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THE PREHISTORIC IMPACT OF MAN ON BIOGEOGRAPHICAL PATTERNS OF INSULAR BIRDS

Through both paleontological and archeological investigations, the past several years have seen an explosive increase in our knowledge of the faunas of islands prior to colonization by man. Analysis of the fossil record has repeatedly shown that prehistoric man has had an extremely adverse effect on insular ecosystems on a global scale. The resulting extinctions have produced completely unnatural faunal assemblages that are grossly misleading with regard both to species diversity and to biogeographical patterns.

I wish to illustrate here some of the problems that have arisen in interpreting biogeographical patterns of extant birds on islands in the Pacific Ocean. It should be remembered, however, that similar problems exist with other groups of organisms and with other groups of islands. For all practical purposes, there are no islands in the world that can be regarded as having an intact fauna and flora. Any assessment of an insular biota should be made with the assumption that it has experienced some degree of human-caused disturbance.

I recently made some rough calculations of the amount of man-caused extinction of native land birds for certain islands of the Pacific, based on the fossil and historic record (Olson, 1989). In all cases, these figures are absolute *minima* because of the inevitable incompleteness of the fossil record. In New Zealand, 46% of the native land birds are extinct, 33% prehistorically. In New Caledonia, at least 40% of the nonpasserine avifauna was exterminated prehistorically (Balouet and Olson, 1989). In the main Hawaiian archipelago, over 50% of the avifauna disappeared prehistorically, and for the two islands; with more complete fossil records the figure is 69% for Oahu and 71% for Maui (Olson and James, 1982, 1984; Olson, 1989). In the Marquesas, analysis of purely archeological deposits, which sample but a fraction of any given fauna, reveal a loss of at least 39% of the avifauna of the archipelago as a whole, and local extinctions reaching 55 to 69% on individual islands (Steadman, 1989; Olson, 1989). On Mangaia in the southern Cook group, 80% of the native land birds were exterminated prehistorically (Steadman, 1985), and on Huahine in the Society Group, the

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figure is a similar 78% (Steadman, 1989; Olson, 1989). Even on remote Henderson Island in the Pitcairn group, which was wrongly presumed to have been uninhabited but had actually been colonized and then abandoned by Polynesians, three species of pigeons, representing 43% of the fauna of native land birds, were extirpated prehistorically (Steadman and Olson, 1985; Steadman, pers. comm.).

These massive extinctions were responsible for the disappearance of entire groups of organisms that consequently have never figured in any consideration of island biogeography. For example, flightless birds, which must once have occurred virtually throughout the Pacific, were almost totally eliminated. Kiwis (Apterygidae) miraculously survived, but all the moas (Dinornithiformes), some 12 species, were totally exterminated. Bizarre flightless derivatives of goose-like birds (Anatidae) evolved in New Zealand and radiated extensively in the Hawaiian Islands, along with flightless ibises (Plataleidae). Other flightless members of these families doubtless remain to be found in other island groups. On New Caledonia, a gigantic flightless galliform bird, *Sylviornis*, possibly derived from megapodes but so divergent as probably to deserve its own family, was exterminated since the island was colonized by man.

Almost every island for which we now have a fossil record has produced one or more flightless rails (Rallidae). For example, at least 9 new species have been found in the main Hawaiian Islands, where only one species of flightless rail persisted into the historic period. I calculate that *hundreds* of populations of flightless rails, particularly of the genera *Porzana* and *Gallirallus*, have disappeared from the Pacific in the past 2000 years or so. Yet outside of the New Zealand region, only 11 species of flightless rails are known historically from Oceania, one of these only from a painting from Cook's second voyage. Of these 11, all but two are now probably extinct, although the Guam Rail (*Gallirallus owstoni*), which was abundant in the 1970's, has been exterminated in the wild by an introduced species of snake, but persists in captive populations.

However, rather than dwell on the tremendous loss of species diversity and all of the prehistorically extinct forms that have been discovered so far on islands, I wish to concentrate here on the manner in which patterns of distribution of extant birds have been unnaturally modified by man-caused extinctions and have thus led to many fallacious systematic and biogeographic conclusions. If we are to salvage anything from present-day distributional patterns we must learn to view them with great scepticism to discern false patterns and to predict the probable former presence of species where they are now absent. For example, the 11 historically known flightless rails mentioned above were scattered over the Pacific in such a haphazard manner on Guam, Kosraï [=Kusai in the Carolines], Wake, Laysan, Hawaii, New Caledonia, Lord Howe, Viti Levu [Fiji], Tahiti, and Henderson Island, that it now seems strange that such a pattern was never adduced to be the unnatural result of numerous extinctions on intervening islands.

Another example of a group with an obviously unnatural pattern of distribution is the megapodes or mound-builders (Megapodiidae). The traditionally accepted historical distribution of these birds in the Pacific includes the species *Megapodius laperouse* in the Marianas and Palau groups, the form *M. layardi* of the New Hebrides and Banks Islands, and the widely disjunct species *M. pritchardii* of the island of Niuafou'ou, a remote northern outlier of the Tonga group between Fiji and Samoa. Such an improbable distribution has attracted some attention and one rather feeble attempt was made (Lister, 1911) to explain this pattern as the result of the birds having been transported to various islands by primitive man. But megapodes do not adjust well to captive conditions and have never been domesticated. Furthermore, since the insular forms are distinct from one another and from those outside Oceania, from where would they have been transported?

Actually, there had long existed some possible historical records of megapodes from islands where they do not now occur (these and fossil records summarized in Balouet and Olson, 1989), but like most facts that do not conform to established ideas, this evidence has long been disregarded. There is a very brief allusion in manuscripts from Cook's second voyage to what was probably a megapode on New Caledonia and a large, extinct species of *Megapodius* has now been found in fossil deposits there. Eggs attributed to megapodes were received at the British Museum from Fiji and Tonga, and were even described as new species, but these have subsequently been ignored by compilers and biogeographers. Bones of megapodes from archeological sites in Fiji, and from the Tongan island of Lifuka, where two large species of megapodes have been recovered (Steadman, in press), now add substance to these early records. Additional material of megapodes has also been recovered from archeological sites in the Santa Cruz Islands and their outlier Tikopia, where megapodes no longer occur. There is even an anecdotal reference to what may have been a megapode in the Kermadec Islands. So the previously puzzling gaps in the distribution of megapodes are being filled in and it now remains to be seen just how extensively these birds were distributed before the arrival of man.

Parrots are another group that have an obviously artificial pattern of distribution in the Pacific. Species of the genus *Cyanoramphus* occur only in the New Zealand region and New Caledonia, except for two species known from the Society Islands, both of which are now extinct. One of these is known only from two specimens from Raiatea collected on Cook's second voyage, and the other is from Tahiti. It is hardly conceivable that no forms of *Cyanoramphus* ever colonized the remaining islands of the Society group or any of the many islands between the Societies and New Caledonia, however.

The distribution of the tiny parrots of the genus *Vini* is similarly suspect. *V. australis* is widely distributed in Fiji, Samoa, and Tonga, *V. peruviana* occurs discontinuously in the Society and Tuamotu groups, *V. ultramarina* is known only from two of the islands of the Marquesas, *V. kuhli* only from

Rimatara in the Australs, and *V. stepheni* only from Henderson Island. It seems obvious, however, that *Vini* probably occurred throughout the southern archipelagos of the Pitcairn, Gambier, Austral, and Cook Islands, a supposition partly confirmed by bones referred to *Vini* from Mangaia in the Cook group (Steadman, 1985). Furthermore, Steadman and Zarriello (1987) have shown from archeological deposits that there was a radiation of *Vini* in the Marquesas that included two species much larger than any now extant, one of which has now been found in archeological deposits on Huahine in the Society Group (Steadman, pers. comm.).

Doves of the genus *Gallicolumba* have a similarly artificial distribution in the Pacific. Three species inhabit Micronesia. *G. sanctaecrucis* is known from 2 islands of the Santa Cruz group and one in the New Hebrides; *G. stairi* occurs in Fiji, Tonga, and Samoa, *G. erythroptera* on several islands in the Society and Tuamotu groups, and *G. rubescens* only on two of the smaller islands of the Marquesas. But from early Pacific voyages there are descriptions and illustrations of species of *Gallicolumba* from the island of Tanna in the New Hebrides, and also from Norfolk Island, where the genus no longer occurs. To these may now be added a medium-sized species from fossil deposits on Mangaia in the Cook Islands (Steadman, 1985), a very large species from fossil deposits in New Caledonia (Balouet and Olson, 1989), and an even more robust species from archeological sites in the Marquesas, Huahine, and Mangaia (Steadman, 1989, pers. comm.). These last two species represent a size-class of *Gallicolumba* that probably once occurred throughout the Pacific but that is now entirely extinct.

The distributions of pigeons of the genus *Ducula*, long heavily hunted by Polynesians, have been severely altered in the past few thousand years. Of the largest forms of the genus, the only species to persist into the historic period in the Pacific are *D. goliath*, of New Caledonia, and *D. galeata*, found only on the island of Nuku Hiva in the Marquesas. In retrospect, that such a large, strong-flying bird as *D. galeata* should not occur at least on some of the other islands of the Marquesas, seems quite improbable. Bones from archeological sites have now shown that the species indeed probably occurred throughout the Marquesas (Steadman, 1989). More importantly, remains of *D. galeata* have also been recovered from Mangaia in the southern Cooks (Steadman, 1985), from Henderson Island (Steadman and Olson, 1985), and from Huahine (Steadman, pers. comm.). In addition, what is almost certainly this species was described from Tahiti on Cook's second voyage. An even larger species of *Ducula* has been found in archeological deposits on Wallis Island and is probably the same as one reported from archeological deposits on Lakeba in the Lau group of Fiji (Balouet and Olson, 1987). This may also be the same species as one of the two giant forms of *Ducula* recovered from midden deposits on Lifuka in the Tonga group (Steadman, in press). Clearly the larger species of *Ducula* must have been distributed throughout the entire Pacific before the arrival of man.

The artificial pattern of distribution of extant populations of *Ducula* has given rise to some very erroneous conclusions regarding the evolution, systematics, and ecological interactions of these birds. *Ducula galeata* was Mayr's (1942) prime example of «extreme morphological differentiation of the most isolated form» of what he considered to be a single «superspecies» that also included the species *D. oceanica*, *D. pacifica*, and *D. aurorae*. Holyoak and Thibault (1978) used these same artificial distributions as evidence for competitive exclusion between the larger and smaller forms of *Ducula* and also as evidence that island size was responsible for restricting the distribution of some species. But we now know that *Ducula galeata* and other large forms of *Ducula* were sympatric with smaller species of *Ducula*, probably throughout the Pacific, and on islands as small and remote as Henderson.

Erroneous biogeographical assumptions seriously undermine Bock's (1970) analysis of evolution in the Hawaiian finches of the tribe Drepanidini. In perhaps the worst of these, he conjectured that the widespread species *Psittirostra psittacea*, found on most of the main Hawaiian Islands, gave rise to *P. cantans* (including *P. ultima*) of the remote Hawaiian Leeward group, and by multiple invasions also gave rise to *P. bailleui*, *P. kona*, *P. palmeri*, and *P. flaviceps*, all of which are known historically only from the island of Hawaii. Morphology alone is sufficient to establish this scenario as hopelessly simplistic and evolutionarily impossible. In addition, we now have fossil records of *P. cantans* from Oahu and Molokai, *P. ultima* from Molokai, *P. bailleui* from Oahu, *P. palmeri* and *P. flaviceps* from Maui and Oahu, and relatives of *P. kona* from Kauai and Oahu (Olson and James, 1982, 1984). We have found that practically all single island distributions of volant birds in the Hawaiian Islands are artifacts of human-caused extinctions on other islands.

Thus, we see the great danger in basing systematic, evolutionary, and ecological hypotheses on present distributional patterns. We must be increasingly aware of the fact that, except for flightless birds, there are probably very few species that are truly endemic to single islands, especially when those islands are part of larger archipelagos. Even flightless species may have very closely related representatives on distant islands. The flightless rail *Porzana atra* on Henderson Island would seem to be a highly distinctive and remote isolate, but a very similar flightless species also occurred on Mangaia in the Cook group (Steadman, 1987) and other derivatives of this same invasion will doubtless be found to have been widely distributed in the Pacific.

Distributions such as that of *Gallicolumba rubescens*, found only on the small, low islands of Fatuhuku and Hatutu in the Marquesas, and *Ducula galeata* found only on the high island of Nuku Hiva in the same group, may now be perceived as simply nonsensical. Both of these species must once have occurred together throughout the archipelago, as shown by bones of both from archeological deposits on Uahuka, Hiva Oa, and Tahuata

(Steadman, 1989; pers. comm.). This example also shows how the variable effects of extinction can produce totally different modern biogeographical patterns and points up a further difficulty with using island area or elevation as predictors of species diversity.

We must also be alert to the fact that allopatric distributions of congeneric birds are not grounds for considering species to be members of the same «superspecies» or «biological species». There has already been much overuse and abuse of the so-called «biological species» concept. With the realization that many allopatric patterns of distribution are probably unnatural, there is all the more reason to call for careful re-evaluation of systematic relationships among insular birds.

If theoretical studies of biogeography of birds of Pacific islands along the lines of MacArthur and Wilson (1967) were not a wasted effort from the outset, most of them have been invalidated by the fact that the data used in such studies are too incomplete and inaccurate, because of man-caused extinctions, to yield any meaningful conclusions. At this point, the only safe generalization in island biogeography is that it is not safe to make generalizations.

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