THE CONTRIBUTION OF FOSSILS TO KNOWLEDGE OF HAWAIIAN BIRDS

H. F. JAMES
Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

ABSTRACT. Fossils of Hawaiian birds reveal at least eight additional avian colonizations of the archipelago, and about 45 additional species of resident birds, thereby raising the number of species in the Holocene avifauna to about 92 and the number of avian colonizations to 20 or more. The colonizing species can be categorized as either waterbirds, raptors, or passerines. Flightlessness and terrestriality developed in over half of the waterbird lineages, adaptations for ornithophagy occur in half of the raptorial lineages, and adaptive radiation occurred in two out of five passerine lineages. The extinction of approximately 61 species of resident Hawaiian birds is attributed to the impact of human settlement of the islands.
Keywords: Hawaiian Islands, fossils, evolution, extinction, human impacts.

INTRODUCTION

Preliminary reports of rich avian fossil deposits in the Hawaiian Islands were published during the 1980's (Olson & James 1982a,b,1984, James 1987, James et al. 1987). Descriptions of seven new genera and 32 new species of birds represented in these fossil collections are in press (James & Olson in press, Olson & James in press), and three fossil genera and species were described earlier (Wetmore 1943, Olson & Wetmore 1976). Knowledge of the fossils has advanced enough to permit a reevaluation of evolutionary and zoogeographic trends in the resident, Holocene avifauna, taking into consideration both the fossil and historically known birds.

Besides the 35 extinct species referred to above, Hawaiian fossil collections include less diagnostic specimens that may represent up to 21 additional new species. A conservative estimate of the number of resident birds that became extinct before the historic period is 45 species, compared to 47 resident species that either still survive or became extinct during the historic period. Thus, there were originally at least 92 resident species in the Holocene avifauna of the main islands, 31 of which still survive, all but 10 of which are now thought to be threatened with extinction (Pyle 1988). These figures exclude species that probably did not colonize until after humans settled in the islands and created appropriate habitat for them (e.g., Black-crowned Night Heron, *Nycticorax nycticorax**, and Short-eared Owl, *Asio flammeus*).

The above figures also do not include an estimate of the number of extinct species for which fossils have not yet been found. Productive fossil deposits are known from only four of the eight main islands (Kauai, Oahu, Molokai, and Maui); a lesser amount of bone material is available from the island of Hawaii, mainly from archaeological

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*Taxonomy follows James & Olson (in press) and Olson & James (in press); common names follow Pyle (1988).

contexts; and little or nothing is available from the other islands. Thus, fossils have added 28 species to the avifauna of Maui, 24 to the avifauna of Oahu, 17 to the avifauna of Molokai, 11 to the avifauna of Kauai, four to the avifauna of Hawaii, one to the avifauna of Lanai, and none to the avifaunas of Kahoolawe or Niihau. More new species and distributional records can be expected as representative fossil collections become known from the poorly collected islands.

COLONIZATION

The historically known resident avifauna can be traced to 14 colonizing species (Mayr 1943), or, subtracting *N. nycticorax* and *A. flammeus* because they are probably post-human arrivals, to 12 natural colonizations of the main islands. Fossil evidence contributes at least eight additional colonizations, bringing the total to 20. This figure is a minimum, as it excludes two obscure fossil geese (*Geochen rhuax* and the Supernumerary Oahu Goose), and it incorporates the following assumptions: 1) the four species of flightless goose-like ducks (*Thambetochen* and relatives) are derived from a single colonization, 2) the flightless rails (*Porzana*) are derived from three colonizations, 3) the three species of Hawaiian crows are derived from one colonization, and 4) the two genera of Hawaiian honeyeaters (Meliphagidae: *Chaetoptila* and *Moho*) are derived from one colonization.

The 20 colonizers were an ibis (Plataleidae), two true geese (Anserinae), a dabbling duck (*Anas*), a second dabbling duck or a shelduck (Anatinae), three rails (*Porzana*), a gallinule (*Gallinula*), a coot (*Fulica*), a stilt (*Himantopus*), a hawk (*Buteo*), a sea eagle (*Haliaeetus*), a harrier (*Circus*), an owl (Strigidae), a crow (*Corvus*), a flycatcher (Myiagridae), a thrush (*Myadestes*), a honeyeater (Meliphagidae), and a finch (Carduelinae). The species that managed to colonize are divisible into three general categories: 11 were waterbirds, four were raptorial species, and five were passerines.

Continental relatives of many of the resident Hawaiian birds are recorded as occasional visitors in the islands (e.g., *Plegadis chihi* (White-faced Ibis), many species of *Anas* (dabbling ducks), *Branta canadensis* (Canada Goose), *Anser albifrons* (White-fronted Goose), *Haliaeetus pelagicus* (Steller Sea-Eagle), *Circus cyaneus* (Northern Harrier), and *Carduelis flammea* (Common Redpoll) (Pyle 1988). Although these species are not necessarily ancestral to related taxa in the resident fauna, their occasional arrival in the islands illustrates how colonization may have taken place.

The possibility also exists of colonization by island-hopping along the hot-spot islands of the Hawaiian-Emperor chain, most of which were submerged long ago and became seamounts (Jackson et al. 1972). This could result in the preservation of relictual taxa from as long ago as the late Cretaceous, the apparent age of the oldest seamount in the Emperor Chain (Scholl & Creager 1973, Worsley 1973). However, despite the growing fossil record there are still no obvious relicts in the Hawaiian avifauna, hence no evidence that avian lineages of extreme antiquity have been preserved by island-hopping from the older seamounts. Colonization of the main islands from the still subaerial Northwestern Hawaiian Islands has been proposed for the Hawaiian finches (Drepanidini) (Sibley & Ahlquist 1982).

EVOLUTION

Waterbirds

Eleven (55%) of the birds that colonized the main islands were waterbirds. An ecological shift from aquatic or semi-aquatic habitats to terrestrial habitats apparently occurred in seven of these lineages (*Apteribis*, *Branta*, a large goose from the island of Hawaii (Anserinae), *Thambetochen* and relatives, and the rails derived from all three colonizations by species of *Porzana*). Fossils of these birds are found in localities that are not near wetlands. Branching speciation, in which more than one endemic species has developed from a single colonization, occurred in at least 6 of the 7 terrestrial lineages, giving rise to 21 or 22 endemic species. Flightlessness is the rule among the terrestrial waterbirds, with all but one of the species in this group being completely (19-20 species) or nearly (one species) incapable of flying. Terrestrial waterbirds are the only group of Hawaiian endemics in which flightlessness evolved.

The four resident waterbirds that remained in aquatic habitats are *Anas wyvilliana* (Hawaiian Duck), *Fulica alai* (Hawaiian Coot), *Gallinula chloropus* (Common Moorhen), and *Himantopus knudseni* (Hawaiian Stilt). So far, no instances of flightlessness or branching speciation have been documented for these lineages, but there are few Holocene fossils of wetland birds.

Raptors

The Holocene fauna of the main islands includes seven raptorial species: *Haliaeetus* sp., *Buteo solitarius* (Hawaiian Hawk), *Circus* sp., and four strigid owls derived from a single colonization. The harrier and the four owls have long legs and short wings compared to related species outside the archipelago. Similar body proportions occur in bird-catching hawks of the genus *Accipiter*. Long-leggedness in Hawaiian raptors has been interpreted as an adaptation for hunting forest birds (Olson & James 1982b,in press).

Passerines

Fossils cast a new light on the spectacular adaptive radiation of the Drepanidini by adding 14 new species, descriptions of which are in press, and up to 8 additional undescribed species that are known from less diagnostic specimens (James & Olson in press). This raises the number of species in the radiation from 34, including three known historically from the Northwestern Hawaiian Islands, to between 48 and 56. Fossils also add to the diversity of the Hawaiian Corvidae and Meliphagidae, with two new species of crows and apparently two undescribed species of honeyeaters.

EXTINCTION

The approximately 45 Holocene extinctions recorded by fossils are attributed to the impact of prehistoric human settlement of the islands (Olson & James 1982a,b,1984, James et al. 1987), which commenced about 1500 years ago (Kirch 1974). Human impacts during the historic period caused 16 additional extinctions of endemic species (Pyle 1988). The prehistoric and historic period extinctions should be viewed as one ongoing "extinction event", which so far has removed roughly as many species of birds from the Hawaiian Islands as there were mammals lost from North America at the end of the Pleistocene (see Anderson 1984 for a list of extinct Pleistocene mammals).

In the Hawaiian Islands, terrestrial waterbirds suffered almost universal extinction. All of the 19-20 flightless species are extinct, as is the one goose that was a weak flier at best. It is no coincidence that the sole surviving member of this group, *Branta sandvicensis*, is also the only species capable of sustained flight. Waterbirds that remained in wetland habitats fared better: these four species are still extant. However, the fact that no extinctions have been documented for wetland birds so far may be due to inadequate fossil sampling of wetland habitats.

All but one raptorial species (*Buteo solitarius*) suffered extinction. Contributing factors may have included low population numbers, disappearance of important prey species, and predation by humans. It is also possible that the raptors, like the flightless birds, were ground nesters. Ground nesters would be vulnerable to nest predation by rats, pigs, and dogs that were introduced by the Polynesians (Olson & James in press).

Among drepanidines, at least 12 (80%) of the species with finchlike bills were lost from the main islands, and 16 (50%) of the species with more derived bill shapes were lost, either during the historic or prehistoric periods. The relatively dry, lowland forests, which are now virtually absent from the islands, may have provided essential habitat for these birds.

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ECOLOGICAL IMPACT OF THE HUMAN DEPLETION OF FRUGIVOROUS BIRDS IN POLYNESIA

DAVID W. STEADMAN
New York State Museum, 3140 CEC, Albany, New York 12230, USA

ABSTRACT. The extinction and extirpation that accompanied the human colonization of Polynesia involved many obligate frugivores (pigeons, parrots) and partial frugivores (megapodes, flightless rails, certain passerines). On most islands, frugivorous species of the forest canopy have been reduced in number, while those of the forest understorey and floor have been eliminated. At first human contact, most islands in the Marquesas supported 2 or 3 rails, 6 pigeons and doves, 3 parrots, and a starling. Only 1 to 3 frugivorous species survive on the same islands today. Similar depletion occurred in the Society and Cook Islands. Even isolated Henderson Island has lost a ground-dove and two pigeons since Polynesians arrived 800 years ago. In Tonga, human impact has eliminated a megapode, 2 flightless rails, 5 pigeons and doves, 2 parrots, and a thrush on 'Eua. Similar losses must have occurred throughout the region. Because of the decline in frugivorous birds, particularly columbids capable of ingesting large fruits, some Polynesian forest trees may be unable to disperse naturally within or between islands today. This situation, now aggravated by mechanized forest clearing, may threaten survival of the forest trees.

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