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Patterns of Avian Diversity and Radiation in the Pacific as Seen Through the Fossil Record

EXTENDED ABSTRACT

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In the past two decades, increased paleontological exploration of the islands of the Pacific has revealed prehistoric man-caused extinctions on a scale never previously imagined. Habitat destruction, along with predation by man and introduced mammals, removed a minimum of 30% to 80% of the avifauna within the past 2000 years or less on most of the prehistorically inhabited islands for which a fossil record is available (Olson, 1989). Such massive extinctions are assumed to have been pervasive, affecting organisms other than birds, and occurred even on islands not currently populated by man, such as Henderson (Steadman & Olson, 1985; Schubel & Steadman, 1989). Consequently, biogeographical and systematic conclusions based on historically known distributions are bound to be to some degree inaccurate, or entirely erroneous (Olson, in press; Steadman, 1986).

Apart from the story of extinction itself, what does the fossil record, as it presently stands, tell us about patterns of avian diversity and adaptive radiation in the Pacific?

In New Zealand, where the first fossil birds were described from the Pacific, there are many extinct lineages documented in the fossil record. The most famous of these is the moas, which were large, wingless herbivores with characters associating them with the so-called "ratite" birds such as emus and ostriches, although these characters may possibly be convergent (Olson, 1983; 1985). The number of species recognized was once exaggerated but has been continually dwindling through systematic revisions so that now there are some 11 species in six genera admitted (Worthy, 1990). I personally doubt that this diversity is entirely the result of *in situ* radiation from a single ancestral species but is more likely due to multiple invasions by several volant ancestors, which may have been closely related. This remains to be proven, however.

Fossils from New Zealand also document the extinction of the Apteromithidae, a family of flightless gruiform birds possibly related to the kagu, *Rhynochetos*, of New Caledonia; *Cnemiornis*, a flightless "goose" related to the Cape Barren Goose, *Cereopsis*, of Australia; *Euryanas*, a flightless or nearly flightless duck probably congeneric with the Australian Wood Duck, *Chenonetta*; *Harpagornis*, a giant eagle that doubtless preyed on large flightless birds; an owlet-nightjar, *Aegotheles novaezealandiae*, with its presumed

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closest relative in New Caledonia; several flightless rails (Rallidae); a swan; several ducks; a hawk; a pelican; a crow; and an extinct genus with two species of the wren-like Acanthisittidae (Millener, 1988).

The overall pattern of avian diversity in the main islands of New Zealand has resulted for the most part from repeated colonizations from the mainland. Thus, each of the 13 species of ducks and geese (Anatidae) and 10 species of rails (Rallidae) represents an independent colonization, mainly from Australia. A single lineage may colonize more than once, as for example, in the rails *Gallirallus*, *Porphyrio*, and *Fulica*. Presumably because there have been at most three, and often only two, main islands in New Zealand to provide opportunities for genetic isolation, there has been very little adaptive radiation here, and when such does occur, the result is usually no more than three species per radiation, as in the case of kiwis (Apterygidae), the wattlebirds (Callaeidae), and the passerine genus *Mohoua* (sensu lato, Olson, 1990). Discounting moas, the only apparent exception is the New Zealand "wrens" (Acanthisittidae), with four genera and six species. But no close mainland relatives of this peculiar family have ever been identified and it has not been confirmed that the Acanthisittidae resulted from a single invasion rather than two or more.

In New Caledonia the fossil record is still very incomplete but at least 11 extinctions have been recorded (Balouet & Olson, 1989), including a giant, flightless galliform bird, *Sylviornis*, which is probably derived from the Megapodiidae but is best considered a separate endemic family. Despite its deep, somewhat raptorial-looking beak, the abundance of *Sylviornis* in fossil deposits indicates that it could not have been at the top of the food chain and it has been postulated to have been a herbivore (Balouet, 1986). The family Strigidae, represented by a species of *Ninox*, is the only other family found as a fossil that does not occur on the island today. A megapode, two pigeons, and a snipe belong to genera that no longer occur in New Caledonia. All other extinct species belong to genera that still exist in the island. No adaptive radiations are apparent among the birds of New Caledonia, which is essentially a single island. Instead, each of the endemic species arose from a separate colonization, the only apparent exception being the kagu, *Rhynochetos*, of which a second fossil species has been described (Balouet & Olson, 1989).

On the opposite side of the Pacific, in the Galápagos, which were not inhabited prehistorically, the fossil record shows only local extinctions of species of birds, all of which are known or assumed to have taken place in the historic period (Steadman, 1986). The only completely extinct lineage of vertebrate not known historically is the large cricetid rodent *Megaoryzomys* (Steadman & Ray, 1982), although bones of these rodents have been radiocarbon dated to historic times (Steadman et al., in press). There are three *in situ* radiations of birds ranging in size from two species (vermilion flycatchers, *Pyrocephalus*), and four species (mockingbirds, *Mimus*), to some 13 species and many more subspecies of the renowned Galápagos finches, which Steadman (1982) considers to belong to a single genus, *Geospiza*. These radiations appear to be very recent. If Steadman (1982) is correct that the mainland grassquit *Volatinia* is congeneric with *Geospiza* (sensu lato) then none of the birds of the Galápagos differs at the generic level from its mainland ancestors. There are no flightless species among any of the land birds. The only real departures from mainland forms are in the bill shapes of the finches and mockingbirds. Presumably the great number of islands in the archipelago is responsible for the diversity of Galápagos finches. The youthfulness of this radiation and the fact that the subspecies, species, and "genera" form essentially a continuum, with considerable hybridization, make this assemblage unique among insular birds.

The Hawaiian Islands combine aspects of the great divergence from ancestral forms seen in New Zealand, with adaptive radiations even more diverse than in the Galápagos. The fossil record documents the extinction of 35 named species and some 22 possible additional species that await description, pending further study or collection of better specimens (Olson & James, 1982a,b; 1984; in press; James & Olson, in press). These come from five of the main Hawaiian Islands, but the fossil record is reasonably complete from only two of these, Oahu and Maui.

In the Hawaiian Islands, the niche of large herbivores was occupied by geese (at least two extinct species) and the moa-nalos (Olson & James, in press), which were heavy-bodied, flightless derivatives of ducks, with strangely shaped bills. These are divided into three genera and four species. Whether these are products of a single colonization from the mainland or several has not been determined. The niche of kiwis on islands of the Maui group was occupied by flightless ibises of the genus *Apteribis*, which contains at least two and perhaps three species. Flightless rails are represented by at least ten species, probably from at least three separate colonizations. An extinct genus of long-legged bird-eating owl is known from four species on as many islands. Other raptors included an extinct eagle, *Haliaeetus*, and a strikingly modified harrier of the genus *Circus*, with very shortened wing elements. Two species of crows, *Corvus*, were added to the one known historically, and the already impressive radiation of Hawaiian finches, Drepanidini (the "Hawaiian honey-creepers" of old), have been augmented by four new genera, fourteen new named species and up to eight yet unnamed species.

Compared to the Galápagos, the avifauna is much more diverse, with many endemic genera, and with most of the endemic species having diverged far more from their main-land ancestors. Compared to New Zealand, there has been much more *in situ* radiation. There are no really "ancient," relictual elements in the Hawaiian fauna comparable to the Acanthisittidae and Apteromithidae in New Zealand or the Rhynochetidae in New Caledonia, none of which has any close living mainland relatives.

Factors contributing to the character of the Hawaiian avifauna are its great isolation from the continents, the large size and large number of islands, the ecological and climatological diversity of the islands, and their relative age, i.e., older than the Galápagos but younger than New Zealand. The fact that the Hawaiian islands are situated so as to have received colonists from at least three different directions (North America, Asia, Australasia/Oceania), has also doubtless contributed to the makeup of its avifauna.

Fossil avifaunas in the remainder of the Pacific are known almost entirely through the recent work of David W. Steadman who has analyzed material from the Marquesas, Pitcairn, Cook, Society, and Tonga groups (Steadman, 1989). Many of these bones are from archeological middens, hence conferring a decided bias in the sample towards edible, catchable species, and also towards larger species in the case of material collected by archeologists who did not use fine enough screen to recover smaller bones. Time of deposition may also affect species composition in archeological samples representing time periods after significant human-caused extinction had already taken place.

Steadman has documented the extinction of many previously unknown species, as well as many range extensions of extant species. Although considerably greater diversity within genera is indicated, so far most of the new species belong to families or genera already well represented in Polynesia. These include megapodes of the genus *Megapodius*, rails of the genera *Gallirallus*, *Porzana*, and *Porphyrio*; pigeons of the genera *Ducula* and *Gallicolumba*; parrots of the genus *Vini*; and starlings of the genus *Aplonis*. New elements for the Polynesian region include the pigeons, *Caloenas*, previously known only as far east as Micronesia and New Caledonia; and *Macropygia*, not known east of Vanuatu (Steadman, in press).

Although large flightless herbivorous birds evolved in New Zealand, New Caledonia, and the Hawaiian Islands, this niche in the Galápagos being filled by tortoises, no such herbivores are known from central or eastern Polynesia. Nor have flightless, long-billed probing birds, such as kiwis and *Apteribis*, been discovered outside of Hawaii and New Zealand. Except for a species of *Accipiter* from Tonga (D. W. Steadman, pers. comm), no raptorial birds have yet been reported from fossil deposits on islands outside the historically known range of hawks and owls.

Except in Hawaii, there are few recognized adaptive radiations of passerines in Polynesia, apart from such possible examples as the diversity of monarchine flycatchers (Myiagridae) in Fiji (Olson, 1980). The fossil record has so far added nothing that would change this impression.

Why should the patterns of great evolutionary divergence or of adaptive radiations such as seen in the avifaunas of Hawaii, New Zealand, New Caledonia, and the Galápagos, not be evident elsewhere in the Pacific? To some extent this may be attributable to the effects of larger land area and/or greater degree of isolation of these archipelagos. But in part it may be an artifact of inadequate paleontological knowledge. The large, high islands of Fiji and Samoa, for example, are essentially unexplored and it would be difficult to imagine that some great evolutionary novelties do not await the paleontologist who first discovers a significant source of fossils, say, on Viti Levu.

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