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## *OVERVIEW*

# HAWAIIAN BIRDS: LESSONS FROM A REDISCOVERED AVIFAUNA

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In the introduction to *Hawaiian Birdlife*, Andrew Berger (1972) wrote with frustration and dismay about his futile search for several species of endemic Hawaiian birds that had been described by collectors in the 1890s, but apparently were extinct by the mid-20th century. He bemoaned the fact that the ecology and behavior of those birds could never be studied. In fact, the loss of diversity and the gaps in our knowledge of the ecology and evolution of Hawaii's birds both are far greater than Berger could have imagined. During the past three decades, paleontological efforts spearheaded by Storrs Olson and Helen James have unearthed an unsuspected number and diversity of extinct birds. Bones collected from sand dunes, lava tubes, sinkholes, and former lakebeds have approximately doubled the number of endemic Hawaiian species. Among the fossil taxa collected and described by Olson and James are at least 15 new species in the spectacular honeycreeper radiation (tribe Drepanidini); several species of raptors unknown in the historical avifauna, including an eagle, a harrier, and a radiation of bird-eating owls; and many flightless birds, including rails, ibises, ducks, and geese (Olson and James 1982a, b, 1991; James and Olson 1991). Olson and James have demonstrated that the historically recorded Hawaiian avifauna, although spectacular, is a meager and biased sample of the fauna that existed prehistorically (i.e. before 1778, the year of the arrival of James Cook in the Hawaiian Islands).

Radiocarbon dating of bones of extinct birds and presence of extinct birds in some archaeological sites have shown that extinctions on Hawaii occurred after humans colonized the archipelago, ~1,600 years ago (Olson and James 1982a, b; James et al. 1987, Burney et al. 2001). That pattern of massive, rapid extinction of endemic birds following human colonization has been found on oceanic islands throughout the world (Steadman 1995). The loss of biodiversity is sobering. Also sobering is the realization of our previous ignorance. Any hypotheses about the evolution and ecology of the birds on oceanic islands based only on extant or historically recorded taxa are likely to be wrong. For the Hawaiian Islands, the paleontological work of Olson and James has provided vital new knowledge to re-address basic questions. In this overview, I attempt to summarize their work in the Hawaiian Islands and to describe how it has altered prevailing notions about the origins of the endemic birds, patterns of colonization and speciation within the archipelago, rates and patterns of morphological change, and the ecological roles of extant and extinct birds.

## Geography of the Hawaiian Islands

The Hawaiian archipelago is located in the middle of the north Pacific, over 3,800 km from North America, the nearest continent, and about the same distance from the Marquesas, the nearest high islands to the south. The Hawaiian Islands are volcanic in origin, formed by eruptions of fluid basalts from a fixed "hotspot" under the Pacific plate, located southeast of the island of Hawaii (Carson and Clague 1995). Volcanoes are formed successively, being built up over the hotspot, then carried to the northwest by the movement of the Pacific plate. The result is a linear chain of volcanoes of increasing age extending from Hawaii in the southeast, to Kure Atoll in the northwest, a distance of ~2,450 km (Fig. 1). Older islands tend to be smaller and lower in elevation, because of the combined effects of subsidence and erosion. The eight high islands in the southeast, from Hawaii to Kauai, constitute 99% of the land area in the entire archipelago Hawaii; the youngest island is ~0.43 Ma old. Kauai and Niihau are the oldest of the high islands, each ~5 Ma old. (Olson and James 1982b, Carson and Clague 1995). Olson and James have collected from sites on the high

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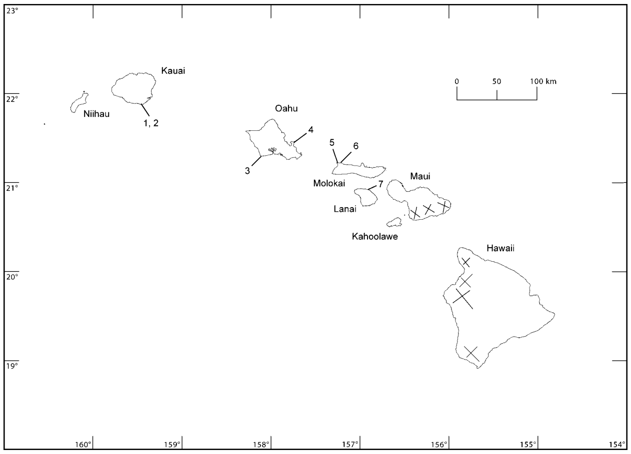

Fig. 1. Map of the Hawaiian Islands showing the principal localities for fossil birds. (1) Makawehi Dunes, (2) Maha`ulepu Cave, (3) karstic solution pits and caves near Barber's Point, `Ewa Plain, (4) Pleistocene wetland sediments at Ulupau Head, (5) Ilio Point Dunes, (6) Mo`omomi Dunes, (7) Maunalei Gulch Cave. On the islands of Maui and Hawaii, the regions with important lava tube sites for fossil birds are indicated with "X".

islands of Hawaii, Molokai, Maui, Lanai, Oahu, and Kauai (Olson and James 1982b, 1991; James and Olson 1991, 2003; Burney et al. 2001).

The extreme isolation of the Hawaiian archipelago has led to a high degree of endemism. For example, for both flowering plants and terrestrial vertebrates, the percentage of endemics is 96–97%, and for insects, >90% (Olson and James 1982b, Carson and Clague 1995). Relatively few lineages have succeeded in colonizing the archipelago, especially vertebrates. The native terrestrial vertebrates include 2 species of bat (1 extant) and at least 70 species of land birds. Some colonists have radiated to produce an abundance of diverse taxa. Among birds, the most extensive radiation is represented by the Hawaiian cardueline finches, tribe Drepanidini. About 13 genera and 27 species, with extremely diverse feeding adaptations, survived to historic times. Another 15 species have been described from fossil bones, bolstering both the number and diversity of species in the radiation (James and Olson 1991, 2003).

## Description of Fossil Sites

*Overview.*—Olson and James have collected bones from a wide variety of sites throughout the archipelago, including sand dunes on Molokai and Kauai, lava tubes on Maui and Hawaii, and sinkholes and caves in a limestone reef on Oahu (Olson and James 1982b, 1991; James and Olson 1991). Collecting sites differ in the quality of preservation, variety and type of taxa recovered, and age of bones. Collectively, the sites provide a broad, although piecemeal picture of prehistoric birds and ecosystems. Some bones have been dated, and the dates provide evidence that at least many extinct taxa were still extant when humans arrived in the islands (James et al. 1987). Additional evidence is provided by sites where archaeological remains are mixed with the bones of extinct birds, suggesting contemporaneous deposition. (Olson and James 1982a, b, 1984).

*Dunes.*—The first large collections by Olson and James were obtained from dune sites on Molokai (Moomomi Dunes, Ilio Point) and Kauai (Makawehi Dunes) (Fig. 1). Most bones were found scattered in loose sand. Samples of land snail shells and crab claws from Ilio Point and Makawehi Dunes yielded radiocarbon ages ranging from 5,145 ± 60 to 6,740 ± 80 years before present (BP) (Olson and James 1982b). One exceptional specimen collected from Moomomi Dunes was the holotype of *Thambetochen chauliodous*, one of four species of extinct, flightless anatids collectively dubbed "moa-nalos." That specimen was preserved as a nearly complete articulated skeleton in weakly cemented sand, and land snails associated with it yielded a radiocarbon age of 25,150 ± 1,000 year BP, much older than the dates associated with other dune sites (Olson and James 1982b, 1991). The dunes on Molokai also yielded additional bones of *T. chauliodous*, bones of an extinct flightless ibis (*Apteribis glenos*), an extinct eagle of the genus *Haliaeetus*, an extinct harrier (*Circus dossenus*), an extinct bird-eating owl (*Grallistrix geleches)*, a large species of *Corvus*, *Branta*, rails, seabirds, shorebirds, and some small passerines. Bones of an extinct species of *Ciridops*, an endemic honeycreeper, were found in a fossilized owl pellet, presumably deposited by the extinct *G. geleches* (Olson and James 1982b, 1991; James and Olson 1991). Fossilized owl pellets were common in dune sites, and Olson and James (1991) suggest that the owls roosted in the dunes.

The dune sites on Kauai yielded a similar mix of fossils, including bones of a second species of moa-nalo (*Chelychelnechen quassus*), a second species of bird-eating owl (*G. auceps*) and owl pellets, *Branta*, seabirds, shorebirds, and small passerines including drepanidines and a meliphagid (*Moho braccatus*) (Olson and James 1982b). The bones from the dune sites vary in quality of preservation, some appearing weathered or stained, and others in near perfect condition (Olson and James 1982b). Attempts to obtain DNA from bones from dune sites have failed, possibly because the bones were exposed to sun or partially mineralized.

*Lava tubes.*—On Maui, bones have been collected almost exclusively from lave tubes found at the southern end of the island, at elevations ranging from 15 to 1,860 m (Olson and James 1991, James and Olson 1991). Some of the lava tubes apparently acted as pitfall traps. Flightless birds and some volant animals fell or flew into openings to the lava tubes; often, those openings were vertical drops. Bones were found lying exposed on the floor of the lava tubes, often in the vicinity of skylights. Taxa represented in those collections include a high proportion of flightless birds (moa-nalos, rails, and ibises), as well as bats, ducks, petrels, gallinules, owls, an eagle, crows, and small passerines (Olson and James 1991, James and Olson 1991). Bones collected from some lava tubes on Maui have yielded DNA, and there appears to be a trend toward longer amplification products (i.e. less degraded DNA) from bones from high elevation sites.

On Hawaii, as on Maui, most bones have been collected from lava tubes, although the collections from Hawaii are less extensive. Lava tube sites on Hawaii range from sea level to ~400 m. The bones recovered include elements of the endangered Laysan Duck (*Anas laysanensis*) and Hawaiian Goose or nene (*B. sandvicensis*), a large extinct flightless goose ("very large Hawaii goose," Olson and James 1991), flightless rails, a petrel, two crows, a meliphagid, and several species of Hawaiian finches (James and Olson 2003, James 1998). Many bones from the lava tubes on Hawaii have yielded DNA, and DNA sequences have been used to study population-level variation in the Hawaiian Goose (Paxinos et al. 2002a) and phylogenetic relationships of the Laysan Duck (Cooper et al. 1996), *Branta* species (Paxinos et al. 2002b), and flightless rails (Slikas et al. 2002).

*Sinkholes, caves, and lakebeds.*—On Oahu, bones were collected from several sinkholes and caverns in an elevated limestone reef at Barber's Point, on the southwestern corner of the island. One unique site in that locality is a flooded cavern in which associated skeletons of extinct birds were found under several meters of fresh water. The skeletons included 12 individuals of two species of raven-sized *Corvus* and 5 or 6 individuals of a large meliphagid, presumably *Chaetoptila* (Olson and James 1982b). Assuming that the bones were deposited when the cavern was dry, the bones probably date to the last glaciation (about 10,000–15,000 years ago), when lower sea levels reduced the water table on the island. Physically, the bones were remarkably well preserved, with even small processes intact (Olson and James 1982b). However, attempts to obtain DNA from those bones have failed, presumably because of the moist conditions of preservation.

Bones also were recovered from sediment-filled sinkholes at Barber's Point. At several sites, evidence of human occupation was found, including human-made items, fish and chicken bones, and shells of edible mollusks. Those cultural remains frequently were associated with large concentrations of bird bones, including bones of Dark-rumped Petrel (*Pterodroma phaeopygia*) and Bonin Petrel (*P. hypoleuca*), both now extinct on Oahu, Wedge-tailed Shearwater (*Puffinus pacificus*), and a few other species either extinct or extirpated on Oahu. The association of cultural remains and extinct birds suggests that those prehistorically extinct species survived until the arrival of humans. The context of those bones also suggests that some extinct Hawaiian birds were food items for Polynesians (Olson and James 1982b).

A second productive locality for bones of extinct birds on Oahu is at Mokapu Point, near the southeastern corner of the island. Bones are exposed in a sea cliff, buried in sediment that was deposited when a lake filled the Ulupau tuff cone (Olson and James 1982b, 1984, 1991; James 1987). The site has been dated at ~120,000 years BP or earlier, making it the oldest known fossil site in the archipelago (James 1987). Bones recovered from that site are heavily mineralized and useless for DNA extraction.

A productive site on Kauai is an excavation in a large sinkhole and cave system at Maha'ulepu on the south coast of the island (Burney et al.

2001). That site is unique in that the goal was to obtain a detailed, comprehensive picture of the complete flora and fauna over time. Sediments were screened for vertebrate bones, invertebrate shells, seeds and other plant macrofossils, pollen, diatoms, and cultural artifacts. The excavation covered a period of ~10,000 years. Bones of 40–43 species of indigenous birds were recovered from that site, including waterfowl, pelagic seabirds, waders and shorebirds, rails, raptors, and passerines (Burney et al. 2001). New fossil taxa include an odd duck with a flattened cranium and small eyes and an endemic gull; there are no resident gulls in the modern Hawaiian avifauna, and no gulls have been collected at other fossil sites. Bones of a koa-finch (*Rhodacanthis*) and Palila (*Loxioides bailleui*) were collected here, extending the known distribution of both taxa. DNA sequences have been obtained from several bones from that site (Burney et al. 2001). Bones from more recent levels in the excavation have proven more likely to yield DNA sequence.

## Fossil Birds

*Passerines.*—The new taxa described by Olson and James from their fossil collections have increased the number of species in the Hawaiian avifauna by ~50%, and many more fossil species await formal description (Olson and James 1982b, 1991; James and Olson 1991, 2003). Among passerines, James and Olson (1991, 2003) described 17 new species from fossils: 2 species of crows (*Corvus*) and 15 species of Hawaiian honeycreepers (tribe Drepanidini). Thus far, fossils have added new species to lineages known from the historic avifauna, increasing the morphological and presumably ecological diversity of those lineages, but fossils have not added any new lineages of passerine birds. Interestingly, most bones of small passerines were found in fossilized owl pellets or originally were deposited in owl pellets, then dispersed over time (James and Olson 1991).

Hawaiian finches, or honeycreepers, constitute by far the most speciose radiation in the Hawaiian avifauna. It is one of the largest and most spectacular avian radiations on any island. The monophyly of the Hawaiian finches is supported by morphological and molecular data (Raikow 1977, Zusi 1978, Johnson et al. 1989, Fleischer et al. 2001, James 1998). Independent studies of mycology (Raikow 1977), osteology (Zusi 1978) and DNA–DNA hybridization data (Sibley and Ahlquist 1982, Bledsoe 1988) support a most recent common ancestor for the Hawaiian finches among the cardueline finches. Elements of the postcranial skeleton tend to be similar among closely related species of Hawaiian finches, so descriptions of new fossil species are based primarily on features of the skull and bill (James and Olson 1991).

Because taxon sampling is known to have a tremendous effect on the accuracy of phylogenetic reconstructions, the inclusion of fossil species in any analysis of relationships among the Hawaiian finches is essential. James (1998) constructed a phylogeny based on osteological characters for 55 Hawaiian finches, including 17 fossil species. She also constructed a phylogeny based on mitochondrial DNA sequences, taken from GenBank, for 12 Hawaiian finches. The sequence data set is limited to extant birds, because obtaining DNA sequence data from the bones of small passerines has proven difficult. The two trees are not congruent. James is preparing a manuscript comparing the two phylogenies and analyzing the points of disagreement.

James and Olson (1991) described two new species of raven-sized crows from Oahu (*Corvus impluviatus)* and Oahu and Molokai (*C. viriosus*). The Hawaiian Crow or alala (*C. hawaiiensis*) is still extant on Hawaii. Bones from lava tubes on Hawaii and Maui might represent additional species. The three named species of Hawaiian crows can be distinguished by bill shape, but osteological characters are insufficient to determine the phylogenetic relationships of the Hawaiian crows with respect to each other and other species in the genus *Corvus* (James and Olson 1991). Studies of their origins and relationship based on DNA sequence data are underway.

*Nonpasserines.*—Among nonpasserines, Olson and James (1991) have described 16 new species. In contrast to passerines, many of those fossil species represent groups unknown in historic times. Several of the Hawaiian nonpasserine birds are flightless (Olson and Wetmore 1976, Olson and James 1982b, 1991). Loss of flight probably has evolved more than once within each clade of flightless birds—a remarkable example of convergence (Olson and James 1991, Sorenson et al. 1999, Paxinos et al. 2002b, Slikas et al. 2002). Another example of convergence is found in the browsing adaptations of flightless Hawaiian geese and moa-nalos; the latter are an endemic clade of ponderous, goose-like birds descended from an ancestor in the dabbling duck group (Olson and James 1991, Sorenson et al. 1999). The origins and relationships of many of the extinct nonpasserines have been studied using DNA sequence data (Cooper et al. 1996; Sorenson et al. 1999; Fleischer et al. 2000; Fleischer and McIntosh 2001; Paxinos et al. 2002a, b; Slikas et al. 2002). Obtaining DNA sequence data from the typically larger, more robust bones of nonpasserines has been more successful than obtaining sequence data from smaller, more fragile passerine bones.

*Anatids.*—The Hawaiian Goose, or nene, (*B. sandvicensis*) is the only endemic nonpasserine land bird that is still extant. In historic times, the nene was restricted to the island of Hawaii, although fossil bones have been collected from Molokai, Lanai, Maui, and Kauai, indicating that it was more widespread in prehistoric times (Olson and James 1991, Paxinos et al. 2002a). Several other goose-like birds have been found in the fossil record. *Branta hylobadistes,* a large robust goose with reduced wings and pectoral girdle, was described from bones found in the Auwahi lava tube (1,145 m) on Maui; bones of a similar-sized goose with reduced wings collected on Oahu and Kauai might represent the same species (Olson and James 1991). Bones of an undescribed species, larger than *B. hylobadistes*, also with reduced wings, were found in lava tubes on Hawaii ("very large Hawaii goose," Olson and James 1991). Fragmentary remains found at Barber's Point on Oahu and at a public works site on Hawaii probably represent two additional species of uncertain affinities: the "supernumerary Oahu goose" (Olson and James 1982b, 1991) and *Geochen rhuax* (Wetmore 1943, Olson and James 1991), respectively.

Paxinos et al. (2002b) assessed the relationships of the nene, *B. hylobadistes*, and the "very large Hawaii goose" using mitochondrial DNA sequences obtained from 13 bone samples representing the three Hawaiian species and homologous sequences of 15 taxa of true geese (tribe Anserini), including several subspecies of the Canada Goose (*B. canadensis*). The three Hawaiian geese formed a clade that was embedded within the Canada Goose clade. The Hawaiian clade was sister to two subspecies of large-bodied Canada Goose; that clade was sister to a clade including the Barnacle Goose (*B. leucopsis*) and several subspecies of small-bodied Canada Goose. Nine of the 13 bones that yielded DNA were radiocarbon dated, yielding ages from 5,100 ± 50 to 510 ± 60 years BP (Paxinos et al. 2002b).

Another group of endemic anatids are the moa-nalos, a radiation of four species of ponderous, flightless browsing birds with massive bills. Bones of moa-nalos have been found on all the main islands where extensive collecting has been done, except Hawaii, the youngest island (Olson and Wetmore 1976, Olson and James 1982b, 1991). The moa-nalos are goose-like in overall appearance, but a few individuals were discovered with an ossified syringeal bulla associated with the skeleton. A syringeal bulla is a feature found only in the males of most genera of ducks, leading Olson and James (1991) to suggest that the moa-nalos were members of the subfamily Anatinae. To test that hypothesis and to determine the ancestor of the moa-nalos, mitochondrial DNA sequences were obtained from bones of three moa-nalo individuals representing two species, *T. chauliodous* and *Ptaiochen pau* (Sorenson et al. 1999). Sequences were compared to sequences from 37 extant waterfowl in 25 genera using parsimony and maximum-likelihood analyses. In all optimal phylogenies, the two moa-nalo species paired as sister taxa, and that pair was sister to a large clade of dabbling ducks (Sorenson et al. 1999). Additional mitochondrial DNA sequence was obtained from another individual of *P. pau*, an individual of *T. xanion*, and two individuals of *C. quassus*, so that all four species of mao-nalo could be represented in a phylogenetic analysis. The new sequences were added to the data matrix of Sorenson et al. (1999). In all optimal trees from parsimony and maximum-likelihood analyses, the moa-nalos formed a clade, and that clade was again sister to a large clade of dabbling ducks (H. F. James et al. unpubl. data). The moa-nalos apparently are descended from a dabbling duck, but their ancestor might be extinct, because the clade does not pair with any particular species or lineage.

The massive bills of all moa-nalo species suggest that those birds were browsing herbivores. In a unique study, James and Burney (1997) examined the chemical composition and pollen and spore content of coprolites attributed to *T.*

*chauliodous*, to determine the diet of this extinct bird. Coprolites were recovered from lava tubes on Maui. The results support the hypothesis that those birds were primarily folivorous and suggest that ferns were important in their diet. James and Burney (1997) discuss the ecological role of the moa-nalos, and the effect of the extinction of large native herbivores on the native vegetation.

*Flightless ibises and rails.*—In addition to flightless geese and ducks, the Hawaiian Islands also harbored a small radiation of flightless ibises and several flightless rails (Olson and Wetmore 1976, Olson and James 1982b, 1991). All the flightless Hawaiian endemics on the main islands were extinct before historic times, except a single species of rail on Hawaii (*Porzana sandwichensis*) (Berger 1972). Presumably, loss of flight made the birds vulnerable to hunting and predation by rats and dogs, particularly on nests (Olson and James 1982b, 1991). Olson and James (1991) speculate that flightless ibises and rails exerted considerable predation pressure on native Hawaiian land snails.

The radiation of flightless ibises included at least two species, *A. glenos* from Molokai and *A. brevis* from Maui (Olson and Wetmore 1976, Olson and James 1991). Bones from lower elevations on Maui are smaller than those attributed to the higher elevation taxon (*A. glenos*) and might represent another species. Olson and James (1991) speculate that the flightless ibises were confined to Maui Nui, the single large island formed when Molokai, Maui, and Lanai were joined at times of low sea level during the Pleistocene. No bones of ibises have been found on any of the other main islands, whereas ibises are relatively abundant on Molokai and Maui. Phylogenetic analysis of mitochondrial DNA sequences (12S rDNA) from an *Apteribis* specimen and 21 other species of ibises yields a tree in which *Apteribis* is sister to the New World White Ibis (*Eudocimus albus*; Fleischer and McIntosh 2001).

Flightless rails are a ubiquitous component of the avifauna of islands and are abundant in the Hawaiian fossil record (Olson and James 1991, Steadman 1995). Bones of flightless rails have been collected from all the main islands where collecting has been done. Size differences among bones collected from single islands suggest that Kauai, Oahu, Maui, and Hawaii each were occupied by two or more species. All the Hawaiian flightless rails were short-billed crakes, provisionally placed in the genus *Porzana*. Mitochondrial DNA sequences have been obtained from some species of flightless Hawaiian rails, including *P. sandwichensis*, the "medium Hawaii rail", and the "large Hawaii rail" from Hawaii, and *P. severnsi* and *P. keplerorum* from Maui. Phylogenetic analyses indicate that the rails from Hawaii and *P. keplerorum* are descended from *P. tabuensis*, a volant rail widespread in northern and eastern Australia and on islands north to Micronesia and the Philippines and east through Polynesia. *Porzana severnsi* appears to be an older lineage, descended from a previous colonization event , although the species from which it descended could not be determined (Slikas et al. 2002; B. Slikas, S. Olson, H. James, and R. Fleischer, unpubl. data).

*Raptors*.—On the basis of the historical fauna, it would seem that Hawaiian passerine birds evolved in a predator-free environment, but the discovery of several raptor species in the fossil record contradicts that notion. In particular, it appears that endemic owls in the genus *Grallistrix* fed primarily on small birds. Four species of those bird-eating owls have been discovered and described, one species on each of the islands of Kauai, Oahu, Molokai, and Maui, and fossilized owl pellets containing bones of passerines and a small flightless rail have been collected from dune sites on Kauai and Molokai (Olson and James 1991). The bird-eating owls have elongated legs and shortened wings compared to owls in the genus *Strix*, believed to be their closest relatives. Those proportions parallel those of bird-eating hawks in the genus *Accipiter* (Olson and James 1991). Studies are underway to determine the relationships of *Grallistrix*, using DNA sequence data.

Other extinct raptorial taxa include a harrier (*C. dossenus*) and an eagle (*Haliaeetus* sp.). The harrier species was described from bones found in the Moomomi Dunes on Molokai (Olson and James 1991). Olson and James (1991) note that the wing and pectoral elements of that harrier are greatly shortened, so that the proportions relative to the body are similar to those of an accipiter. They hypothesize that *C. dossenus* was adapted to living in the forest, feeding on birds and insects. The eagle is represented by bones from at least five individuals from sites on Maui, Molokai, and Oahu. Olson and James (1991) placed it in the genus *Haliaeetus* based on the fusion of the phalanges of the inner toe. They suggested a close relationship with either *H. leucocephalus* of North America or *H. albicilla* of Eurasia, on the basis of the overall size of the bird, but they could find no osteological characters to distinguish the two species. Fleischer et al. (2000) obtained mitochondrial DNA sequence from a single bone of the eagle, collected from a lava tube on Maui, and compared it to sequences obtained from GenBank for other species of *Haliaeetus*. The sequence from the bone was almost identical to that from *H. albicilla*, and the two sequences paired in a phylogenetic analysis, suggesting that the Hawaiian eagle is descended from the Eurasian *H. albicilla.*

## Summary

During almost three decades of field and museum work, Olson and James have been collecting, describing, and analyzing thousands of avian bones collected from sites scattered throughout the main Hawaiian Islands. Those sites include dunes, lava tubes, limestone sinkholes, and former lakebeds, most dating to the Holocene. The fossil finds have more than doubled the endemic avifauna of the islands, increasing the number and diversity of species known from groups that are recorded historically and revealing an unsuspected diversity of extinct nonpasserine groups, including several raptors and flightless taxa. Also, the fossil record shows that some species historically, found on a single island were more widely distributed in the past (James 1987; Olson and James 1982b, 1991; James and Olson 1991, 2003; Burney et al. 2001). Those discoveries force a re-evaluation of the prehistoric ecology and biogeography of the islands and greatly increase the number of colonization events contributing to the endemic avifauna.

Using osteological traits and DNA sequence data, Olson, James, and colleagues have studied the origins and relationships of several groups of endemic Hawaiian birds, and demonstrated striking examples of convergent evolution and rapid and drastic morphological change (James and Olson 1991; Olson and James 1991; James 1998; Sorenson et al. 1999; Fleischer and McIntosh 2001, Fleischer et al. 2000, 2001; Paxinos et al. 2002b; Slikas et al. 2002). Examples include loss of flight within and between flightless groups and the browsing adaptations of flightless Hawaiian geese and moa-nalos (Olson and James 1991, Sorenson et al. 1999, Paxinos et al. 2002b, Slikas et al. 2002). Using radiocarbon dating of the bones of extinct birds as well as other organic material from fossil sites, Olson and James have shown that the bulk of extinctions in the Hawaiian Islands occurred prehistorically (prior to 1778) but after the arrival of humans in the archipelago. That pattern of destruction has been repeated on oceanic islands throughout the world (Olson and James 1982a, 1984; James et al. 1987; Steadman 1995).

Olson and James are continuing to collect bones in the Hawaiian Islands and to describe new taxa from their collections. In addition, they are using their collections to study causes and ecological consequences of extinctions and patterns of evolution and biogeography. Their ongoing work is creating a more complete picture of the avifauna and ecology of prehistoric Hawaii and contributing to a better understanding of extinction and evolution on oceanic islands.

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