978). It is a domed cavern about 11 m in diameter that is two-thirds filled with fresh water that deepens at one point to nearly 10 m. The water level fluctuates as a result of tidal influences, indicating that this is part of a subterranean lens floating above salt water. The site is about 1.3 km from the present coastline. The entrance to the cavern at the time of our visit was a 3 × 4 m hole in the ceiling that was made during quarrying operations in 1975. Prior to this, the cavern had evidently been almost completely sealed off by several feet of limestone overburden covering the present entrance. The total absence of any cultural material indicates that the cavern was not open during the prehistoric Polynesian period. The original entrance by which birds gained access to this chamber is no longer evident, and the remains we encountered probably have been entombed for several thousands of years.

Because of the depth of the water, all collecting was done with the aid of SCUBA gear. The major paleontological finds at this site were the remains of 12 individuals of two species of raven-sized *Corvus* and 5 or 6 individuals of a large meliphagid, presumably *Chaetoptila*. Most of these bones were found as nearly complete, associated skeletons (Figure 11) lying in a part of the cavern about 4.5–5 m deep, fairly near the present entrance. The deeper crevices were nearly sterile. Skeletons of petrels (*Pterodroma phaeopygia*) and isolated elements of other species such as the extinct owl, flightless rail, and the extinct thrush (*Phaeornis obscurus oahuensis*) were encountered here as well. Specimens were either lying directly on the rock surface or partially buried in soft, white sediment that appeared to be a precipitate of calcium carbonate crystals in the form of small flakes.

Along an underwater ridge in a shallower part of the cavern was a rather thick deposit of a more rubbly sediment containing abundant bones of *Pterodroma phaeopygia* as well as a few bones of a new species of small extinct petrel, and a few passerines and other birds, as well as many shells of small land snails. The bones here were disas-

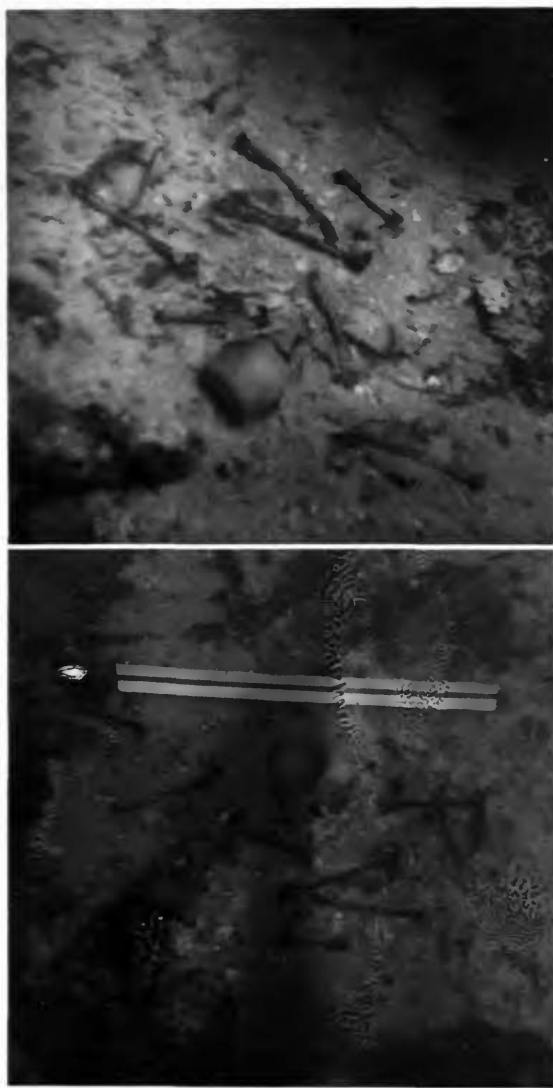


FIGURE 11.—Two views of an associated skeleton of the deep-billed *Corvus* in place at the bottom of a flooded cavern (50-Oa-B6-139), at Barber's Point, Oahu. The negatives were damaged by water. (Photographs by Aki Sinoto.)

sociated and many had a blackened appearance. These bones were removed partly by screening underwater (which had the effect of turning the water the color of milk) and partly by removing the matrix in screens for subsequent washing under more favorable circumstances. There must

have been a small crevice opening to the outside that was at least partly responsible for the deposition of bone in this limited area, as bones of *Rattus exulans*, and the postcontact introduced rodents, *Mus musculus* and *Rattus* sp. (either *rattus* or *norvegicus*), were recovered here.

As no remains of flightless birds other than a very few bones of small rails were represented at this site, we believe that the original opening through which large birds such as crows entered was a lateral one, and that the sink was not a vertical pitfall trap. The fact that no terrigenous sediments had accumulated on the floor of the cavern is further evidence of this. The cave could not have been filled with water at the time the corvid and meliphagid skeletons were deposited, as is indicated by their high degree of association. Had there been water in the cave, the carcasses would have floated and bones would have been scattered randomly about as decomposition progressed. Furthermore, stalactites occur under ledges at least a meter below the present water level, and a skeleton of *Pterodroma phaeopygia* (BBM-X 154815) found about 6–8 m below the surface was almost completely encased in drip-stone, which could not have formed had the cave been filled with water at the time. Thus, the age of the associated skeletons is perhaps no younger than Wisconsinan, when lowered sea levels would have depressed the water table. Considering that these skeletons are then at least 10,000–15,000 years old, their preservation is more than extraordinary, as most of them are absolutely perfect, appearing like modern bone with very delicate processes intact.

Generally it is the larger and deeper of the open, sediment-filled sinkholes that are most productive of fossils. Of the many sites examined, four stand out as particularly significant: Bishop Museum Nos. 50-Oa-B6-78, 50-Oa-B6-148 (data from Sinoto, 1978), and State of Hawaii Nos. 50-80-12-2624 (formerly 9670-P1) and 50-80-12-2763 (formerly 2706-22b) (data from Hammatt and Folk, 1981). Site 50-Oa-B6-78 is a large sinkhole with an opening 1.5×2.5 m in diameter and a depth of 1.9 m to the surface of the sediment. It

contained a crudely built wall of limestone slabs but the sediment contained no other sign of cultural activity. This site was dug to a depth of about 250 cm (not counting the overlying recent layer of largely organic material). Bird bones, including those of extinct species, were found mainly in the upper 50 cm of brownish alluvium and eolian silt, whereas the lower 150 cm were sterile. Site 50-Oa-B6-148 had an opening 1×1.5 m and a depth of 270 cm to the surface of the sediment. Beneath 6 cm of recent overburden were two layers of yellowish-brown to reddish-brown sediment containing bird bones, including extinct species, to a depth of about 28 cm, beneath which the sediments were sterile.

Site 50-80-12-2624 is a large sinkhole with no apparent manmade modifications or cultural evidence. The opening is about 1.5×3.5 m and the profile is somewhat bell-shaped with considerable overhang, so that the floor of the sink is about 3×4 m in diameter. Depth to sediment surface was about 4 m. The areas nearest the walls were more productive, and excavations were carried out around virtually the entire perimeter. Beneath the recent organic layer at the surface were largely homogeneous deposits of brownish or reddish sediment that were excavated to a depth of 30–40 cm. Bones of birds, including extinct species, occurred throughout these sediments but were more abundant in the upper 20 cm; extinct species were often found within the upper 5–10 cm. Remains of the Polynesian-introduced rat, *Rattus exulans*, were common at this site and were found at most levels, but were concentrated in the upper 20 cm. These were disassociated and appeared to have been deposited in the same manner as the bird bones, rather than being intrusives as a result of the rats burrowing into the sediment.

Site 50-Oa-B6-22 (data from Sinoto [1976] and our field notes) is among the largest and most important of the sinkholes in the Barber's Point area and shows considerable evidence of cultural modification and use (Figure 12). It is about 9 m in diameter and 6 m deep, with large areas of the floor being well-protected by overhang. Near one

wall is a large man-made stone cairn that was probably built to facilitate entrance to and exit from the sink. Fossils were obtained here from two quite different areas. Because detailed descriptions of the stratigraphy and lithology of these deposits will be presented elsewhere (James I. Mead et al., in prep.), we present only a brief discussion here. The richest deposits were located in the southwest part of the sink in an area protected above by a large overhang and further sheltered by a wall of rubble separating it from the main part of the sink (Figure 12). A test pit was excavated in this area by A. Sinoto and other members of a Bishop Museum survey team in 1976, and we extended this pit slightly in 1980. We conducted extensive excavation of this area in 1981. The sediments in this sheltered area were extremely dry and dusty. The upper 10 cm or so consisted of a darker layer beneath which was a homogeneous deep layer of whitish or grayish sediment that appeared to consist mainly of limestone dust. In places there were numerous thin layers or lenses of whiter sediment, almost certainly ash. This deposit had to be excavated very carefully to prevent slumping. Excavation could be done with fine brushes and all sediment was removed and screened through window screen (ca. 1.6 mm mesh). A firepit was uncovered in the original test pit but this secondary disturbance did not appear to extend into the areas excavated in 1981. Bones from this protected area are very well preserved.

The bones of extinct birds were more abundant in the upper parts of the lighter colored sediment layer, where they were invariably disassociated and lying in a more or less horizontal plane. Bones were less abundant deeper in the sediment. We did uncover a partial tibiotarsus, tarsometatarsus, and basal pedal phalanges of a juvenile individual of *Thambetochen* in articulation lying approximately 80–90 cm below the surface, but this was the only definitely articulated specimen recovered at this site.

Not only were bones of extinct birds disassociated, but it also appears that the birds were not deposited as complete skeletons. Although we



FIGURE 12.—Eric Komori (left) and Aki Sinoto (right) at the big sinkhole at Barber's Point, Oahu (Site 50-Oa-B6-22). The most and the best fossils from this site came from dry dusty sediments in the darkened area beneath the overhang at the top of the picture. The stone cairn behind Komori, and the rock wall extending from it to the large rockfall behind Sinoto, are part of the archeological features of this site. A test pit in the exposed sediments in the middle of the sinkhole shows at the right. (Photograph by C.J. Ralph.)

recovered virtually every bone from the greater part of the sediments in the sheltered overhang, we do not have close to a complete representation of skeletal elements for the number of individuals represented. For some of the rarer species only a few bones were found. Apart from the fire pit found in the original test excavation, there was little cultural evidence in the sheltered sediments, although a few shells of marine mollusks were recovered and fish bones were also present. Some of the latter may have come in as stomach contents of petrels, but others are too large to have arrived in this manner. Bones of the Pacific Rat were found commonly in these deposits, often in

direct association with those of extinct birds (page 31).

Bones of extinct birds were also recovered from pits excavated in the moister and more rubbly sediments in the exposed central portion of the sinkhole, although they were much less abundant and not as well preserved as in the sheltered area. Cultural evidence was more frequently encountered here, however. Excavations revealed that large pits had been dug previously in this part of the sinkhole, suggesting that it may once have been used for agricultural purposes. In 1981, McCoy and his associates uncovered a hearth in this area that yielded datable charcoal and bird bones (see page 31).

Another interesting archeological site at Barber's Point is Site 50-80-12-2763, a small bell-shaped sinkhole about 2.5 m in diameter with an opening about 1 × 0.5 m (Hammatt and Folk, 1981). The sediments here contained abundant cultural evidence, including a grindstone and other artifacts, marine mollusks, and bones of fish, chicken (*Gallus*), *Rattus exulans*, and a larger mammal, probably dog. The most abundant remains were those of the Dark-rumped Petrel (*Pterodroma phaeopygia*), which were present in a great concentration of thousands of bones from dozens, more likely hundreds, of individuals. Interestingly, all elements of the skeleton were represented and there was no evidence of breaking or charring, suggesting that the birds were cooked by steaming. This is in contrast to the archeological sites on southeastern Oahu (see below), where bones of petrels were most often broken. In addition to *P. phaeopygia*, which is now extinct on Oahu, remains of seven species of birds that are either extinct altogether or extinct on Oahu were recovered at this site (p. 30).

We have also examined and identified bird bones from two archeological sites excavated by the Bishop Museum in 1950 and 1951 in the southeastern part of Oahu (Emory and Sinoto, 1961). The first of these is known as the Kuliouou Shelter (or on specimen labels as "Niu rock shelter") and is Site O 1 of Emory and Sinoto (1961) (now designated as 50-Oa-A2-1). This site was described as "a remnant of a lava tube which forms a spacious natural shelter . . . a little more than 100 feet above sea level and 200 yards in from the beach" (Emory and Sinoto, 1961:4). Sediments on the floor of this shelter contained abundant evidence of former occupancy by Polynesians, including many artifacts and food remains. Charcoal taken from a limited area at depths between 18 and 24 inches yielded a radiocarbon age of A.D. 1004 ± 180 years. It is interesting that the excavators noted that bird bones tended to be most numerous as one "neared the sterile [lower level of the] floor, particularly at its juncture with the fertile [upper level]," thus possibly indicating "the start of occupation on this

part of the coast, when sea birds would have been most numerous" (Emory and Sinoto, 1961:17). The most abundant bird remains from this site are those of Dark-rumped Petrels and Newell's Shearwaters (*Pterodroma phaeopygia*, and *Puffinus puffinus*), as well as one bone of the Bonin Petrel (*Pterodroma hypoleuca*); all three of these species are now extinct on Oahu. Also included is a tibiotarsus of a medium-sized extinct rail and a humerus of the extinct, flightless goose (*Thambetochen* sp.). Unfortunately, there is no longer any record of the exact level from which these specimens were recovered.

The other site in this area from which we have examined bird bones is known as the Hanauma shelter, or Site O 3 (Emory and Sinoto, 1961) and is also designated as "Koko Head" on specimen labels. This site was situated under an overhanging portion of the sea cliff at Hanauma Bay. Its former inhabitants were obviously heavily dependent on the sea, the principal food remains here being shells of marine mollusks and fish bones. In contrast to the Kuliouou shelter, the most abundant bird bones here are those of the Wedge-tailed Shearwater (*Puffinus pacificus*) and *Pterodroma hypoleuca*. Whereas the former manages to persist in small numbers on Oahu, the latter is extinct there.

Ages of the Fossil Deposits

We have used three methods of dating deposits from which we obtained bird remains, of which the only direct means was by radiocarbon analysis. Otherwise we have inferred the ages of specimens either by their occurrence in a certain cultural context or by their association in deposits with organisms known to have been introduced to the archipelago by Polynesians before European contact.

The radiocarbon ages that are available thus far are shown in Table 2. Snail shells associated with the holotype of *Thambetochen chauliodous* at Moomomi, Molokai, were dated at 25,150 ± 1000 radiocarbon years B.P. (Stearns, 1973a). This at first prejudiced us toward considering that the

TABLE 2.—Radiocarbon ages in radiocarbon years B.P. from materials obtained in Hawaiian fossil sites (SI = Smithsonian Institution Radiation Biology Laboratory; HIG = Hawaii Institute of Geophysics (from Stearns, 1973a))

Sample No.	Material	Locality	Age
HIG-35	land snail shells	Site 1, Molokai	25150 ± 1000
SI-3791A	small land snail shells	Site 20, Molokai	5245 ± 60
SI-3791B	large land snail shells	Site 20, Molokai	5510 ± 65
SI-3792	land snail shells	Site K-2, Kauai	6740 ± 80
SI-3793	crab claws	Site K-2, Kauai	5145 ± 60
SI-5136	charcoal from hearth	50-Oa-B6-22, Oahu	770 ± 70

remaining dune deposits on Molokai and Kauai were likewise probably of Pleistocene age. This prejudice was strengthened by the considerable faunal differences found among the various deposits, which we were inclined to attribute to differences in chronology. Radiocarbon ages from land snail shells and crab claws from the dune deposits on Molokai and Kauai, however, indicate a Holocene age for these deposits (Table 2). It should be noted that the flightless goose skeleton from Site 1, where Stearns (1973a) obtained a Pleistocene age, was articulated and exposed in place in a vertical outcrop near sea level, whereas other bones found on Molokai were generally found on or near the surface of blowouts at higher elevations.

Radiocarbon ages from land snail shells are prone to error because the snails in life may take up carbonate containing "dead" carbon in their shells. This has the effect of making the radiocarbon ages obtained from carbonate in snail shell appear older than they actually are. Thus, the dates from the land snail shells from Molokai and Kauai are maxima, and the deposits from which they came could possibly be younger than the ages given for them in Table 2. Interestingly, the crab claws from Kauai gave a younger age than the snail shells from the same deposits, and if the

discrepancy is due to dead carbon in the snail shells, then the Molokai ages may be too old by a similar amount. Regardless, there are remains of many extinct species of birds from Molokai and Kauai that are almost certainly much younger than Pleistocene, so that something other than Pleistocene climatic changes must have caused the extinction of these species.

Polynesians apparently arrived in the Hawaiian Islands only about 1500 years ago, so any bird remains found in a cultural context are likely to be less than 1500 years old. Absolute age, however, is of less biological consequence than establishing the contemporaneity of extinct birds and Polynesians, as it is our main concern to show that prehistorically extinct species survived until the arrival of man.

We have found bones of *Branta* sp. in an archeological deposit on Molokai, where no resident geese are known to have occurred historically. In the cultural deposits from the Mauna Kea adz quarry on Hawaii there are two species of small rails, whereas only one species was recorded on the island in the historic period. From Site 50-80-12-2763 at Barber's Point, Oahu, where deposits appear to be purely cultural midden, we have bones of *Pterodroma phaeopygia*, *Oceanodroma castro*, and *Branta* sp., which are extinct on Oahu, as well as those of an extinct species of petrel (*Pterodroma*), an extinct flightless goose (*Thambetochen*), an extinct crow (*Corvus*), an extinct meliphagid (*Chaetoptila*), and an extinct flightless rail, none of which are known to have survived into the historic period. From the archeological sites on southeastern Oahu are individual bones of *Thambetochen* and an extinct rail, as well as numerous bones of seabirds that are now extinct on Oahu, or in the entire main archipelago, in the case of *Pterodroma hypoleuca*. Because of the absence of precise excavation data, the possibility that the goose and rail bones may have come from a lower, noncultural layer cannot be ruled out, although the excavators of this site would have been unlikely to have spent much time digging in the culturally "sterile" lower layers. The seabirds

from these sites are definitely of cultural derivation.

Among the many remains of extinct birds excavated from the large sinkhole (Site 50-Oa-B6-22) at Barber's Point, Oahu, are some that were found in and around a hearth. Some of these are fire-blackened. A charcoal sample from this hearth was dated at 770 ± 70 years B.P. (Table 2). The bones associated with this date include those of *Pterodroma phaeopygia*, *Branta* sp. (a form larger than recent examples of *B. sandvicensis*), a vertebra of a goose larger and quite different from *Branta*, and two bones of *Rattus exulans*.

Contemporaneity of extinct birds and man can also be inferred from the co-occurrence of bones of extinct birds with remains of organisms that were introduced adventitiously to the Hawaiian Islands by Polynesians, before the arrival of Europeans. The Pacific Rat, *Rattus exulans*, is a notable example. Lizards also arrived with the Polynesians and should prove useful as temporal indicators. But the greatest potential for such relative "dating" may lie in stratigraphic studies of land snails (Kirch and Christensen, 1981; Christensen and Kirch, 1981).

Land snails in Hawaii can be classified as follows: (1) native endemics, (2) species introduced by Polynesians prior to European contact, or (3) species introduced subsequent to European contact. Thus, by identifying land snails in cores from Barber's Point the deposits could be divided roughly into three units distinguished by the two introduction events (Kirch and Christensen, 1981; Christensen and Kirch, 1981). In samples from Site 50-Oa-B6-78, the prehistorically introduced snail genus *Lamellaxis* was found only in the upper two-thirds of the layer that produced the most bones of extinct birds. At Site 50-80-12-2624, *Lamellaxis* occurred throughout the deposit, as did bones of *Rattus exulans* and extinct birds. Bones of *Rattus exulans* were found in place adjacent to bones of extinct birds in the fine dust deposit of Site 50-Oa-B6-22, and bones of these rats and of lizards were obtained in screens at almost all levels. As an indication of the recency of deposition of bones of extinct birds at this site,

an intact mandible of the giant Oahu grosbeak finch ("*Chloridops*") was uncovered in sweeping away the dust and rubble from part of the sheltered sediments preparatory to excavation. This specimen was at the surface among rocks that formed part of the wall that had been built to enclose the sheltered area and was not buried at all. Evidently much of the deposition of bird bones at Barber's Point was subsequent to the arrival of Polynesians, about 1500 years ago.

Species Accounts

We intend to give here only a bare outline for each of the species obtained as fossils. In some instances we depart from currently accepted nomenclature. The Hawaiian finches we consider to be no more than a tribe (Drepanidini) within the subfamily Carduelinae. We place this group in the Fringillidae as delimited by Sibley (1970), who includes among them all the so-called "New World nine-primaries oscines" except the vireos. This treatment is supported by Raikow's (1978) myological studies, although Raikow adopted a more conservative nomenclature. It has proven convenient to refer as "subgenera" to the various generic names that were once applied to different sections of the genus *Psittirostra* (see also Banks and Laybourne, 1977). We recognize the genus *Heterorhynchus* for the species *lucidus* and *wilsoni*, now usually included in *Hemignathus*. Also, our studies show that the six allopatric populations that Amadon (1950) considered to be subspecies of *Loxops maculata* comprise a minimum of four species in three different genera. When it comes to lumping taxa, however, we have not made all of the changes in nomenclature that we will eventually adopt. It should also be noted that the studies of Ames (1975) suggest that there is little or no evidence to ally the Monarchinae (represented in the Hawaiian Islands by *Chasiempis*) with the true Muscicapidae, and that *Phaeornis* (along with *Myadestes*) is doubtfully referable to the Turdinae (see also Sibley, 1973). In the case of *Chasiempis*, we have followed the familial and

subfamilial nomenclature proposed by Boles (1981).

PROCELLARIIFORMES

DIOMEDEIDAE

Diomedea immutabilis: The Laysan Albatross breeds in the Leeward Islands, evidently nests sporadically on Niihau, and has recently colonized (or recolonized, as the case may be) Kauai. Fossils of this species occur rarely in the Kauai deposits.

PROCELLARIIDAE

Pterodroma phaeopygia: The Dark-rumped Petrel is known historically from all of the larger main Hawaiian islands except Oahu. It was subsequently extirpated from all but Hawaii, Maui, and Lanai. Remains were found abundantly in lava tubes on Hawaii, and in fossil and midden deposits on Molokai and Oahu. It was not found in the Kauai deposits. The species also occurs in the Galapagos Islands.

Pterodroma hypoleuca: The Bonin Petrel breeds only in the Bonin and Volcano Islands and in the Hawaiian Leeward Islands. Hitherto it was unknown in the main Hawaiian chain, but remains were sparsely scattered in a number of sites on Molokai (Moomomi and Ilio Point), and were abundant at Site 6, which may be partly or entirely archeological midden. A single bone was found in Kahuhako Crater on the Kalaupapa Peninsula, Molokai. The species occurs among the archeological material from Hanauma and Kuliouou shelters on Oahu, but has not been positively identified from Barber's Point, where the following species occurs regularly. *P. hypoleuca* also occurs uncommonly in the Kauai deposits. The species once inhabited the main Hawaiian islands, where it was evidently extirpated subsequent to the arrival of Polynesian colonists.

Pterodroma sp.: This curious undescribed species was found in several different sites at Barber's Point, Oahu, including the flooded cavern. It is

smaller than *P. hypoleuca* and larger than *Bulweria bulwerii* and has numerous distinctive characters of its own. It is definitely not referable either to *Bulweria fallax*, which has been taken once in the Leeward Islands (Clapp, 1971), nor to *Pterodroma macgillivrayi* (*Bulweria macgillivrayi* auct.), known from a single specimen from Fiji.

Bulweria bulwerii: Bulwer's Petrel breeds on various islands in the Atlantic and Pacific Oceans. It is found in the Hawaiian Leeward chain and on offshore islets in the main Hawaiian group. Remains were found uncommonly both in midden and fossil deposits on Molokai and Oahu, and as fossils on Kauai.

Puffinus pacificus: The Wedge-tailed Shearwater is a widespread species that is still found breeding through most of the Hawaiian Leewards and in the main group on Niihau, Kauai, Mokolini Islet off Maui, and islets off Oahu. Abundant remains were found in the loess deposits on the south end of Hawaii and in virtually all of the Molokai sites. On Oahu, very recent bones were found at Kahuku Point, at the northern tip of the island, where the birds possibly still attempt to nest. Bones were also recovered from the Hanauma shelter and were very rare in the Barber's Point deposits. This species dominates the seabird fossils found in the Kauai dunes, where some birds still attempt to nest, although many of them are killed by dogs.

Puffinus puffinus: Of the widespread forms of the Manx Shearwater, the subspecies *P. p. newelli* is endemic to the main Hawaiian Islands, where it is known to have bred historically on Hawaii, Maui, Molokai, and Kauai, with occasional individuals taken on Oahu. The only certainly known breeding populations of this subspecies are now restricted to Kauai. Remains of this species occur sparsely in the deposits on Molokai, and at Barber's Point and the Kuliouou shelter on Oahu. It did not occur in the Makawehi deposits on Kauai, but we found two bones, one of which, a humerus, had been made into an awl, in midden deposits at the northern end of the island at Kalihi Point. We have no fossil record of the osteologically similar species *Puffinus nativitatis*,

which breeds in the Leeward Islands and on islets off Oahu.

Puffinus lherminieri: Audubon's Shearwater is a circumtropical species that is found through much of the Pacific but was hitherto unknown in the Hawaiian Islands. As a fossil it was found very rarely on Molokai and Oahu. Although found at six sites on Molokai, no more than one individual is indicated at any one site. On Oahu, the only site at Barber's Point yielding this species contained bones of at least two individuals, however.

OCEANITIDAE

Oceanodroma castro: Harcourt's Storm Petrel has a disjunct distribution in the Atlantic and Pacific Oceans. In the Hawaiian chain it has been taken only on Kauai, though its breeding grounds there remain unknown. Bones of *O. castro* were found in many of the fossil sites at Barber's Point, Oahu, in some of which it was common. We obtained only a few scraps of it on Molokai, however, and then only from Site 20, where we conducted the most intensive screening for small bird remains. Curiously, we did not recover any fossils of this species from Kauai. The Sooty Storm Petrel, *Oceanodroma tristrami*, which breeds in the Leeward chain, is not known historically from the main Hawaiian Islands, nor does it occur in any of the fossil deposits we studied.

PELECANIFORMES

SULIDAE

Sula dactylatra: Fossils of the Masked Booby are very scarce on Molokai (two bones from Ilio Point) and only slightly commoner in the Kauai dunes, with individuals from four sites, including one nonflying juvenile. All three species of tropical boobies occur in the Hawaiian chain. The Red-footed Booby (*Sula sula*), however, nests mainly in trees, and the Brown Booby (*Sula leucogaster*) nests on cliffs. Therefore, it is not unusual that these two species are not represented as

fossils, whereas *S. dactylatra*, the largest of the three, nests on level ground; thus its remains have a better chance of being preserved. Tropicbirds (Phaethontidae) and frigatebirds (Fregatidae), both common seabirds in the Hawaiian archipelago, are probably absent as fossils in the Hawaiian deposits because they are likewise mainly cliff- and tree-nesters, respectively. A similar pattern of differential preservation was noted among the Pelecaniformes of the South Atlantic islands of St. Helena and Ascension (Olson, 1975; 1977).

CICONIIFORMES

PLATALEIDAE

Apteribis glenos: Site 6 on Molokai is the type-locality of this flightless ibis (Olson and Wetmore, 1976), which occurs in fossil deposits both at Moomomi and Ilio Point. A single bone is also known from the Kalaupapa Peninsula, Molokai.

Apteribis sp.: An incomplete associated skeleton of a flightless ibis was recovered from the lower Waihoi Valley lava tube on the east side of East Maui. This was tentatively referred to *A. glenos* by Olson and Wetmore (1976). Since then, however, additional material from Molokai has established that the Maui bird represents a different species. The genus *Apteribis* appears to have been restricted to the islands that once formed Maui Nui. It is unlikely that an ibis occurred on Oahu, for if it had, it seems probable that its remains would have been found at Barber's Point by now.

ANSERIFORMES

ANATIDAE

Branta sandvicensis and *Branta* sp.: The Hawaiian Goose, or Nene, is known historically mainly on sparsely vegetated lava flows at high elevations and in mountain parklands on the island of Hawaii, although early in the historic period there may have been a population in a

similar habitat at the summit of Haleakala on Maui (Kear and Berger, 1980).

Fossil remains of *Branta* have now been found on Hawaii, Molokai, Oahu, and Kauai. Originally, all of the main islands were probably home to *B. sandvicensis* or closely related taxa. Because some of the fossil material differs from the few skeletons of *B. sandvicensis* available for comparison, final determination of the status of the various fossil populations awaits our more detailed study. Nevertheless, the specimens from Hawaii, Molokai, and Kauai are very similar to the extant form, whereas those from Oahu appear to be different and for the time being, can only be referred to as *Branta* sp. (but see the following species).

Fossils of *Branta* from Molokai, Kauai, and Oahu are all from the lowlands near the present shore line, showing that the genus is not naturally restricted in the Hawaiian Islands to the high altitudes and harsh environments it generally inhabits at present. We also have remains from middens on Oahu and Molokai, indicating that *Branta* became extinct on those islands after Polynesian settlement. It probably was able to survive into the historic period on Hawaii, and possibly Maui (Baldwin, 1945), because these are the only islands in the chain with subalpine zones that provide suitable (although perhaps marginal) habitat for the Nene, but not for Polynesians.

Geothen rhuax: The bones of this extinct goose, found fortuitously under a lava flow during the digging of an irrigation tunnel on Hawaii, were the first fossil bird remains to be described from the Hawaiian Islands (Wetmore, 1943). Additional bones, probably belonging to the same species, have been recovered recently from a lava tube north and west of the original site. This species was considerably larger than *Branta sandvicensis* and was thought by Wetmore (1943) not to be closely related.

Medium Kauai goose: Associated bones representing much of the skeleton of one individual of an extinct goose were found in the Makawehi dunes on Kauai. This goose is larger than *Branta*

sandvicensis but the wings are considerably reduced, though they were perhaps still functional. The relationship of this goose to other taxa is as yet uncertain; it may belong to an undescribed genus.

Thambetothen chauliodous: This was the second fossil bird to be discovered in the Hawaiian Islands. It is a large, flightless goose with an extremely reduced wing, keelless sternum, very robust hind limb, and a heavily ossified bill having bony toothlike projections on the rostrum and mandible (Olson and Wetmore, 1976). The holotype is a nearly complete associated skeleton. Much additional material has subsequently been found both at the Moomomi dunes and at Ilio Point, Molokai. Fragments of thick eggshell, probably belonging to this species, are not uncommon at these sites. A few similar fragments were also found in dunes at Waiehu, Maui, the only possible indication so far that this, or a similar species, occurred on that island.

Thambetothen sp.: Remains of an undescribed species of *Thambetothen* are abundant in the sediment-filled sinkholes at Barber's Point, Oahu. It resembles *T. chauliodous* but has a less robust hind limb and differs in bill morphology. Bones of this species were also found in midden sites at Barber's Point and at Kuliouou Shelter, suggesting that the goose survived into the prehistoric Polynesian period.

Supernumerary Oahu goose: Just when we thought we knew all about the Barber's Point fossils, we uncovered a partial rostrum of a goose that is so distinctive that it can only represent a third species for the island. It bears some similarity to the rostrum in *Thambetothen* but has no tooth-like projections and is not as heavily ribbed and grooved on the palatal surface. We have not yet determined how to identify the postcranial elements of this species and it is possible that the seemingly greater variation in the *Branta* from Oahu may be partly due to inclusion of specimens of this species.

Large Kauai goose: Another massive flightless goose is represented by an incomplete, partially associated skeleton and a few additional

remains collected in the Makawehi dunes on Kauai. It is presumably related to *Thambetothen*, as the elements of the wing and leg are similar in general proportions, and it is at the same evolutionary grade of flightlessness. The rostrum and mandible, however, are so distinct from those of *Thambetothen*, or any other known bird, that a new genus will be required to accommodate it.

Large Hawaii goose: Evidence of a third goose from the island of Hawaii comes from a lava tube above Kailua that had been occupied by prehistoric Polynesians (see p. 14). Scant remains from this site include a partial cranium indicating a goose perhaps larger than any of the other species yet found in the archipelago and certainly larger than either *Branta sandwicensis* or *Geochen rhuax*. Its affinities cannot be determined without additional material, however.

Anas cf. *platyrhynchos wyvilliana*: The Hawaiian Duck, or Koloa, has been recorded historically from all the main islands except Lanai. It is usually regarded as being a subspecies of the Mallard, *Anas platyrhynchos*. Bones of a species of *Anas* the size of *A. p. wyvilliana* were very rare in the Moomomi dunes on Molokai, and on Kauai and Oahu.

ACCIPITRIFORMES

ACCIPITRIDAE

Haliaeetus sp.: In the historic period, two species of eagles have been recorded in the Hawaiian Islands as vagrants. The fossil record, however, shows that an endemic species of the genus *Haliaeetus* once existed here. Bones of this eagle, from at least three individuals, have been collected in the Moomomi dunes on Molokai, and at least one, and probably two other individuals are represented at Barber's Point on Oahu.

Buteo solitarius: The Hawaiian Hawk is known historically only from the island of Hawaii, a distribution that puzzled Amadon (1950), as he could think of no convincing reason for the apparent failure of the species to colonize other islands in the chain. That it once had a wider

distribution is established by three bones from a single site on Molokai. Bones of this species have also been found in a lava tube on Hawaii.

Accipiter sp.: A coracoid, tibiotarsus, tarso-metatarsus, and carpometacarpus from two sites at Barber's Point, Oahu, are from a small species of *Accipiter* somewhat larger than *A. striatus*. This is the first and only indication of hawks of this genus in the Hawaiian Islands. The fossils may be presumed to be from an endemic species, but the material is possibly insufficient to establish this with certainty.

GRUIFORMES

RALLIDAE

Porzana sandwichensis: Apart from the extant subspecies of *Gallinula chloropus* and *Fulica americana*, only one species of rallid is certainly known to have survived into the historic period in the main Hawaiian Islands. This was a small flightless species from the island of Hawaii, for which the name *Pennula sandwichensis* is often used, though Olson (1973b) has suggested synonymizing *Pennula* with *Porzana*. It apparently became extinct in the late 1880s (Greenway, 1958). Other names have been applied to small flightless rails supposedly from the main Hawaiian islands, but the exact provenance of most of these early specimens is unknown. Apparently there are two different plumages represented in the few specimens still extant (Greenway, 1958). As we shall see, there were definitely more than two flightless rails present in the main islands. Some detailed detective work will be required to determine if any of the other names already available are applicable to any of the newly discovered fossil taxa. We tentatively assign the smaller of the two species of Rallidae present in the archeological remains from the adz quarry on Mauna Kea and from the Pohakuloa shelter to *P. sandwichensis*.

Larger Hawaii rail: A few bones from the Mauna Kea adz quarry are from a species of rail larger than *P. sandwichensis*.

Small Maui rail: The lava tube in the Lower

Waihoi Valley on Maui that produced the remains of *Apteribis* sp. also yielded the remains of a small flightless rail similar in size to *P. sandwichensis* of Hawaii or perhaps slightly larger. As both were flightless and occurred on separate islands, they probably represent different species.

Larger Maui rail: Remains of several individuals of a flightless rail larger than any of the other species of fossil rails known from the Hawaiian Islands were found in the same lava tube on Maui as the preceding species.

Very small Molokai rail: Fossils of a very small flightless rail, probably the smallest known member of the Rallidae, are abundant in the Ilio Point and Moomomi deposits on Molokai. Curiously, no other species of rail is represented by fossils from this island. Perkins (1903:453) mentions hearsay evidence that a small flightless rail survived on Molokai until the mid-1800s, but no confirmation of this ever surfaced subsequently.

Small Oahu rail: Remains of an extinct flightless rail only slightly larger than the very small Molokai bird are fairly common in sinkholes at Barber's Point, Oahu, including one of the cultural midden deposits there.

Medium-large Oahu rail: This species is very rare in the Barber's Point deposits and there is a single bone of it from the Kuliouou shelter, Oahu. This rail is smaller than the two larger species from Hawaii and Maui and larger than any of the other fossil rails.

Medium Kauai rail: A flightless rail is quite uncommon in the dune deposits on Kauai. This species is larger than the two smaller species from Hawaii and Maui and smaller than the larger species on those islands, or the medium-large species on Oahu.

Thus there were no less than eight species of flightless rails in the main Hawaiian Islands, with a ninth, *Porzana palmeri*, having occurred on Laysan Island well into this century. Without much more study it is impossible to say how many separate colonizations from the mainland were responsible for this diversity of Rallidae, but two or more for the main chain alone is probably a reasonable estimate.

Gallinula chloropus: The Common Gallinule now exists as a supposedly distinct endemic subspecies in suitable places on Kauai, Oahu, and Molokai, having been recorded previously from all the main islands except Niihau and Lanai (Berger, 1972). Remains of it were found only on Oahu, both at Barber's Point and in the archeological material from the Kuliouou shelter.

Fulica americana: The American Coot is represented in the Hawaiian Islands by an endemic subspecies that has been recorded historically from all the main islands except Lanai. As with the gallinule, its remains have been found only at Barber's Point and in the Kuliouou Shelter, Oahu.

CHARADRIIFORMES

CHARADRIIDAE

Pluvialis dominica: The Golden Plover is the most abundant and ubiquitous wintering shorebird in the archipelago. It is also the most frequently encountered charadriiform in the fossil deposits, where it has been found on Molokai, Oahu, and Kauai.

Pluvialis squatarola: The Black-bellied Plover is an uncommon, though regular, winter visitor to the Hawaiian Islands. At least one bone from the Moomomi dunes on Molokai is referable to this species and there may be other specimens among the shorebird remains that are as yet unidentified.

SCOLOPACIDAE

Numenius tahitiensis: The Bristle-thighed Curlew winters fairly commonly in the Leeward Islands but is much less abundant in the main Hawaiian chain. This may be a relatively recent pattern, however, as fossils of this species were found in fair numbers on Molokai and Kauai, and less frequently on Oahu.

Heteroscelus incanum: The Wandering Tattler is a regular winter resident throughout the archipelago. It is usually coastal and solitary, however, which probably accounts for its being known as

a fossil only from a few bones from the Moomomi dunes on Molokai.

Arenaria interpres: The Ruddy Turnstone is mainly a winter resident and occurs in the fossil deposits on Molokai and Kauai.

LARIDAE

Anous minutus: The Black Noddy occurs virtually throughout the Hawaiian chain and is found in tropical waters around the world. Probably because they nest on cliffs or in trees, noddies (*Anous* spp.) seldom are found as fossils (Olson, 1975; 1977). Nevertheless, a few bones of *A. minutus* were found both at Moomomi and at Ilio Point on Molokai.

Sterna sumatrana: Two complete humeri and a coracoid, probably of a single individual, are unquestionably from a Black-naped Tern. All other species of *Sterna* (including *Chlidonias* and *Thalasseus*) are either distinctly larger or smaller than *S. sumatrana*. There are no valid sight records of this species from the Hawaiian Islands; all previous specimen records are based on misidentifications (Roger B. Clapp, pers. comm.). *Sterna sumatrana* now breeds in the western Pacific. The nearest existing populations to the Hawaiian archipelago are in the Marshall Islands. It is impossible to know if the fossil occurrence on Molokai represents the fortuitous preservation of a vagrant bird or indicates that the species formerly inhabited the Hawaiian chain. In this regard, however, it may be worth noting that neither the Sooty Tern (*Sterna fuscata*) nor the Gray-backed Tern (*S. lunata*) were found as fossils, yet both of these species still breed on offshore islets in the main Hawaiian group as well as in the Leewards. Thus, terns may be restricted to the offshore islets by choice. It is possible, therefore, that the history of *Sterna sumatrana* in the Hawaiian group may parallel that of *Puffinus lherminieri*, a species also of tropical waters that apparently was never abundant in the Hawaiian Islands and that became extinct there prehistorically.

Larus? sp.: A worn proximal end of a tarso-

metatarsus consisting mainly of shaft from Moomomi, Molokai, differs from any of the other species of birds recovered as fossils and appears to be from a medium-sized gull. Several species of gulls have been recorded as vagrants to the Hawaiian Islands but, as elsewhere in Oceania, they have failed to colonize (Sibley and Macfarlane, 1968). A fossil of a presumed vagrant gull was found in Pleistocene deposits on St. Helena Island in the South Atlantic (Olson, 1975), so the Hawaiian record would not be without precedent.

STRIGIFORMES

STRIGIDAE

Asio flammeus: The Short-eared Owl is a resident both of native forests and of disturbed habitats, such as fields and towns, on all of the eight main islands. It feeds primarily on House Mice (*Mus musculus*) and Pacific Rats (*Rattus exulans*) (Tomich, 1971), but also takes insects and birds. *Asio* is absent from the deposits on Molokai and Kauai but does occur in the Barber's Point deposits on Oahu, most of which, however, appear to be post-Polynesian in age. The subspecies *Asio flammeus sandwichensis* is very poorly, if at all, differentiated from the subspecies of mainland North America. Vagrants in the Leeward Islands are almost certainly of continental origin. It seems possible that this species did not become established in the Hawaiian Islands until after the Polynesians introduced suitable prey in the form of the Pacific Rat and also created more open habitat. For these reasons, we do not consider it among the endemic native land birds.

Long-legged Molokai owl: Before the arrival of humans, the principal predator of small land birds in the Hawaiian Islands was a very distinctive new genus of long-legged strigid owl. The first species of this genus was discovered in the dunes at Moomomi and Ilio Point on Molokai, where it is rather common and is represented by excellent material, including a complete skull and almost all other parts of the skeleton. These owls apparently fed principally on birds, and their

long tarsi and short wings are perhaps convergent toward the ornithophagous hawks of the genus *Accipiter*. The owls of this new genus were certainly the agents responsible for the deposition of many small passerines in the dunes on both Molokai and Kauai; fossil pellets have been found on both islands.

Long-legged Oahu owl: A species of the same genus as represented on Molokai occurs regularly in the sinkholes at Barber's Point, Oahu. It is, however, clearly specifically distinct from the Molokai bird.

Long-legged Kauai owl: The same genus is represented on Kauai by a species distinct from either the Oahu or Molokai birds. It is known from a partial associated skeleton and quite a few other elements from the Makawehi dune area.

PASSERIFORMES

CORVIDAE

Corvus sp., slender-billed: The remains of many individuals of this undescribed species have been found at Moomomi and Ilio Point, Molokai, and in lesser quantity in the deposits at Barber's Point, Oahu. The bill morphology is similar to that in the extant Hawaiian Crow, *Corvus tropicus*, and is termed slender mainly to contrast it with the following species. This species is much larger overall than *Corvus tropicus*, which is known so far only from the island of Hawaii.

Corvus sp., deep-billed: A second undescribed corvid with a high, arched bill occurred sympatrically with the above species on Oahu, where it is well represented in deposits at Barber's Point, particularly the flooded cavern. The two new species of crows are similar in size but differ so markedly in osteological characters that we assume they represent two independent colonizations of the archipelago from the mainland.

MUSCIPIDAE, TURDINAE

Phaeornis obscurus: Various subspecies of the Hawaiian Thrush are known historically from

Hawaii, Molokai, Lanai, Oahu, and Kauai. All are now either extinct or endangered, except the population on Hawaii. Although we do not as yet have adequate comparative material for definite identifications, we are referring fossils from Kauai, Oahu, and Molokai to this species. The bones from the Barber's Point deposits are the only specimens now in existence of *P. o. oahuensis*, a subspecies hitherto known only from descriptions of skins collected in 1825 that were subsequently lost.

Phaeornis palmeri: The Small Kauai Thrush is known only from the island of Kauai. Based on the size of the hind-limb elements, two species of thrushes are present as fossils in the Kauai deposits. We assume that one of these is conspecific with *P. palmeri*, and that the other represents *P. obscurus*.

PACHYCEPHALIDAE, MYIAGRINAE

Chasiempis sandwichensis: Populations of the Elepaio exist today on Hawaii, Oahu, and Kauai, but the species does not occur on the central islands that once formed the island of Maui Nui. So far, the fossil record has not helped to explain this perplexing distribution. Fossils of *Chasiempis* were found on Kauai and Oahu, but not on Molokai.

MELIPHAGIDAE

Moho braccatus: The Kauai Oo, now an extremely rare and endangered species, survives only in the far recesses of the Alakai Swamp of Kauai. It is common as a fossil in the Makawehi dunes, however, and its present restriction to upland rain forests obviously does not reflect the former extent of its natural distribution.

Moho apicalis: The Oahu Oo became extinct in the last century. A meliphagid that is almost certainly this species is found in the fossil deposits at Barber's Point, Oahu.

Moho bishopi: The Molokai Oo has not been seen on Molokai since the early part of this century and is presumed extinct there. No meli-

phagid bones occur in the extensive collections of small passerines from Ilio Point, and from the Moomomi dunes there is only a single meliphagid humerus that we assume is referable to *M. bishopi*. No species of *Moho* has ever been collected on Maui but there are early sight records and even a few recent ones (Sabo, 1982), suggesting that *M. bishopi* (or a closely similar form) may yet persist on that island.

Chaetoptila sp.: The only historically known species in this genus, *C. angustipluma*, occurred on the island of Hawaii, where it has long been extinct. The first of the four specimens in existence was collected in 1840 and the last around 1859. Beautifully preserved bones of a large meliphagid, presumably *Chaetoptila*, were recovered from the flooded cavern at Barber's Point, Oahu, and also from the sediment-filled sinkholes in the same area. Because of zoogeographical considerations, it is probable that the Oahu population represents a distinct species, though we have not been able to determine this yet. As presently known, the distribution of *Chaetoptila* is somewhat enigmatic, as it is unrecorded from the islands between Oahu and Hawaii.

FRINGILLIDAE, CARDUELINAE, DREPANIDINI

Psittirostra (Telespyza) cf. *cantans*: Historically, the *Telespyza* group of finches is known only from the Leeward Islands, with *P. cantans* on Laysan, and *P. ultima* on Nihoa. Fossils reveal that this group was once widespread in the main islands, however. The species of *Telespyza* obviously occupied lowland habitats and may have been restricted to them.

A few specimens from Barber's Point, Oahu, cannot be separated at the specific level from the Laysan Finch, *P. cantans*. A very fragmentary mandibular articulation from Ilio Point, Molokai, appears to be from a *Telespyza* of this size and is tentatively referred to the same species.

Psittirostra (Telespyza) cf. *ultima*: A species of *Telespyza* very close in size and morphology to the Nihoa Finch, *P. ultima*, is fairly common in the owl pellet deposits from Ilio Point, Molokai, and

a single rostrum has also been found in the Moomomi dunes.

Psittirostra (Telespyza), medium species: A species smaller than *P. ultima* occurs in fossil deposits both on Kauai and Oahu. Although the population from Oahu appears to have had a more robust bill than that from Kauai, at present we consider the two to be conspecific, though perhaps subspecifically distinct.

Psittirostra (Telespyza), small species: This is the most abundant species in the fossil owl pellet deposits from Ilio Point, Molokai. Its bill is smaller than that of the preceding species or any other form of *Telespyza* known thus far.

Psittirostra (Loxioides) bailleui: The Palila has had an extremely restricted distribution during the historic period, being found only in the forests of mamane (*Sophora chrysophylla*), often associated with naio (*Myoporum sandwicense*), that now occur in regions of high elevation and relatively low precipitation on the island of Hawaii. It feeds primarily on the seeds and flowers of *S. chrysophylla*, and it is now rare and endangered. Its present and former historical distribution on Hawaii have been detailed by van Riper et al. (1978).

Fossils of *P. bailleui* were found in the deposits at Barber's Point, Oahu, revealing that the species was once more widely distributed in the archipelago. As the Barber's Point deposits are only a few hundred meters from the present shoreline, near sea level, it is evident that the Palila is not naturally restricted to high elevations. Its principal food, *Sophora*, grows from sea level to timberline (Rock, 1913), although it is rarely found in lowland regions at present. *Sophora* has been collected on both slopes of the Waianae range on Oahu (Chock, 1956). *Psittirostra bailleui* provides a striking example of how the distribution of native birds has been artificially modified in the Hawaiian archipelago.

Psittirostra (Rhodacanthis) flaviceps: The two species of koa finches of the subgenus *Rhodacanthis* (*P. palmeri* and *P. flaviceps*) are known historically only from the island of Hawaii, where they disappeared very shortly after their discovery. Al-

though there has been some dispute as to whether *P. flaviceps* is really distinct from *P. palmeri*, our studies of the cranial osteology fully support Amadon (1950) in maintaining these as separate species. A rostrum from Barber's Point, Oahu, is sufficiently similar to the smaller *P. flaviceps* to be referred to that species.

Psittirostra (Chloridops), Kauai species: A single species of grosbeak finch, *Psittirostra (Chloridops) kona*, is known historically from a very circumscribed area in the western part of the island of Hawaii. It apparently became extinct about ten years after its discovery in 1887.

A new species of *Chloridops* is represented by a few individuals from the Makawehi dunes on Kauai. The bill is smaller and less heavily ossified than that of the highly specialized *P. kona*.

Psittirostra (Chloridops), lesser Oahu species: In this species, known from the deposits at Barber's Point, Oahu, the bill is similar in size to the fossil *Chloridops* of Kauai, but differs in construction.

Psittirostra (Chloridops), giant Oahu species: The largest new species of grosbeak finch, known from fossils from Oahu, has a massive mandible that rivals in size that in the largest finchlike birds in the world. The structure of the rostrum of this bird is very strange and differs substantially from that in other forms of *Chloridops*, whereas the mandible does not.

Psittirostra (Psittirostra) psittacea: Once one of the most abundant and widespread of the drepanidines, the *Ou* now exists in small populations only on the island of Hawaii and perhaps on Kauai. It formerly occurred on all the main islands that were forested in historic times and had not differentiated into subspecies. Fossils of this species were scarce on Kauai but somewhat commoner at Barber's Point, Oahu.

cf. *Psittirostra*, ridge-billed finch: The bill of this species is about the size of that of *P. ultima* of Nihoa Island, but is unlike that of any other species of drepanidine except perhaps the following one. The bill is conical and the dorsal bar of the rostrum is distinctively flattened. The assignment of this species to the genus *Psittirostra* is tentative at present. Fossils of the ridge-billed

finch are fairly common in the deposits at Ilio Point, and less abundant at the Moomomi dunes, Molokai. What appears to be the same species is also found at Barber's Point, Oahu.

cf. *Psittirostra*, cone-billed finch: This species is known from two distinctive rostra recovered from the Makawehi dunes on Kauai. In general shape, these rostra most resemble those of the ridge-billed finch listed above, but they are much larger and the dorsal bar is not flattened. Neither this nor the preceding species appears to have any particularly close relatives among historically known taxa.

cf. *Psittirostra*, additional Kauai finch: This species is represented only by a mandibular articulation that is typically finchlike in shape but differs in details from all known taxa. It was found in the deposits at Makawehi, Kauai.

cf. *Psittirostra*, additional Oahu finch: This species, known from the deposits at Barber's Point, is likewise known only from a single articular end of a mandibular ramus. Its structure is unique and there is little doubt that it belongs to an unknown species. Although it is finchlike in several respects, it may not be referable to *Psittirostra*.

Pseudonestor xanthophrys: The Parrotbill now occurs only on the island of Maui, on the windward slope of Haleakala between 1300 and 1900 m, and usually above 1675 m (C.B. Kepler, pers. comm.). Bones of *Pseudonestor*, apparently belonging to the extant species, are present, but very rare, in the fossil deposits at Ilio Point, Molokai. As with *Psittirostra bailliei*, it is evident that the present restriction of *Pseudonestor* to upland habitats is unnatural.

Heterorhynchus lucidus: Three races of the Nukupuu are known historically, one each from Kauai, Oahu, and Maui. The species is nearly extinct. An additional species, *H. wilsoni*, is restricted to Hawaii. Fossils of *Heterorhynchus*, probably referable to *H. lucidus*, have been found in the deposits at Barber's Point, Oahu, and at Ilio Point, Molokai, the latter occurrence extending the distribution to another island in the Maui Nui group.

Hemignathus obscurus: Populations of the Aki-aloa existed on Kauai, Oahu, Lanai, and Hawaii during the historic period, although all are now probably extinct. The birds from Kauai have been recognized as belonging to a distinct species, *H. procerus*, supposed to be much larger than the birds from other islands. Our investigations, however, suggest that the most distinct taxon is *H. o. obscurus* of Hawaii, which is considerably smaller than the other forms of *Hemignathus*. For the present, we recognize only one species in the genus *Hemignathus*. Very rare fossils of a *Hemignathus*, larger than *H. o. obscurus*, were found at Ilio Point, Molokai, thus filling in a gap in the distribution of the species. Fossils of *H. o. procerus* are fairly abundant in the collections from the Makawehi dunes on Kauai.

Oreomystis bairdi: This is one of the taxa previously included in "*Loxops maculata*." It is actually a distinct genus and species endemic to Kauai, where fossils have been recovered from the Makawehi dunes.

Paroreomyza maculata: The four taxa of this distinctive genus of warbler-like drepanidines constitute part of the remainder of "*Loxops maculata*" of Amadon (1950), the remaining species being *Loxops mana* of the island of Hawaii. We recognize two species in *Paroreomyza*: *P. maculata*, with subspecies on Oahu (*maculata*), Maui (*newtoni*), and formerly on Lanai (*montana*), and *P. flammea*, a considerably larger extinct species with very distinctive plumage that occurred on Molokai. Fossils of *P. maculata* were obtained at Barber's Point, Oahu. Fossil specimens of *Paroreomyza* from Ilio Point, Molokai, are puzzling in that they are the size of *P. maculata* and thus smaller than *P. flammea*, the species known historically from Molokai.

Hoopoe-like sickle-bill: This new species has a long, decurved bill very like that of *Hemignathus* at first glance but differing from all other long-billed drepanidines in one rather remarkable aspect. The dorsal surface of the mandibular symphysis, rather than being excavated to accommodate a long, tubular tongue, is completely flat. Thus the bill resembles that in such long-billed

probing birds as hoopoes and woodhoopoes (Upupidae and Phoeniculidae) or the neotropical scythebills (*Camptylorhampus*; Dendrocolaptinae). This new species is known from the fossil deposits at Barber's Point, Oahu, and the Makawehi dunes on Kauai, but it is uncommon at both localities.

Icterid-like gaper, Molokai: This new genus of rather large drepanidines is characterized by having the bill long, straight, pointed, and flattened dorsally, resembling that of a meadowlark (*Sturnella*, Icteridae). The retroarticular process of the mandible is extremely well developed, indicating that it was a powerful gaper. This species has been found both at Ilio Point and Moomomi, Molokai.

Icterid-like gaper, Oahu: Uncommonly encountered bones from the Barber's Point deposits are evidently from the Oahu representative of the preceding genus, which is, however, specifically distinct from the Molokai bird.

Sickle-billed gaper, Oahu: An additional species from Barber's Point, Oahu, resembles the two preceding gaping birds in certain details, but differs in having a narrower, more decurved bill. Its generic affinities have not yet been determined.

Loxops virens: The Amakihi is one of the more abundant and widespread of the extant species of Drepanidini. Four subspecies are recognized from the six largest islands of the archipelago. Fossils clearly referable to the morphologically distinct subspecies *L. v. stejnegeri* were abundant in the deposits on Kauai. The species is also represented among the fossils from Barber's Point, Oahu. *Loxops virens* is unexpectedly absent from the extensive collections of passerine fossils from Molokai.

Loxops parva: The Anianiau is endemic to the island of Kauai, where it survives in fair numbers. It is also fairly common in the fossil deposits in the Makawehi dunes.

Himatione sanguinea and *Himatione* sp.: The Apapane is the most common and widespread drepanidine in the remaining native forest, where it is known from the six largest islands and has

not differentiated into races. (The historically extinct population of Laysan Island we consider to be a distinct species, *H. freethi*.) Despite its present ubiquity, *Himatione sanguinea* is very rare in the fossil deposits, having been positively identified only from Barber's Point, Oahu. A single mandibular articulation from Ilio Point, Molokai, appears very similar to *H. sanguinea*, but it is too fragmentary for positive identification. Some better-preserved specimens from the Kauai dunes are also similar to *Himatione* but apparently differ somewhat from *H. sanguinea*.

Vestiaria coccinea: The Iiwi is a monomorphic species known from the six largest islands. It is now common only on Hawaii, Maui, and Kauai. As a fossil, this species occurs only at Barber's Point, Oahu.

Ciridops sp., Molokai: The single historically known species of the genus, *Ciridops anna*, of the island of Hawaii, became extinct in the last century; only five specimens of it are known to exist. The distinctive bill and uniquely stout hind-limb elements of *Ciridops* permit it to be readily identified in fossil material. *Ciridops* is now known from Molokai from a partial associated skeleton removed from an intact fossil owl pellet found in the Moomomi dunes. Although this is one of very few small passerines found at Moomomi, the species is lacking in the nearby Ilio Point deposits, in which other small passerines are abundant. The Molokai *Ciridops* is more similar to *C. anna* than are either of the following species, but it is smaller and represents a distinct species.

Ciridops sp., Oahu: This new species is fairly common in the deposits at Barber's Point, Oahu. The bill is much shorter than in any of the other species of *Ciridops*.

Ciridops sp., Kauai: Another species of *Ciridops* is well represented in the deposits from the Makawehi dunes on Kauai. The hind-limb elements are less robust and thus are seemingly less specialized than in the populations from the other islands.

Effects of Habitat Modification by Polynesians on Avian Extinction and Distribution

Our studies of fossils indicate that the avifauna of the Hawaiian Islands experienced an extraordinary period of extinction within relatively recent time. Fossils have contributed no less than 39 extinct species of endemic land birds that are unknown historically (Table 3). Most of the new forms come from only three of the eight main islands, so our knowledge of the total avifauna of the archipelago is probably still quite incomplete. According to the classification we will adopt in our proposed taxonomic papers, the historically known avifauna comprises 36 endemic species of land birds from the main islands and 5 from the Leeward Islands. Hence, taking into account the number of extinctions that probably occurred on islands for which we have a poor fossil record or none at all, it is likely that well over half of the species of endemic land birds that were present in the archipelago before the arrival of Polynesians became extinct between that event and European contact.

On the main islands, all endemic species of nonpasserine land birds were exterminated except one goose, one hawk, and one small flightless rail. These are definitely known to have survived into the historic period only on the island of Hawaii. The prehuman fauna of nonpasserine endemic land birds is far greater and includes at least eight species of geese, an eagle, two hawks, two flightless ibises, eight flightless rails, and three owls. Although a greater proportion of the fossil passerines survived into the historic period, at least 18 species were lost, including 15 in the tribe Drepanidini. Whereas certain species became totally extinct, others became more restricted in distribution through the extinction of populations on individual islands. We have documented that on the three islands with fairly comprehensive fossil faunas (Molokai, Oahu, and Kauai), there was a total of at least 74 island populations of land birds. Of these 74 island populations that occur as fossils, only 20 (27 percent) are known to have survived into the historic period.

That seabirds also suffered prehistoric extinctions and depletions is amply demonstrated by the fossil material. An enigmatic new species of *Pterodroma* was entirely eliminated. *Puffinus lherminieri*, apparently a rare species in any case, also vanished from the archipelago, as may have *Sterna sumatrana*. *Pterodroma hypoleuca* was extirpated from the main islands and persists in the Hawaiian chain only in the Leeward group. *Pterodroma phaeopygia*, the most abundantly represented bird in the Oahu deposits, was wiped out on that island before it could be recorded by ornithologists.

Extinctions of insular populations of birds can be caused by Pleistocene changes in climate and vegetation, as has been documented for the West Indies (Pregill and Olson, 1981). Pleistocene climatic fluctuations would have affected not only the number and size of the Hawaiian islands through changes in sea levels, but also, to some extent, their environment. Reduction in land area and the creation of water barriers by rising sea levels at the close of the Wisconsin stage doubtless affected some avian populations. But the area and configuration of most of the main islands were not dramatically altered by rising sea levels (Juvik and Austring, 1979). Only the central islands, whose conjoined lavas were once exposed to form the single island of Maui Nui (page 8) experienced fragmentation and a significant reduction in land area.

Little is known about the effects of world-wide climatic fluctuation on climate and vegetation in the archipelago during the Pleistocene. Wentworth and Powers (1941), Wentworth (1966), and Porter (1979) have documented that Mauna Kea, on Hawaii, experienced multiple glaciations during the past 300,000 years. Selling (1948) studied pollens from cores of peat bogs in the rain-forest belts on Maui, Molokai, and Kauai, between 1200 and 1765 m (3940–5790 ft) elevation. Although these studies have been criticized (Fagerlind, 1949), they succeeded in showing fluctuations in the limits of wet and dry forests, and clearly demonstrate that the distribution of vegetation types on the main islands has not been constant in the past. None of these studies, how-

ever, contributes directly to our knowledge of how climatic change may have affected relatively dry, lowland habitats, where all of our significant fossil finds have originated.

However, as we have seen, the effects of the Pleistocene are irrelevant because most, if not all, of the extinct species found as fossils survived into the Holocene and into the period of Polynesian colonization of the archipelago (pages 29–31). Thus, Pleistocene changes in climate and vegetation will not account for the disappearance of half of the endemic land birds of the islands.

A more probable explanation is that most species were driven to extinction as a result of predation and habitat destruction by Polynesians (see also Olson and James, 1982; in press). Although it has been generally assumed that the era of human-caused extinctions in the Hawaiian biota began after 1778, when Captain Cook first visited the archipelago, a growing body of evidence indicates that the period of Polynesian settlement was one of equal or greater environmental perturbation.

Not all the casualties of Polynesian interference were necessarily extinct by the time of European contact, however. A variety of historically known species were extremely rare when first discovered, and became extinct shortly afterward. Some of these species may well have been reduced in number or range as a result of previous habitat destruction, and thus made more susceptible to extinction. One example of this is *Ciridops anna*, a species of drepanidine known from five specimens taken on the island of Hawaii during the nineteenth century. New fossil species of *Ciridops* are now known from lowland sites on three other islands, and on two of them the fossils are fairly abundant (page 42). Only the species from Hawaii is known to have survived into the historic period, but because there was a hiatus of about a century between European contact and the arrival of the first systematic bird collectors (Newton, 1892), it cannot be established that some of the species of *Ciridops* known only as fossils did not survive in low numbers into the early part of the historic period. As another example, hearsay

TABLE 3.—Continued

Species	Laysan	Nihoa	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii*	Species	Laysan	Nihoa	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii*
(<i>Loxioides</i>)									<i>Paroreomyza flammea</i>					H			
<i>bailliei</i>				F			H		Hoopoe-like sickle-bill			F	F				
(<i>Rhodacanthis</i>)									Icterid-like gaper, Molokai sp.					F			
<i>palmeri</i>							H		Icterid-like gaper, Oahu sp.				F				
<i>flaviceps</i>				F			H		Sickle-billed gaper				F				
(<i>Chloridops</i>)									<i>Loxops mana</i>								H
Kauai species			F						<i>Loxops sagittirostris</i>								H
Lesser Oahu species				F					<i>Loxops virens</i>			H,F	H,F	H	H	H	H
Giant Oahu species				F					<i>Loxops parva</i>			H,F	H				H
<i>kona</i>							H		<i>Loxops cocinea</i>			H					H
(<i>Psittirostra</i>)									<i>Himatione freethi</i>	H							
(Subgenera incertae sedis)									<i>Himatione sanguinea</i>								
Ridge-billed finch			H,F	H,F	H	H	H		<i>Himatione</i> sp.								
Cone-billed finch				F	F				<i>Palmeria dolei</i>								
Additional Kauai finch			F						<i>Vestiaria cocinea</i>				H	H,F	H	H	H
Additional Oahu finch			F						<i>Drepanis funerea</i>								
Other Drepanidines									<i>Drepanis pacifica</i>								
<i>Melamprosops phaeosoma</i>									<i>Ciridops anna</i>								H
<i>Pseudonestor xanthophrys</i>									<i>Ciridops</i> sp., Molokai								
<i>Heterorhynchus lucidus</i>									<i>Ciridops</i> sp., Oahu								
<i>Heterorhynchus wilsoni</i>									<i>Ciridops</i> sp., Kauai								
<i>Hemignathus obscurus</i>			H,F	H	F	H	H										
<i>Oreomystis bairdi</i>			H,F														
<i>Paroreomyza maculata</i>				H,F	F	H	H										

* Except for *Geochen rhuax*, a second large goose, and two species of Rallidae, we have not included the species from archeological sites and lava tubes on the island of Hawaii.

evidence suggests that the flightless rail known from fossils on Molokai survived into the historic period (Perkins, 1903:453), though it was never seen or collected by a naturalist.

We have already discussed the paleontological and archeological evidence that Polynesians and prehistorically extinct birds were contemporaneous (pages 29–31). We shall now treat the possible means by which the birds were exterminated.

Polynesians may have colonized the Hawaiian archipelago as early as A.D. 400 (Kirch, 1974). They imported at unknown dates a variety of food plants, including taro, sweet potatoes, bananas, and coconuts, as well as dogs, pigs, and chickens (*Gallus gallus*). Other foreign plants, the Pacific Rat (*Rattus exulans*), land snails (Kirch and Christensen, 1981), and lizards (Cook, 1784; Stejneger, 1899) probably arrived with the Polynesians adventitiously.

By the time Cook reached the archipelago, it had long been home to a large human population with a complex social and agricultural system. Crude contemporary estimates of the size of the Polynesian population at the time of Cook's contact range from 200,000 to 400,000, but more recently Schmitt (1971) has advocated an estimate between 200,000 and 250,000. Even with Schmitt's lower estimates, at least six of the eight main islands supported a larger human population in 1778 than in 1970.

The Hawaiians depended mainly on food crops, and to a lesser extent on domestic animals and marine resources, for their sustenance. In their most developed stage, the prehistoric Hawaiian agriculturalists combined two basic methods—intensive pond-field cultivation in wetter regions, where sufficient water for irrigation was available, and extensive slash-and-burn or shifting cultivation in drier areas. The principal crops were taro in the irrigated pond-field complexes and sweet potatoes on drier land.

Polynesians, with pigs, dogs, and rats as accomplices, could have extirpated some of the native birds, or at least reduced their numbers to a state of extreme vulnerability, by direct predation. Of

the 13–15 species of flightless birds now known to have inhabited the main islands, only one species of small rail is positively known from the historic period. The large, ungainly flightless geese and ibises would have been easy prey for humans and introduced mammals, as would flightless rails and ground-nesting and burrowing seabirds, for which the fossil record documents the extinction of numerous species and island populations.

Among the Hawaiians were accomplished hunters of small forest birds that were taken both for their decorative feathers and for food. It would have been virtually impossible, however, for the Hawaiians to hunt dozens of populations of small forest species to extinction with the limited technology available to them. Ultimately, the cause of most of the prehistoric extinctions of Hawaiian birds was probably not predation but habitat destruction, particularly of the drier lowland forest.

Archeological research in windward Halawa Valley, Molokai, provides evidence that the slopes of the valley were denuded up to 300 m elevation by prehistoric land clearing (Kirch and Kelly, 1975). Removal of the natural vegetation through fires and clearing apparently resulted in an accelerated rate of soil erosion and the extermination of local faunas of endemic land snails as well. Yen et al. (1972) found parallel evidence of disruption of the native vegetation and accelerated erosion due to prehistoric slash-and-burn methods in the upper Makaha Valley on Oahu.

Archeological surveys in the Kohala Mountains on Hawaii have revealed that the leeward slopes were once covered by extensive agricultural field systems extending in a continuous band from 60 to 900 m (200–3000 ft) elevation, encompassing land that receives between 50 and 150 cm (20–60 in) of rainfall annually (Smith and Schilt, 1973). Areas with lower annual precipitation and steeper terrain had scattered fields only along stream gulches.

Kirch and Christensen (1981) document probable habitat degradation at Barber's Point, Oahu, on the basis of changing concentrations of land snail shells in the deposits there. Many endemic

species became less abundant and eventually disappeared, while species that are more tolerant of disturbed areas increased through time.

Archeological research on prehistoric land use and its effect on the environment is usually restricted to considering one valley or region at a time, but a somewhat broader view may be derived from the accounts of early western voyagers to the islands. In an undisturbed state, virtually all land in the Hawaiian islands would have been covered with forest of one type or another; exceptions include recent lava flows, sand dunes, and areas above the tree line. But this contrasts sharply with what was reported at the time of European contact. In general, the early journals describe well-populated islands with large-scale agricultural operations in the lowlands, and lush, verdant forests in the mountains. One also finds frequent mention of extensive grasslands in drier regions of low and middle elevation. Cook (1784, 2:225) described the view of the leeward slopes of Kauai from his anchorage at Wymea (=Waimea) Bay in 1778 as follows:

From the wooded part to the sea, the ground is covered with an excellent sort of grass, about two feet high, which grows sometimes in tufts, and though not very thick at the place where we were, seemed capable of being converted into plentiful crops of hay. But not even a shrub grows naturally on this extensive space.

He also mentions that “no wood can be cut at any distance convenient to bring it from” (Cook, 1784, 2:224).

Fourteen years later, Vancouver (1798, 1:170) supplied additional details in his account of the same scene:

I...found the low country which stretches from the foot of the mountains towards the sea, occupied principally with the *taro* plant, cultivated in the same manner as at Woahoo [Oahu]; interspersed with a few sugar canes of luxuriant growth, and some sweet potatoes.... The sides of the hills extending from these plantations to the commencement of the forest, a space comprehending at least one half of the island, appeared to produce nothing but a coarse spiry grass from an argillaceous soil, which had the appearance of having undergone the action of fire

Vancouver’s suspicions that the plains sur-

rounding Waimea Bay were periodically burned were confirmed when he (Vancouver, 1798, 1:175–176) “observed the hills to the eastward of the river to be on fire from a considerable height, in particular directions, down towards the water’s edge.” Menzies (1790–1792), a member of Vancouver’s expedition, had seen fires in the same area a few years earlier, while visiting Kauai on a trading vessel. Vancouver (1798, 2:221) also sailed along the windward side of Kauai, and although he describes the scenery of the Lihue District as more verdant than on the leeward side, the lowlands were nevertheless in a “high state of cultivation.”

Descriptions of other Hawaiian islands in the journals of these and other explorers are basically similar to those for Kauai. The drier lowlands were often devoid of trees, including, as far as King (1784:114) could ascertain from his ship, southwest Molokai and the entire island of Kahoolawe. Unpublished journals of other members of Cook’s expedition confirm these observations and add that Lanai and Niihau also appeared to be barren of trees (E. Wilson, 1977).

Intensive cultivation occupied valleys and slopes of hills where the water was sufficient, and few of the early explorers failed to express their admiration for the ingenuity of the natives in building irrigation works and exploiting every available space for their plantations. Of leeward Oahu, Chamisso (1830:316) observed:

The culture of the vallies which lie behind Hanaruru [Honolulu] is really astonishing. Artificial irrigations enable the natives to form, even upon the hills, large aquatic plantations of *Tara* [taro], which are at the same time employed as fish ponds, while all kinds of useful plants grow on the banks which form their borders.

Menzies (1790–1792) made inland trips from the western shore of Hawaii to ascend Hualalai and Mauna Loa, and he marveled at the extent and intensity of dryland plantations in that region. He estimated that the plantations he walked through reached 6–7 miles (8–11 km) inland from Kealakekua Bay, his point of departure, and when he marched still farther inland he found extensive banana plantations in a region that,

from a distance, had appeared to be woodland. The cultivated land occupied a broad band along the coast as far as he could see in both directions. On the leeward slopes of the Kohala Mountains of Hawaii, which still exhibit evidence of extensive prehistoric field systems, Menzies (1790–1792:478) reported:

From the North West point of the Island [of Hawaii] the Country stretches back for a considerable distance with a very gradual ascent & is destitute of Trees or Bushes of any kind, but it bears every appearance of industrious Cultivation by the number of small fields into which it is laid out

Although the food supply in some regions had been depleted by warfare when Vancouver visited, the natives were able to supply Cook and King with a seemingly inexhaustible store of vegetables and meat. King (1784:118) was particularly impressed by the abundance of swine:

The supply of hogs which we got from them, was really astonishing. We were near four months, either cruising off the coast, or in harbour at Owyhee [Hawaii]. During all this time, a large allowance of fresh pork was constantly served to both crews: so that our consumption was computed at about sixty puncheons of five hundred weight each. Besides this, and the incredible waste which, in the midst of such plenty, was not to be guarded against, sixty puncheons more were salted for sea-store. The greater part of this supply was drawn from the island of Owyhee alone, and yet we could not perceive that it was at all drained, or even that the abundance had in any way decreased.

Despite all evidence to the contrary, many naturalists who have studied the Hawaiian biota have adopted without scrutiny the popular view that the archipelago was in a nearly pristine state when it was first visited by Europeans. Botanists who recount the sorrowful state of the dry lowland vegetation in the islands have frequently assumed that its destruction began after 1778 (e.g., Rock, 1913; St. John, 1947). Even after reading Cook's and Vancouver's descriptions of the grasslands covering leeward Kauai, Selling (1948:44) enigmatically concluded that "these early observations almost preclude the idea of any great cultural effects having cooperated in originating this type of vegetation." Similar prejudices among ornithologists led Amadon

(1950:210) to surmise that "no serious inroads were made on the native birds by the Hawaiians," though there is no basis for making such a statement.

On the other hand, Zimmerman (1963), Degener and Degener (1974), and Atkinson (1977) have adopted the view that extensive deforestation, particularly of coastal areas and leeward slopes, resulted from Polynesian land use. In this connection, Atkinson's (1977:116) remarks are especially germane:

The lowland forest of the drier parts of the Hawaiian Islands was considered by Rock (1913) to have been the most diverse of all Hawaiian forests. It is possible that endemic birds specifically adapted to these dryland forests became extinct as a result of the destruction of the lowland forest during the Polynesian period.

The fossil record has substantiated this prediction in a most spectacular manner.

In this regard, it may be significant that in Puerto Rico and probably elsewhere in the West Indies, arid lowland habitats have been found to be richer, both in species and in numbers of individuals of birds, than are montane rain forests (Kepler and Kepler, 1970; Pregill and Olson, 1981). This might explain why the elimination of native forest in the dry lowlands of Hawaii caused such a high number of extinctions, even though rain forests persisted.

Habitat alterations were perhaps not universally detrimental in that certain modifications created conditions that were more favorable for some species. The extensive Polynesian cultivation of taro in flooded pond-fields would have provided much more suitable habitat for aquatic birds such as ducks, gallinules, and coots, than ever existed previously. Berger (1972:23) has noted that the cessation of taro growing in recent times has reduced suitable habitat for waterbirds. The Polynesians' construction of fishponds along the coasts provided sheltered areas for coots and, especially after silting, for herons. The Black-crowned Night Heron in the Hawaiian Islands has probably benefited further by the introduction in this century of mangroves (*Rhizophora mangle*), which has created foraging and nesting

habitat. Some of these modifications may likewise have benefited the Hawaiian Stilt, though this species may have been less dependent on man-caused changes.

In light of the above, it is of interest that the five species of freshwater birds in the Hawaiian chain are either only subspecifically distinct from their mainland relatives (the duck *Anas platyrhynchos wyvilliana*, the gallinule *Gallinula chloropus sandvicensis*, the coot *Fulica americana alai*, and the stilt *Himantopus himantopus knudseni*), or have not differentiated at all from their mainland ancestor (the night heron *Nycticorax nycticorax hoactli*).

The Short-eared Owl (*Asio flammeus*) falls into much the same category as the species just mentioned. It is poorly, if at all, differentiated from North American populations and does not occur in any of the deposits that are known to date from the period before man's arrival. The species may have become established in the archipelago only after open habitats were created by Polynesians and after suitable prey, in the form of the Pacific Rat, *Rattus exulans*, was introduced.

The available evidence points toward the Short-eared Owl and the freshwater birds of the Hawaiian Islands being recent colonizers. Of these, the duck and the stilt are the most strongly differentiated and the least dependent on man-altered environments, and they could well have arrived prior to Polynesian colonization. The differences from their mainland ancestors shown by the gallinule, coot, and Short-eared Owl could perhaps have evolved within 1500 years or less. Therefore, not only do we see that the arrival of man brings about drastic changes in terms of extinction, but also may be responsible for increasing the number of successful colonizations.

Analysis of Fossil Samples

An understanding of the distribution of taxa within the archipelago is partly contingent on how completely the fossil samples from the various islands represent the land bird fauna that was in existence at the time of deposition. Knowledge of the prehistoric avifauna of most of the

main Hawaiian islands is as yet either nonexistent (Niihau, Lanai, Kahoolawe) or very incomplete (Maui, Hawaii). Only for Molokai, Oahu, and Kauai do we have what appears to be a fairly representative sample of fossil land birds. Yet even for these three islands it is extremely unlikely that all of the taxa that were present at the time of deposition have been found.

In our initial assessment of the fossil collections from the dune deposits on Molokai and Kauai, we were impressed by the great differences between the number of historically known endemic species of land birds (13 from Kauai and 9 from Molokai) and the number of species represented by fossils (21 from each island; see Table 4). Because the fossil avifaunas are so much larger than the historic avifaunas of these islands we initially assumed that the fossil samples were reasonably complete. Under such an assumption, the differences in species composition among the fossil and historic avifaunas could be interpreted as reflecting evolutionary and distributional changes through time.

Our views changed, however, when the fossil sample from Barber's Point, Oahu, was expanded, and also when it became evident that most of the Hawaiian fossil deposits are considerably younger than Pleistocene (page 30). On Oahu, 32 endemic species of land birds are now known from the Barber's Point deposits, while only 11 species are known historically (Table 4). In light of these figures, it seems probable that

TABLE 4.—Numbers of endemic species of land birds in historic and fossil avifaunas from three of the main Hawaiian Islands, excluding *Asio flammeus* and aquatic birds not specifically distinct from mainland species

Avian Group	Molokai		Kauai		Oahu	
	His- toric	Fos- sil	His- toric	Fos- sil	His- toric	Fos- sil
Nonpasserines	0	7	0	5	0	8
Nondrepanidine passerines	2	3	4	4	3	6
Drepanidini	7	11	9	12	8	18
Total	9	21	13	21	11	32

more species were present on Molokai and Kauai at the time of deposition than are represented in the fossil samples from those islands. In fact, it is quite likely that more than 32 species of land birds were present on Oahu.

Each of the major fossil deposits lacks certain species that survived into the historic period on their respective islands. On Kauai, the drepanidines *Heterorhynchus lucidus*, *Loxops coccinea*, *Vestiaria coccinea*, and possibly *Himatione sanguinea*, are absent from fossil deposits, whereas all are known from the island in the historic period. Despite the large number of species present in the fossil sample from Oahu, two historically known species of drepanidines, *Loxops coccinea* and *Hemignathus obscurus*, are lacking as fossils. The fossil collections from Molokai are much more anomalous; of the 21 endemic species of land birds found as fossils, only *Phaeornis obscurus*, *Moho bishopi*, and possibly *Himatione sanguinea*, are known historically from the island.

If the deposits are as recent as the radiocarbon ages and other evidence indicate, we could make the assumption that all of the species in the historically known avifauna of an island were present at the time the fossil deposits were formed. We could thus derive new figures of at least 23 endemic species of land birds formerly present on Kauai, at least 34 on Oahu, and at least 27 on Molokai. Even these figures, however, probably do not truly reflect the original species diversity of these islands, because we cannot include the unknowable quantity of prehistorically extinct populations that remain to be discovered. In some cases, this figure would probably be rather large.

Eagles and hawks are rare as fossils, perhaps because of lower population densities or because their habits are not conducive to frequent fossilization (in contrast to flightless species, for example). The absence of fossils of *Accipiter* everywhere except Oahu, and of *Buteo* everywhere except Molokai, probably does not reflect the true former distribution of these genera in the Hawaiian islands. Although on Kauai the representation of species and individuals of small passerines is good because of the discovery of two rich pockets of

bone, the absence of fossils of *Corvus*, hawks, and eagles is almost surely a reflection of the limitations of the fossil deposits and cannot be taken as evidence that these taxa never occurred on the island. That *Loxops coccinea* is unknown as a fossil is possibly a result of its being the smallest species of a native bird in the archipelago. Its absence from fossil deposits may thus be due to a sampling bias either in deposition or collecting.

It should be emphasized that not all of the unexpected absences of species from fossil deposits can be easily attributed to incomplete samples. For instance, the avifauna from Ilio Point, Molokai, is remarkable in that all of the fossil land birds except *Phaeornis obscurus* are either new species or are known historically only from other islands. Various species of finch-billed drepanidines dominate the small passerine fauna. Most of these belong to the *Telespyza* group, whereas the *Chloridops*, *Loxioides*, *Psittirostra*, and *Rhodacanthis* groups are absent. Meliphagids are also absent and the nectarivorous group of drepanidines is represented only by a single mandibular articulation resembling that of *Himatione*. Thus *Ciridops*, *Drepanis*, *Palmeria*, *Vestiaria*, and all of the species of *Loxops* (in our restricted sense) are strangely missing. Among these taxa are some of the commonest and most widespread native land birds of the Hawaiian Islands today. Several of these occur commonly as fossil on other islands; for example, *Loxops virens*, *Moho*, and *Ciridops* have been found on Kauai. Fossils of small passerines have been found only incidentally in the Moomomi dunes, Molokai. Nevertheless, the few identifiable specimens include *Ciridops* and *Moho*, genera that are absent among the much more numerous remains of small passerines from nearby Ilio Point.

Differences in habitat may have affected faunal composition in particular deposits. Unfortunately, almost all we know about the natural avifauna of lowland areas in the Hawaiian chain comes entirely from the fossil record. We have repeatedly seen that species that are now confined entirely to montane regions were present, and often apparently abundant, in the lowlands near

sea level. Although it is quite possible that certain species not represented in the fossil record existed only in rain forests at high elevations, this would now be difficult to prove. The two species of *Drepanis*, for example, may have been restricted to the wet forest zone where the lobelioids on which they apparently preferred to feed were most abundant.

The peculiar composition of the avifauna from Ilio Point, Molokai, may be due in part to differences in ecology and climate. Ilio Point is situated near the end of a peninsula in one of the drier parts of the island and simply may have presented an unsuitable environment for certain birds, such as the nectarivorous species that are absent from the deposit. Nevertheless, there was enough forest in the area to attract such birds as *Pseudonestor*, *Hemignathus*, *Heterorhynchus*, and other probably arboreal types such as the icterid-like gaper. The absence of certain taxa at Ilio Point, such as *Loxops virens*, which occurs in lowland deposits on Oahu and also on Kauai, where it was common, or *Ciridops* and *Moho*, which both occur in the deposits on Oahu and Kauai as well as at the Moomomi dunes, Molokai, is not easily accounted for. At present, we have no satisfactory way to explain the species composition of the sample obtained from the Ilio Point dunes.

Biogeography

Although the Hawaiian avifauna is renowned in part for having been derived from so few colonizing ancestors, we now see that the fossil record greatly alters the statistics for successful colonizations. The historically known avifauna of the main islands was probably derived from 14 separate colonizations (Mayr, 1943), and the Leeward Islands would add another one or two. Several colonizations of the main islands may have taken place since the arrival of Polynesians. If we consider just endemic species, however, the historically known avifauna of the entire archipelago resulted from only 10 colonizations.

Whereas only one endemic species of goose is known historically from the archipelago, at least

seven others are now known as fossils. The two species of *Thambetochea* and the large flightless goose of Kauai were probably derived from a single colonization. *Geochea rhuax* of Hawaii, the medium Kauai goose, and the supernumerary Oahu goose appear to have been derived from at least one, and more likely two, additional colonizations.

The two species of fossil ibises add a new family to the endemic fauna of the archipelago and, of course, represent an additional colonization. The eagle, *Accipiter*, and long-legged owls were each derived from separate colonizations and in our opinion it is likely that the deep-billed *Corvus* did not come from the same ancestor that gave rise to the slender-billed species of *Corvus* and *C. tropicus*. It may never be possible to determine how many colonizations were responsible for the nine species of flightless rails now known from the archipelago, but we would guess that two or more would be necessary to account for the observed diversity of rallids.

Therefore, we calculate that the minimum number of additional colonizations indicated by the fossil record is 10, which exactly doubles the number needed to derive the total historic avifauna of endemic species. Clearly, any discussion of the number and kind of birds that were able to establish themselves in the Hawaiian Islands would be meaningless without reference to the species that existed there prior to the arrival of man.

It should be noted that the Hawaiian Islands once had more predatory birds than was previously apparent. Small passerines co-evolved with a genus of highly efficient bird-eating owls and at least one species of hawk of the ornithophilous genus *Accipiter*. In addition, *Buteo solitarius* had a wider distribution than was known historically, and probably fed mainly on birds and insects before rodents were introduced. Thus, to the extent that evolution is influenced by natural selection through predation, Hawaiian passerines would certainly have been subject to such pressures. Finally, the larger birds of the archipelago were not without a predator either, as the extinct

eagle would surely have taken seabirds, geese, ibises, and perhaps crows as well.

Most of the low islets and atolls of the Leeward chain were once larger and higher and doubtless supported more diverse biotas than they do at present. Thus, there is a possibility that elements of the present biota of the main Hawaiian islands have been in existence longer than the main islands themselves. Organisms may have dispersed southeastward through the Hawaiian-Emperor chain as new islands emerged and as the more northwesterly ones eroded and subsided. Organisms from Nihoa, for example, could have colonized Kauai when Nihoa was a larger island and before any of the other main islands emerged. Documenting that dispersal took place in this manner would be extremely difficult. We know of no direct evidence that any of the endemic birds or any other part of the biota of the main Hawaiian islands arrived via the Leeward Islands, despite the possibility that this could have happened in some instances.

A bizarre notion is that advanced by Croizat (1979:251), who has cited our fossil discoveries as marking "the demise of the claim that Ascension and Hawaii are 'oceanic islands.'" To conclude that the fossil birds of the Hawaiian islands are ancient continental relicts merely because they have diverged markedly from their ancestral stock is a ridiculous nonsequitur. We hasten to disassociate ourselves from any such argument.

In fact, we see no reason why the age of colonization of the ancestors of the endemic Hawaiian birds, fossil or otherwise, need be any greater than the age of the main Hawaiian chain. Propagules are still arriving regularly in the islands. Many of the same kinds of birds that gave rise to the endemic avifauna have been known to occur in the Hawaiian islands as vagrants from mainland areas. For example, geese of several different species are of fairly regular occurrence, as are various ducks. Glossy Ibis (*Plegadis falcinellus*), the Osprey (*Pandion haliaetus*), and two species of eagles are also known as vagrants. One of the few passerines that have strayed to the Hawaiian chain is the Snow Bunting (*Plectrophenax nivalis*), an

emberizine, rather than a cardueline, but nevertheless a boreal fringillid, as probably was the ancestor of the drepanidines.

Land bridges probably made various connections between the islands of Maui, Molokai, Lanai, and Kahoolawe at times during the Pleistocene epoch, but no such connections ever existed between any of the other Hawaiian islands. Therefore, all of the flightless species of birds in the archipelago must have evolved their flightless characteristics on the islands (or island group, in the case of Maui Nui) on which they occurred. Flightlessness and the morphology associated with it may evolve very rapidly through neoteny (Olson, 1973a). The ibises of Molokai and Maui evolved their flightlessness in less than 1.8 million years, the age of the West Molokai volcano, which has the oldest rocks found on any of the islands that formerly constituted Maui Nui. Because ibises have not been found, and probably did not occur on the older islands of Oahu and Kauai, it is unlikely that the ancestors of *Apteribis* once lived there and arrived on Molokai from the west before becoming flightless. Therefore, the most reasonable assumption at present is that the ancestor of *Apteribis* arrived from the mainland and established itself in the archipelago only after one or more of the volcanoes that later became Maui Nui emerged and developed soil, vegetation, and an invertebrate fauna sufficient to sustain an ibis. In other words, the very divergent genus *Apteribis* evolved in considerably less than 1.8 million years.

The entire avifauna of the Galapagos evolved very rapidly, probably during the late Quaternary period (Steadman, 1982). Given a somewhat longer period of subaerial exposure for the Hawaiian islands, we find no compelling reason to assume that the ancestors of any of the elements of the endemic avifauna need have arrived in the archipelago before the appearance of the main islands.

Since the debut of MacArthur and Wilson's (1967) equilibrium theory of island biogeography, we have witnessed a great proliferation of research attempting to apply numerical theory to

distributional data from island groups and other situations where distributions are patchy. Equilibrium theory has recently been applied to the endemic land birds of the Hawaiian islands by Juvik and Austring (1979). They found a strong positive correlation between island area and both the total number of species of land birds and the number of species of drepanidines on the islands. They also found other geographic and ecological factors, such as maximum elevation and number of "ecozone patches," to be highly correlated with numbers of avian species on islands. The slopes of species-area curves fit very well with the values predicted by the theory. Juvik and Austring (1979:205) concluded that the drepanidines have "achieved species-area saturation through adaptive radiation in evolutionary time," and that both the drepanidines and the total endemic land bird fauna are probably in natural equilibrium.

Our fossil evidence unequivocally controverts this interpretation. As seen in Table 5, although the number of historically known species of land

birds on individual islands appears to be related to island area and elevation, this relationship has not been achieved through a gradual evolutionary increase in the number of species on the larger islands, which is the assumption of the equilibrium theory. On Molokai and Oahu, over twice as many species occur in the fossil deposits as in the historically known fauna, and Kauai likewise has substantially more species in the fossil sample (Tables 4 and 5). Although the island of Hawaii has by far the greatest number of historically known species of land birds (23), the fossil deposits from Barber's Point, Oahu, an island with one-seventh the land area of Hawaii, contain many more species (32), and the still smaller islands of Kauai and Molokai have nearly as many species (21 each) in their fossil deposits as are known historically for Hawaii. The figures for the fossil avifaunas are minima, as some of the species that are known historically are absent from the fossil deposits (page 50), and there are undoubtedly additional extinct fossil taxa that are unrepresented as well.

Obviously, the recent history of the endemic Hawaiian avifauna has been one of massive extinction without natural replacement—not one of slow increase in numbers of species on islands, as Juvik and Austring (1979) concluded. This extinction was caused largely by human modification of the environment. Data from islands that have suffered from human disturbance, which would include most of the islands of the world, should not be relied upon for numerical studies of island biogeography unless the impact of such disturbance is known.

The fossil record has provided evidence that prehistoric Polynesian habitat modification and predation had a devastating effect on the endemic Hawaiian avifauna. We can only speculate on the effects of such perturbations on plants and insects. Therefore, great caution should be used in future attempts to interpret historical distributions of the Hawaiian fauna and flora in a biogeographical sense. This is particularly true of taxa that are likely to have inhabited lowland regions.

TABLE 5.—Maximum elevations and areas of the main Hawaiian Islands, and numbers of endemic species of land birds, excluding *Asio flammeus* and aquatic birds not specifically distinct from mainland species; no search has been made for fossil deposits on Niihau or Kahoolawe

Island	Maximum elevation (m)	Area (km ²)	Species	
			Historic	Fossil
Hawaii	4206	10464	23	— ^a
Maui	3056	1880	10	3
Oahu	1227	1536	11	32
Kauai	1598	1422	13	21
Molokai	1515	676	9	21
Lanai	1027	362	7	—
Niihau	391	184	0	—
Kahoolawe	449	115	0	—
Total			36	63 ^b

^a There are three extinct species of birds from Hawaii known only from fossils, but we have not computed the number of species in the archeological material from Mauna Kea or included the number known from lava tubes on Hawaii.

^b Does not include taxa listed in Table 3 as "*Branta* sp.," "*Himatione* sp.," or "additional Kauai finch."

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