

Quaternary Extinctions

A PREHISTORIC REVOLUTION

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EDITORS



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The Role of Polynesians in the Extinction of the Avifauna of the Hawaiian Islands

STORRS L. OLSON AND HELEN F. JAMES

BECAUSE A GREAT PROPORTION of the native land birds of the Hawaiian archipelago became extinct or very rare in the period since European discovery of the islands, it has often been assumed that the "serious degradation of the Hawaiian environment... began in earnest within a few years after the arrival of Captain Cook and his successors," whereas the "new balance [that] was established between the Hawaiians and their environment during the centuries following the first colonization of the islands will never be known" (Berger 1972:7). Discoveries of major deposits of fossil and subfossil bird bones on four of the main Hawaiian Islands, as well as lesser finds on another island, drastically change these assessments. Contrary to the stated belief that "no serious inroads were made on the native birds by the Hawaiians" (Amadon 1950:210), we find that the destruction of the greater part of the avifauna took place well before Cook's arrival.

The Fossil Sites

The sites that have produced bones of extinct birds (fig. 35.1), along with bones of extant species, encompass a surprising variety of geologic settings on five of the eight main Hawaiian Islands. Detailed information on these sites and the composition of the fossil faunas is provided elsewhere (Olson and James 1982b); here we limit ourselves to a brief recapitulation, adding new information from our latest excavations on Maui and Oahu.

On the island of Molokai a large collection of fossil material has been recovered from numerous individual sites in aeolian sand dunes at Ilio Point, on the northwestern tip of the island, and near Moomomi Beach. Aeolian dunes at the southern end of the island of Kauai are the source of another extensive fossil avifauna. Four samples of land snail shells and crab claws from the dunes on Kauai and from Ilio Point, Molokai, yielded radiocarbon ages ranging from $5,145 \pm 60$ to $6,740 \pm 80$ yr B.P. (Olson and James 1982b), indicating that the extinct species in these deposits persisted well into the Holocene. At least one specimen of fossil bird from the Molokai dunes appears to be Pleistocene in age, however, as land snails associated with the holotype of the flightless goose *Thambetothen chauliodous* yielded a radiocarbon age of $25,150 \pm 1000$ yr B.P. (Stearns 1973).

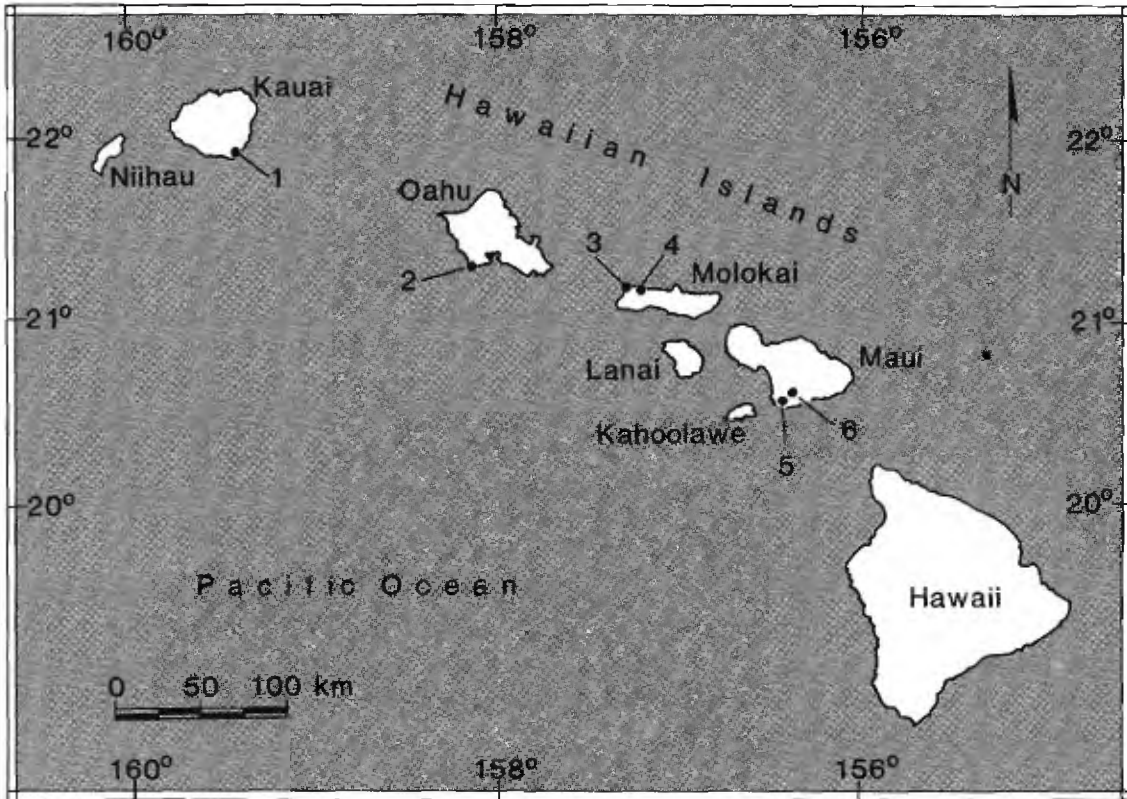


Figure 35.1. Outline map of the main Hawaiian Islands to show the location of principal fossil sites: 1, Makawehi dunes; 2, Barber's Point sinkholes; 3, Ilio Point dunes; 4, Moomomi Beach dunes; 5, Pau Naio lava tube; 6, Auwahi lava tube.

On Oahu we obtained a very rich avifauna from various sinkholes and caverns in an elevated limestone reef at Barber's Point, on the southwestern corner of the island. A unique site here is a flooded cavern, exposed during limestone quarrying operations, in which associated skeletons of extinct birds were found under 5 or more meters of fresh water. These skeletons must have been deposited at a time when most of the cavern floor was dry, presumably when lowered sea levels depressed the water table, indicating that fossils from this site are probably at least Wisconsinan in age. Apart from this site, however, the bones from Barber's Point were recovered from sediment-filled sinkholes and appear to be Holocene in age.

Recently, a new fossil bird site on Oahu was located by G. Paulay near Mokapu Point. Well-mineralized bird bones are exposed here in a sea cliff in sediment that was apparently deposited when a crater lake filled the center of the Ulupau tuff cone. The bird-bearing sediments underlie a beach deposit that has been identified as part of the Waimanalo Formation, dated radiometrically at 120,000 yr B.P. (Ku et al. 1974). Fossils from this deposit will add a new dimension to our knowledge of evolution in Hawaiian birds, but because they greatly antedate the arrival of man in the archipelago, they are not relevant to the present discussion and are not included in our calculations.

Until recently, few bird remains had been found on Maui (Olson and James 1982a,b), but two richly fossiliferous lava tubes were discovered in 1982 by R. M. Seaverns on the southeast slope of Haleakala on east Maui. Both are at considerably greater elevations than any of the productive sites on other islands. The first of these, the Auwahi Tube, is situated at 1145 m in a once-forested area that is now cattle pasture. Access to this tube was through two roof collapses about 58 m apart, both of which probably acted as pitfall traps. By far the majority of bird remains recovered here were those of flightless geese, ibises, and rails. Bones were concentrated near the entrances

but were also scattered throughout the remainder of the tube. Many were exposed at the surface, while others were buried in the shallow sediment that had accumulated near the entrances. Preservation was usually excellent. The bones are unmineralized and do not appear to be of great age.

The second site, the Puu Naio Tube, is at roughly 300 m elevation. The entrance to this tube is at the bottom of a sinkhole about 10 m in depth. Both the uphill and downhill portions of this lava tube had in the past been used for Polynesian burials. Bird remains were found only in the somewhat drier upslope portion of the tube. Bones of geese and ibises were found among the coarse rockfall at the rear of this cave; for the most part these were more friable and poorly preserved than those obtained in the Auwahi Tube, due presumably to greater moisture and degree of exposure. Extensive deposits of sediment occur back from the entrance of the upslope cave for a distance of at least 25 m. A small test pit here yielded remains of several species of extinct birds, and more extensive excavations should yield bones of a greater variety of small passerines than previously recovered from Maui.

A few bird bones have also been found in lava tubes on Hawaiï, and it is hoped that further exploration will expand our knowledge of the former birdlife of that island. Archaeological sites are another source of remains of extinct birds, and on Oahu, Molokai, and Hawaiï they have provided unequivocal evidence of contemporaneity of Hawaiians and extinct species of birds.

The Extinct Birds

The prehistorically extinct species of birds in our faunal samples (Table 35.1) include one small petrel, ten or eleven species of geese, most of them bizarre flightless forms, three species of flightless ibises, eight species of flightless rails, at least three species of a new genus of long-legged owl, an extinct eagle (*Haliaeetus*), an extinct hawk (*Accipiter*), two large species of extinct crows (*Corvus*), one species of large meliphagid (*Chaetoptila*), and as many as fifteen species of the so-called "Hawaiian honeycreepers," or drepanidines, which are actually finches belonging to the subfamily Carduelinae of the Fringillidae. Among the last mentioned are numerous taxa of finch-billed forms, as well as extinct genera not known historically.

We recognize thirty-six endemic species of land birds in the historically known avifauna of the main Hawaiïan Islands and five from the Leeward Islands. Sixty-eight endemic species of land birds occur in fossil deposits, forty-four of which became extinct before they could be recorded in life by ornithologists. Fourteen of the historically known species have not yet been collected as fossils, giving a total of eighty-two endemic species of land birds known from the main Hawaiïan Islands. Of this total, 53 percent became extinct prehistorically. These figures are constantly being updated, and the addition of taxa recovered during our excavations on Maui accounts for the difference between these figures and those in Olson and James (1982a,b).

Although the historic period in the Hawaiïan Islands began with Captain Cook in 1778, to avoid the tedious repetition of such phrases as "before thorough ornithological collecting took place," we define the historic avifauna as comprising all species that have been described as living birds in the scientific literature. Many of these descriptions were published a century or more after 1778, and it is quite possible that some of the species we count as prehistoric extinctions may have survived into the early part of the historic period. It is extremely unlikely, however, that an appreciable portion of the extinct fossil species survived this long.

Many of the extinct species are found in fossil deposits on more than one island. For instance, one species of fossil crow occurs both on Molokai and on Oahu; thus, two separate island populations of this crow became extinct. By analyzing the avifauna at the

**Table 35.1. Species or Populations of Fossil Land Birds
that Became Extinct Prehistorically in the Hawaiian Islands**

KAUAI

Anatidae

**Branta sandvicensis* (Hawaiian Goose)

Medium Kauai goose

Large Kauai goose

Rallidae

Medium Kauai rail

Strigidae

Long-legged Kauai owl

Fringillidae

Drepanidini

Psittirostra (Telespyza) (a finch), medium sp.

Psittirostra (Chloridops) (a grosbeak finch), Kauai sp.

Psittirostra (Subgenus incertae sedis) Cone-billed Finch

Psittirostra (Subgenus incertae sedis) Additional Kauai Finch

Hoopoe-like sickle-bill

Ciridops sp. (related to Ula 'ai hawane), Kauai

OAHU

Anatidae

†*Branta* sp. (a goose)

Supernumerary Oahu goose

Oahu *Thambetochen* sp. (a flightless goose)

Accipitridae

Haliaeetus sp. (an eagle)

Accipiter sp. (a hawk)

Rallidae

Small Oahu rail

Medium-large Oahu rail

Strigidae

Long-legged Oahu owl

Corvidae

Corvus sp., slender billed (a crow)

Corvus sp., deep billed (a crow)

Meliphagidae

Chaetoptila sp. (similar to Kioea)

Fringillidae

Drepanidini

**Psittirostra (Telespyza)* cf. *cantans* ("Laysan" finch)

Psittirostra (Telespyza) medium sp. (a finch)

**Psittirostra (Loxioides) bailleui* (Palila)

**Psittirostra (Rhodacanthis) flaviceps* (Lesser Koa Finch)

Psittirostra (Chloridops) Lesser Oahu sp. (a grosbeak finch)

Psittirostra (Chloridops) Giant Oahu sp. (a grosbeak finch)

Psittirostra (Subgenus incertae sedis) Ridge-billed Finch

Hoopoe-like sickle-bill

Icterid-like gaper, Oahu

Sickle-billed gaper

Ciridops sp., Oahu (related to Ula 'ai hawane)

MOLOKAI

Plataleidae

Apteribis glenos (a flightless ibis)

Anatidae

**Branta sandvicensis* (Hawaiian Goose)

Thambetochen chauliodous (a flightless goose)

Accipitridae

Haliaeetus sp. (an eagle)

**Buteo solitarius* (Hawaiian Hawk)

Table 35.1. Species or Populations of Fossil Land Birds that Became Extinct Prehistorically in the Hawaiian Islands

(continued)

Rallidae	Very small Molokai rail
Strigidae	Long-legged Molokai owl
Corvidae	<i>Corvus</i> sp., slender billed (a crow)
Fringillidae	
Drepanidini	
	* <i>Psittirostra</i> (<i>Telespyza</i>) cf. <i>cantans</i> ("Laysan" Finch)
	* <i>Psittirostra</i> (<i>Telespyza</i>) cf. <i>ultima</i> ("Nihoa" Finch)
	<i>Psittirostra</i> (<i>Telespyza</i>) small sp. (another finch)
	<i>Psittirostra</i> (Subgenus incertae sedis) Ridge-billed Finch
	* <i>Pseudonestor xanthophrys</i> (Maui Parrotbill)
	* <i>Heterorhynchus lucidus</i> (Nukupu'u)
	* <i>Hemignathus obscurus</i> ('Akialoa)
	* <i>Paroreomyza maculata</i> ('Alauwahio)
	Icterid-like gaper, Molokai
	<i>Ciridops</i> sp., Molokai (related to Ula 'ai hawane)
MAUI	
Plataleidae	
	Maui <i>Apteribis</i> sp. A (a flightless ibis)
	†Maui <i>Apteribis</i> sp. B (a flightless ibis)
Anatidae	
	Maui <i>Thambetochen</i> sp. A (a flightless goose)
	Maui <i>Thambetochen</i> sp. B (a flightless goose)
	†Maui <i>Branta</i> sp. A (a goose)
	†Maui <i>Branta</i> sp. B (a goose)
Rallidae	
	Smallest Maui rail
	Small Maui rail
	Larger Maui rail
Strigidae	
	†Long-legged owl
Muscicapidae	
	* <i>Phaeornis</i> sp. (a thrush)
Meliphagidae	
	* <i>Moho</i> sp. ('O'o)
Fringillidae	
Drepanidini	
	† <i>Psittirostra</i> sp. (a finch)
HAWAII	
Anatidae	
	<i>Geochen rhuax</i> (a goose)
	Large Hawaii goose
Rallidae	
	Large Hawaii goose

NOTE: Nomenclature follows Olson and James (1982b)

*Taxa that survived into the historic period, but not on island where listed.

†Taxon may not be specifically distinct from one occurring on another island.

level of individual island populations rather than species, we find that a minimum of eighty-nine populations of endemic species of land birds occur as fossils, sixty-seven (75 percent) of which became extinct prehistorically.

We can also document through fossils that many extant taxa with historically restricted distributions were, once, more widespread in the archipelago. Some of the

better examples are among the species known historically only from the Leeward Islands or the island of Hawaii. A number of species absent from the historically known avifauna of Maui are known historically from islands on either side of Maui [e.g. the thrush (*Phaeornis*), flycatcher (*Chasiempis*), meliphagid (*Moho*), and drepanidine (*Hemignathus obscurus*)]. Our recent excavations have now begun to fill in some of these gaps, although even when prehistoric human disturbance is considered it is still difficult to explain the absence from the large island of Maui of many taxa that managed to survive on smaller islands.

So far we have limited our discussion of the fossil evidence to endemic land birds. Seabirds, particularly petrels (Procellariidae), which come to land to breed and are essentially helpless in their nesting burrows, also suffered extinctions. Among the bones from Oahu are remains of a new extinct species of small *Pterodroma*. Another species, the Bonin Petrel, *Pterodroma hypoleuca*, is found in the Hawaiian chain today only in the Leeward Islands, yet it occurs in the deposits from the main islands and is particularly well represented in a site at Moomomi on Molokai that consists in part of cultural midden. The Dark-rumped Petrel, *Pterodroma phaeopygia*, once occurred on all the main islands, where the Polynesians used it extensively for food. It is now found as dwindling populations only in the higher parts of Maui and Hawaii, its decline being attributed to predation by mammals introduced after European colonization. Although unknown historically from Oahu, the Dark-rumped Petrel is by far the most abundant species represented in each of the many sinkholes at Barber's Point. Munro (1960) has suggested that Polynesians exterminated the Oahu population.

The number of Holocene extinctions in the Hawaiian avifauna was undoubtedly considerably greater than the figures presented here suggest. Certainly, many extinct species and populations remain to be discovered. Only from three of the eight main islands (Kauai, Oahu, and Molokai) are fossil collections comprehensive enough to include most of the species that were present on the island before human disturbances took place. But even on these islands, the samples do not include the entire naturally occurring avifauna (Olson and James 1982b). Niihau and Kahoolawe have not been searched for fossils yet, and efforts to find fossils on Lanai have so far produced only some eggshell fragments, probably of a goose. Fossil collections from the island of Hawaii are meager at present. Productive fossil sites on Maui eluded us for years, but new discoveries are beginning to increase the number of species known from fossils on that island.

Contemporaneity of Prehistoric Humans and Extinct Fossil Birds

What can account for the massive extinction of species of birds as diverse as flightless geese, eagles, petrels, and small insectivorous and granivorous passerines? While Pleistocene changes in climate and habitat can be correlated with extinctions of vertebrates in the West Indies (Pregill and Olson 1981), they cannot be invoked to explain the massive extinction of Hawaiian birds, since in most cases the extinct species persisted well into the Holocene. Further, we can show that many of the prehistorically extinct birds survived long enough to be contemporaneous with the Polynesians. The best evidence for this comes from finding bones of extinct birds in archaeological sites.

The Hawaiian Goose, *Branta sandvicensis*, is known historically only from the island of Hawaii. Remains of *Branta* (the systematics of the fossil populations have not yet been resolved) have been found in cultural midden deposits on Molokai and Oahu. A small sinkhole on Barber's Point, Oahu, contained bones of hundreds of individuals of the Dark-rumped Petrel, and, in addition to *Branta*, the following taxa that are either extinct altogether or extinct on Oahu: Bonin Petrel, *Pterodroma hypoleuca*; Harcourt's

Storm Petrel, *Oceanodroma castro*; a small flightless rail; a flightless goose, *Thambetochen* sp.; an extinct crow, *Corvus* sp.; and a large passerine, probably the extinct meliphagid, *Chaetoptila* sp. These were in association with a grindstone and bones of fish, chicken (*Gallus gallus*), Pacific rat (*Rattus exulans*), and a larger mammal (probably dog), as well as shells of marine mollusks commonly taken as food by Hawaiians. Of the myriad petrel bones from this site, all elements of the skeleton are represented, and none is broken or burned, indicating that cooking must have been accomplished by steaming or boiling. Thus, bird bones from Hawaiian middens will not necessarily exhibit either cut marks or charring.

In contrast to the Barber's Point cooking site, seabird bones from archaeological sites on southeastern Oahu almost always have the ends broken off. Bones of an extinct goose (*Thambetochen* sp.), an extinct rail, and locally extirpated seabirds were also recovered from these sites (Olson and James 1982b).

On the island of Hawaii, remains of a prehistorically extinct rail were found in cultural deposits high on Mauna Kea. A partial cranium of a large extinct goose was recovered from an occupation site in a lava tube at a level slightly below one dated at 606 ± 90 radiocarbon yr B.P. (Olson and James 1982b), but the association of this specimen with cultural deposits we now consider doubtful.

Two of the fossil sites in the Moomomi dunes on Molokai are composed at least partially of cultural midden, including bones of fish and chickens (*Gallus*), limpet shells ("opihī"), other edible mollusks, and crab claws. However, because of the unstable nature of dune deposits, we cannot be certain that the midden material was not deposited in an area that already contained bones of extinct birds. At one of these sites there is an unusually large concentration of bones of the Bonin Petrel, *Pterodroma hypoleuca*, a species now extinct in the main Hawaiian Islands. Along with the petrel bones are those of the flightless goose *Thambetochen chauliodous* and the flightless ibis *Apteribis glenos* (Olson and Wetmore 1976), an extinct long-legged owl, an extinct crow (*Corvus* sp.), a nene-like goose (*Branta* sp.), and a hawk (*Buteo solitarius*), the last two being extinct on Molokai, although still present on the island of Hawaii.

One of the most significant sites on Oahu is a very large, deep sinkhole with signs of considerable human modification (fig. 35.2). Beautifully preserved bones of extinct birds were obtained here from a deposit of fine, dry limestone dust that had accumulated under a sheltered overhang. Additional bones were recovered from the sediments in the central part of the sinkhole. Excavations here indicated that the sinkhole may have been used by Polynesians for agricultural purposes. A hearth uncovered in the central area contained charred bones of *Branta* sp., a larger extinct goose, Dark-rumped Petrel, and *Rattus exulans*. Charcoal from the hearth gave a radiocarbon age of 770 ± 70 yr B.P. (Olson and James 1982b), indicating that at least some species of extinct birds may have survived well after the original human colonization of the archipelago about 1,500 years ago.

In the dusty sediments of the sheltered portion of the sinkhole, bones of *Rattus exulans* were found in place in the same levels as bones of extinct birds. These were disassociated, isolated elements, all of which lay in a horizontal plane and thus were evidently not deposited as a result of burrowing by the rats. Thus, bones of extinct birds and *Rattus exulans*, which was imported by Polynesians, were being deposited simultaneously. These deposits must, therefore, postdate the arrival of man in Hawaii.

The remains of "marker" taxa such as *Rattus exulans*, that indicate Polynesian introduction, offer great potential for showing contemporaneity of extinct birds and Polynesians. Land snails also may be important indicators (Kirch and Christensen 1981, Christensen and Kirch 1982). At least one species, *Lamellaxis gracilis*, is believed to have been introduced to the Hawaiian Islands before European contact. It now appears likely that most of the species of lizards that occur at present in the Hawaiian archipelago were introduced prehistorically by Polynesians (G. K. Pregill in prep.), so that lizard bones, too, should provide good indicators.



Figure 35.2. The largest of the fossiliferous sinkholes in the raised limestone reef at Barber's Point, Oahu. The large stone cairn at the left and the rock wall extending from it are prehistoric Polynesian modifications of the site. Bones of extinct birds were recovered in association with Polynesian-introduced marker taxa in the fine dusts beneath the overhang at the top of the picture. Additional bones of extinct birds, cultural remains, a radiocarbon-dated hearth, and evidence of agricultural use of the sinkhole were uncovered in the unsheltered sediments. A test pit, later greatly expanded, may be seen in these sediments at the right of the picture.

In another of the larger soil-filled sinks excavated at Barber's Point, bones of extinct birds were found in the upper 5 cm of sediment and to depths of nearly 40 cm. Disassociated bones of *Rattus exulans* occurred throughout the deposit, although they were more abundant in the upper portions. In cores taken from this site, shells of *Lamellaxis* were distributed throughout the column. In another sinkhole with deeper sediments, *Lamellaxis* was found two-thirds of the way down into the layer that produced the most bones of extinct birds. It is evident that much of the deposition of bones of extinct birds at Barber's Point took place during the prehistoric Polynesian period. Kirch and Christensen (1981) also document the decrease in abundance and eventual extinction of a number of species of endemic land snails up through the stratigraphic column.

Causes of Extinction

Having shown that the majority of prehistorically extinct species of birds were not victims of Pleistocene climatic changes or other natural causes, and having implicated man in the demise of these birds, we now turn to possible mechanisms of extinction. Direct predation for food could have been responsible for the reduction in numbers or total obliteration of some species. The large flightless geese, the flightless ibises, and

ground-nesting or burrowing species of seabirds had no defenses against man or the dogs, pigs, and rats the Polynesians brought with them. To account for the loss of population after population of small forest birds, which could hardly have been hunted to extinction by any means available to the Polynesians, some other mechanism must have been at work. The most likely explanation is that relatively dry lowland forests in the Hawaiian islands were largely destroyed by clearing, mostly by fire, for agriculture.

In general, the pattern of extinctions within the avifauna corroborates the idea that human disturbances were involved. Possibly as many as twenty-two of the extinct fossil species of birds found so far were flightless or nearly so, and it is obvious that conditions in the archipelago were ideally suited to the evolution of flightlessness. However, only one of these flightless species is known certainly to have survived into the historic period. It is hardly likely that climatic changes or any other natural force would have been so intolerant of an adaptation that had been selected for repeatedly throughout the evolutionary history of the Hawaiian avifauna.

Except for some of the lava tubes, all of our fossil sites are from lowland areas; most are within a few hundred meters of the present shoreline. Although the Maui sites are at higher elevations, they are on the drier, leeward slope of Haleakala. During the historic period, native forest birds have been found almost exclusively in wet montane forests, and in fact some authors have considered them to be "montane species," unable to exist in lowland habitats (e.g. Juvik and Austring 1979). Fossil evidence conclusively shows not only that many prehistorically extinct species once flourished in the lowlands, but also that virtually all extant species occurred there as well.

With such exceptions as recent lava flows, active sand dunes, and the alpine regions of the highest mountains, there is no reason to believe that the vegetation in any part of the Hawaiian Islands before man's arrival consisted of anything other than forest of one kind or another. This was definitely not the case at the time of European contact, however. Early explorers described much of the drier lowlands as being barren or grassy and destitute of trees. On the leeward slopes of Kauai, Cook (1784) reported that on his visit "no wood can be cut at any distance convenient to bring it from," and fourteen years later Vancouver (1798) confirmed that this area was periodically burned when he "observed the hills to the eastward of the river to be on fire to a considerable height, in particular directions, down towards water's edge." From shipside, King (1784) could discern no tree growth on southwest Molokai or on the 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 (Wilson 1977).

On Vancouver's expedition, Menzies (1790-1792) found continuous plantations reaching six or seven miles inland from Kealahou Bay on the west coast of Hawaii, stretching in a broad band along the coast as far as he could see in either direction. Of the land farther north, he reported that "from the northwest point of the island [of Hawaii] the country stretches back for a considerable distance with a very gradual ascent and 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. . . ."

Of leeward Oahu, Chamisso (1830:316) gave the following account: "The culture of the vallies which lay behind Hanaruru [Honolulu] is really astonishing. Artificial irrigations enable the natives to form, even upon the hills, large aquatic plantations of *Tarra* [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." Archaeological studies of prehistoric land use on Molokai and Oahu provide further evidence that the natural vegetation of many lowland regions was removed, probably for agricultural purposes, and that an accelerated rate of erosion and the extermination of native land snail faunas ensued (Yen et al. 1972, Kirch and Kelly 1975).

The nature of the original vegetation of lowland regions is a matter of conjecture, as the forests here were virtually destroyed before botanists arrived to collect in them. Fosberg (1972) believes that "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." In sampling a few remnants of lowland forest, Rock (1913:15) was surprised to find a much greater diversity of species of trees than in wet montane forests, and he remarked that "not less than 60 percent 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 suggests that there was a greater diversity of feeding niches in these lowland forests, a view supported by the number of new species of drepanidines that we found in the lowland fossil deposits.

In the West Indies, arid scrub forest in Puerto Rico was found to have twice the species diversity and three times the number of individuals of birds as montane rain forest (Kepler and Kepler 1970). For this reason, and with support from the fossil record, it has been postulated that loss of arid habitats in the West Indies since the last glaciation probably caused the extinction of many species (Pregill and Olson 1981). By removing such habitats from the Hawaiian Islands, the Polynesians wrought a greater change in the total biota of the archipelago than has been accomplished by all post-European inroads in the wet montane forests.

Implications for Island Ecosystems Elsewhere

There is no reason to regard the prehistoric fate of the Hawaiian Islands as exceptional. It is known that practically the entire flora of Easter Island was eliminated by Polynesians, and in fact the eventual absence of wood strongly influenced the cultural development of the islanders (McCoy 1976). The Maoris in New Zealand were responsible for extensive deforestation by burning shortly after they colonized those islands (McGlone 1978). Zimmerman (1938) lamented that at least three quarters of the forest had been eliminated from Rapa by fire and grazing animals. When queried whether there were any islands in the Pacific that are "sufficiently virgin to enable a study of the primitive conditions" Zimmerman (1963:63) responded that: "From my experience, I would say there are very few, almost no such islands as a matter of fact, and that in the eastern or central south Pacific there are none."

Entomologists, however, can do little more than speculate on what the consequences of this deforestation might have been for insects, as few insects are preserved as fossils under the usual conditions of deposition met with in these islands. With the fossil record of birds from Hawaii we get a better picture of the magnitude of the destruction. With the possible exception of some Galapagos islands (D. W. Steadman pers. comm.), probably no islands in the Pacific have a relatively intact fauna with a full complement of naturally occurring species. Preliminary studies of a few archaeological remains from the Lakeba Islands in the Fiji group, for example, have shown that megapodes (Megapodiidae) and a very large pigeon were eliminated from the avifauna since the arrival of man (D. W. Steadman pers. comm.).

Exercises based on MacArthur and Wilson's (1967) "island biogeography," using statistics derived from present island ecosystems without considering the human history of the islands involved, are now seen as unlikely to be biologically meaningful. As an example, Juvik and Astring (1979) calculated species-area curves for native land birds of the Hawaiian Islands on the basis of historically known taxa. They found a high correlation between number of species and island area. It seemed reasonable to conclude that the Hawaiian avifauna was in natural equilibrium when the islands were first visited by Europeans. The fossil record, however, has shown that the historically known

Table 35.2. Area, Elevation, and Number of Endemic Species of Land Birds Known Historically and as Fossils from the Five Largest Hawaiian Islands

		Molokai	Kauai	Oahu	Maui	Hawaii
Endemic Species of Land Birds	Fossil	21	21	32	12+*	3*
	Historic	9	13	11	10	23
Island Area (km ²)		676	1,422	1,536	1,880	10,464
Maximum Elevation (m)		1,515	1,598	1,227	3,056	4,206

*Fossil samples from these islands are still too small to reflect true prehistoric species diversity.

avifauna of the archipelago constitutes only a fraction of the natural species diversity of the islands (Table 35.2). For example, thirty-two endemic species of land birds occur in the fossil deposits on Oahu, yet only eleven species are known historically. Even with the inclusion of the available data from fossils, there would be little chance of deriving a realistic correlation based on numbers of species per island because of the deficiencies of the fossil record.

Biotas of oceanic islands outside the Pacific region have also been depleted by human-caused extinctions. Fossils indicate that the small islands of the South Atlantic underwent a period of extinction immediately after their discovery by Europeans early in the sixteenth century. A flightless rail was exterminated on Ascension Island (Olson 1973), a rail and a rodent disappeared from Fernando de Noronha (Olson 1981), and two rails, a cuckoo, a hoopoe, and at least five species of seabirds, including one endemic, vanished from St. Helena since the coming of man (Olson 1975). In the North Atlantic, fossil evidence of man-caused extinctions is as yet known only from Bermuda (Olson et al. in prep.), whereas the nature of the prehuman faunas of the Azores, Canaries, Madeira, and Cape Verde islands, which have longer histories of occupation by man, are yet unknown. The absence of any endemic species of birds in the Azores is almost certainly an artifact of human interference. In the Indian Ocean, the ill fate of the biota of the Mascarene Islands since their discovery in the fifteenth century is renowned (e.g. Greenway 1958), although the fauna of these islands is still incompletely documented in the fossil record.

We have only begun to appreciate the effects of the Polynesian invasion on the biotas of Pacific islands. Heretofore, the best evidence, though often not recognized as such, came from New Zealand. We have now shown in the Hawaiian Islands that the devastation was more widespread and comprehensive than previously imagined (Olson and James 1982a, b). If the Hawaiian archipelago, which was colonized by humans considerably later than most of Polynesia, can be taken as an indication of the extent to which other Pacific Islands suffered from prehistoric human-caused alterations in environment, then the period of the original peopling of the diverse islands of Oceania, with their highly endemic biotas, may have been marked by one of the greatest waves of rapid extinction of species of animals and plants in the history of the earth. As a consequence, at least for vertebrate zoologists, scientific exploration of the Pacific Islands must be conducted anew. Until these islands are investigated paleontologically, we will not know what their natural diversity may have been.

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Figure 35.3. Extinct flightless ibis (left) and flightless rail from the Hawaiian Islands. (Courtesy of B. P. Bishop Museum, Honolulu. Painting by H. Douglass Pratt)

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