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Fossil Birds from the Hawaiian Islands: Evidence for Wholesale Extinction by Man Before Western Contact

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Abstract. *Thousands of fossil bird bones from the Hawaiian Islands collected since 1971 include remains of at least 39 species of land birds that are not known to have survived into the historic period; this more than doubles the number of endemic species of land birds previously known from the main islands. Bones were found in deposits of late Quaternary age; most are Holocene and many are contemporaneous with Polynesian culture. The loss of species of birds appears to be due to predation and destruction of lowland habitats by humans before the arrival of Europeans. Because the historically known fauna and flora of the Hawaiian Islands represent only a fraction of natural species diversity, biogeographical inferences about natural processes based only on historically known taxa may be misleading or incorrect.*

Since 1971, tens of thousands of fossil bird bones have been found in various geological settings on five of the main Hawaiian islands (*1*). At least 39 endemic species of land birds and one species of seabird are now known only from fossil remains (*2*); only three of these have been named previously (*3*). We have completed a general overview of the fossil deposits and their faunas (*1*), but systematic revisions and descriptions of new taxa are not completed (*4*). We now report on the role of Polynesians, who colonized the Hawaiian Islands by A.D. 600, and perhaps as early as A.D. 400 (*5*), in the disappearance of native birds.

The largest collections of fossil birds were found on the islands of Molokai, Oahu, and Kauai (*6*) (Fig. 1), and a few remains were found in lava tubes on Maui and Hawaii. Bones of prehistorically extinct birds (that is, extinct before Europeans arrived to keep written records, beginning in 1778) have also been recovered from archeological midden sites on Hawaii, Molokai, and Oahu.

The endemic species of land birds (*7*) that survived into the historic period on the main Hawaiian Islands include a goose, a hawk, a flightless rail, a crow, two thrushes, a flycatcher, five honeyeaters, and 27 Hawaiian finches (Drepanidini, previously called "Hawaiian honeycreepers"). To these, the fossil record now contributes the following additional endemic taxa: at least seven species of geese (many of them flightless), two species of flightless ibises, a sea eagle (*Haliaeetus*), a small hawk (*Accipiter*), seven flightless rails (Rallidae), three species of owls belonging to an extinct genus, two large crows (*Corvus*), one honeyeater (*Chaetoptila*), and at least 15 Hawaiian finches (Drepanidini). Thus, the number of species of endemic land birds known for the main islands has been more than doubled by the fossil taxa. The number of colonizations by birds that are known to have produced endemic species in the main islands has likewise now been doubled (*1*).

In addition to providing evidence of the extinction of many species, the fossil record shows that numerous taxa with restricted ranges in the historic period were formerly more widely distributed. For instance, certain species that are known historically only from the Hawaiian Leeward Islands (*Pterodroma hypo-*

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leuca, *Psittirostra cantans*, and *Psittirostra ultima*) or only from the island of Hawaii (*Branta sandvicensis*, *Buteo solitarius*, *Chaetoptila angustipluma*, *Psittirostra bailleui*, *Psittirostra kona*, *Psittirostra flaviceps*, and *Ciridops anna*) are represented in fossil deposits from other islands by the same or closely allied species.

As an indication of the extent of extinction, a combined total of only 33 island populations of endemic land birds were recorded from Molokai, Oahu, and Kauai during the historic period, whereas 74 populations are known from the same islands as fossils (Table 1). Only 22 (30 percent) of these fossil populations survived long enough to be recorded by ornithologists. In addition, at least five species of marine birds became extinct or were reduced in range prehistorically (*1*).

Extinction took varying proportions of different elements of the avifauna. Of the 24 endemic species of nonpasserine land birds now known from the main Hawaiian Islands, only three (12.5 percent) are definitely known to have survived into the historic period, whereas 62 percent of the species of passerines discovered so far survived. Of the 13 to 17 species of flightless birds that occur as fossils, only one small rail is known historically. Only one endemic species of raptorial bird (*Buteo solitarius*) now exists in the archipelago, whereas at least five species in three genera became extinct prehistorically, a situation that must alter assumptions concerning the role of predation in the evolution of the Hawaiian avifauna. Because the fossil record is incomplete, the figures on the extent of survivorship may actually be exaggerated.

Although at least one of the Hawaiian fossil deposits is of late Pleistocene age (*1*, *8*), most of the important sites appear to be late Holocene. The major deposits on Molokai and Kauai have yielded maximum radiometric ages ranging from 5145 ± 60 to 6740 ± 80 years before present (B.P.) (*9*), an indication that the extinct species in these deposits survived any Pleistocene climatic perturbations that may have affected the Hawaiian Islands.

Table 1. Island areas and numbers of species of endemic land birds in the historic and fossil avifaunas of Oahu, Kauai, and Molokai. For comparison, the large island of Hawaii (10,464 km^2) has only 23 historically known endemic species of land birds.

Island	Area (km^2)	Endemic species of land birds	
		Historic	Fossil
Oahu	1536	11	32
Kauai	1422	13	21
Molokai	676	9	21

At least 12 species that are either extinct, or that were extirpated on the island where their bones were found, have been collected in prehistoric archeological sites; these provide evidence that prehistorically extinct species of birds persisted until Polynesians colonized the islands. Charcoal from a hearth in a large sinkhole at Barber's Point, Oahu, was associated with charred bones of extinct birds and yielded a radiocarbon age of 770 ± 70 years B.P. (*1*). Noncultural deposits at Barber's Point also provide evidence of the contemporaneity of prehistoric man and extinct birds. In these sites, the Pacific rat *Rattus exulans* and the adventive land snail *Lamellaxis* (*10*), both introduced by Polynesian colonists, are ubiquitous in the same stratigraphic levels that contain the greatest concentrations of bones of extinct birds. This evidence suggests that all of the 23 extinct populations of land birds from the Barber's Point deposits were present on Oahu when Polynesians first arrived.

The Polynesian residents may have been responsible for the disappearance of more than half the endemic avifauna of the Hawaiian Islands. We attribute the extinction that occurred to a combination of habitat destruction and predation. Flightless species, as well as ground-nesting land birds and burrowing seabirds, would have been particularly vulnerable to predation by humans and by the dogs, pigs, and rats that arrived with them. Predation, however, was probably not the principal factor in the prehistoric extinction of most Hawaiian birds. It is unlikely, for instance, that 29 extinct populations of small passerines succumbed to hunting pressure. A more plausible explanation for the disappearance of these and many other Hawaiian land birds is the clearing of lowland forest, primarily by fire, for agricultural purposes. Journals of early western voyagers to the islands, including those of James Cook, James King, and George Vancouver, record extensive deforestation and heavy cultivation of the lowlands, as well as the use of fire in clearing (*1*). Archeological research on prehistoric land use supports these early descriptions (*1*). Changes through time in the land snail fauna in the Barber's Point deposits on Oahu also reflect habitat alterations that took place in the prehistoric Polynesian period (*10*).

In the historic period, endemic Hawaiian forest birds have been reported mainly from the wet montane regions where native forest persisted. Yet evidence from the fossil deposits shows that many of these species once occurred, sometimes abundantly, in relatively dry regions near sea level. Early botanical surveys have shown that the drier lowland regions of the Hawaiian Islands once supported a distinctive forest vegetation with many endemic species of plants, although only scattered remnants of this flora were in existence when they were first described by botanists (*11*). Species of birds that were restricted entirely to such habitats would have become extinct. Wet montane forest was probably not the optimal habitat for many others, which perhaps accounts for the scarcity of certain species of Hawaiian birds throughout the historic period.

We should emphasize that the fossil record for the Hawaiian Islands is still incomplete. We have good fossil samples from only three of the main islands, and even these samples lack species that must have been present at the time of deposition (*1*). Fossil material from the

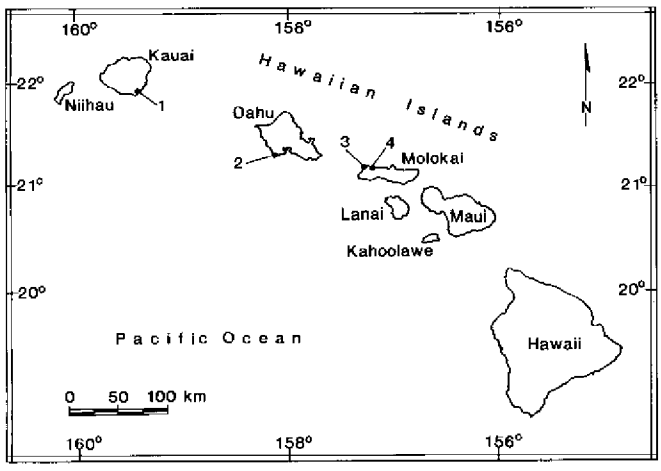

Fig. 1. The main Hawaiian Islands, showing the more important collecting localities for fossil birds: 1, Makawehi dunes, Kauai; 2, Barber's Point, Oahu; 3, Ilio Point, Molokai; and 4, Moomomi dunes, Molokai.

two largest islands, Hawaii and Maui, is scant, and there is as yet no way to assess changes in the avifaunas of these islands caused by prehistoric man, although three species of birds are known to have become extinct prehistorically on each. There is no fossil record from the islands of Lanai, Kahoolawe, or Niihau. No endemic species of land birds were ever recorded from the last two, although the absence of endemic birds cannot be a reflection of natural conditions. It is probable that the historically known avifauna represents only a third, or less, of the total number of endemic species of birds that were present in the Hawaiian Islands when man first arrived there.

These findings have implications for studies of island biogeography. The equilibrium theory of island biogeography (*12*), for example, was applied to the historically known avifauna of the Hawaiian Islands, with the results being congruent with the theory (*13*); the fossil record shows these results to be spurious, however (*1*). The assumption that the historically known biota of a prehistorically inhabited island contains an intact complement of species in a natural state of equilibrium is invalid for the Hawaiian Islands, and is most likely invalid for other islands as well.

Note added in proof: Much more extensive deposits of bird bones have very recently been found in lava tubes on Maui. Two or three species of geese, including flightless forms, are represented, along with other birds.

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References and Notes

1. S. Olson and H. James, *Smithsonian Contrib. Zool.*, in press.
2. We use the term "fossil" to refer both to fossil and "subfossil" bones, including those from archeological midden sites.
3. The three previously described fossil species are *Geochen rhuax*, a goose known from fragmentary remains from the island of Hawaii [A. Wetmore, *Condor* **45**, 146 (1943)], *Thambetochen chauliodous*, a large flightless goose, and *Apteribis glenos*, a flightless ibis, both from Molokai [S. Olson and A. Wetmore, *Proc. Biol. Soc. Wash.* **89**, 247 (1976)].
4. S. L. Olson and H. F. James, in preparation.
5. P. Kirch, *Archaeol. Phys. Anthropol. Oceania* **9**, 110 (1974).
6. On Molokai and Kauai the major collecting localities are in calcareous dune sand. Those on Oahu are from a raised coral-algal reef replete with sinkholes and caverns containing abundant fossil birds.
7. We exclude taxa that are not endemic at the species level from the calculations; that is, five freshwater birds that are only subspecifically distinct from mainland species, as well as the short-eared owl *Asio flammeus*, which appears to have colonized the archipelago subsequent to the arrival of man (*1*).
8. H. Stearns, *Occas. Pap. Bernice Pauahi Bishop Mus.* **24**, 144 (1973).
9. Radiocarbon ages from dune deposits are based on three samples of land snail shells and one of crab claws (Smithsonian Radiation Biology Laboratory, Washington, D.C.).
10. P. Kirch and C. Christensen, "Nonmarine mollusca and paleoecology at Barber's Point, Oahu (unpublished report prepared for the U.S. Corps of Engineers; manuscript No. ARCH 14-115; copy deposited in Smithsonian Institution Libraries) (1981), pp. 242–286; C. Christensen and P. Kirch, *Bull. Am. Malacol. Union* **1981**, 31 (1981).
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14. We thank the many persons who aided our research and who are acknowledged in detail in (*1*); we also thank A. Kaeppler and D. W. Steadman for reading the manuscript.

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