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Evolution

Bird remains from an archaeological site on Henderson Island, South Pacific: Man-caused extinctions on an "uninhabited" island

(anthropology/conservation/island biogeography)

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ABSTRACT **Long thought never to have been inhabited and to be in a pristine ecological state, Henderson Island (southeast Pacific) is now known to have been colonized and then abandoned by Polynesians. Bones from an archaeological site on the island associated with ^{14}C dates of ≈800 and ≈500 years B.P. include specimens of 12 species of birds, of which 3, a storm-petrel and two pigeons (*Nesofregetta fuliginosa, Ducula* cf. *aurorae* or *D. pacifica*, and *Ducula* cf. *galeata*), no longer occur on Henderson, and two others (*Puffinus nativitatis* and *Sula sula*) still visit but are not known to breed. The vanished species were presumably exterminated by Polynesians and the biota of Henderson Island can thus no longer be regarded as being in an unaltered state. The prehistoric abandonment of various small, unarable islands by Polynesians may have been due to the depletion of seabirds and pigeons, the only readily available food source. The species of pigeons identified from Henderson are known historically only from distant archipelagos and have never before been found sympatrically. Distributional patterns resulting from man-caused extinctions may give rise to erroneous interpretations of the relationships and evolutionary history of insular organisms. Certain endangered species, such as *Ducula galeata*, might effectively be preserved by reintroduction to abandoned islands that they occupied before human intervention.**

> Over the whole extent of the South Seas, from one tropic to another, we find traces of a bygone state of over-population, when the resources of even a tropical soil were taxed, and even the improvident Polynesian trembled for the future. . . . we may suppose, more soberly, a people of sea-rovers, emigrants from a crowded country, to strike upon and settle island after island, and as time went on to multiply exceedingly in their new seats. In either case the end must be the same; soon or late it must grow apparent that the crew are too numerous, and that famine is at hand. [Robert Louis Stevenson (ref. 1, p. 34)]

Henderson Island, belonging to the "Pitcairn Group" along with Pitcairn, Ducie, and Oeno, is one of the most remote islands of the South Pacific (Fig. 1), with only Ducie and Easter Islands lying farther to the east in Polynesia. There has been little scientific exploration on Henderson, the few known aspects of its natural history having been compiled recently by Fosberg *et al.* (2).

Henderson was discovered by European voyagers in 1606, at which time it had no human inhabitants. Some 200 years elapsed before the island began to be visited infrequently in the 19th and 20th centuries (table 1 of ref. 2), although no permanent human habitation ever resulted. The assumption has been made, therefore, that Henderson "still seems to be in its natural state," being "now one of the few islands of its size in the warmer parts of the world still little affected by human activity" (ref. 3, p. 233). The recent discovery of several Polynesian occupational sites on Henderson (2, 4) shows that the island had, in fact, been inhabited in prehistoric times. On the basis of vertebrate remains from one of these sites, we can now show that this period of human occupancy was accompanied by extinctions and a consequent decrease in the species diversity of the island.

Henderson Island (24°22′S, 128°20′W) has an area of 37 km^2 (9.6 × 5.1 km), with a maximum elevation of ca. 33 m. The nearest islands are Pitcairn (200 km west-southwest), Oeno (200 km west), and Ducie (360 km east). Of these, only Pitcairn is inhabited. Steep cliffs of bare limestone surround Henderson, and the terrain consists of densely vegetated, highly weathered and pinnacled Tertiary limestone riddled with pits and crevasses up to 7 m deep, making travel difficult and hazardous. Annual rainfall is estimated at about 1500 mm but fresh water occurs only as drippings in caves and as a spring of unknown flow and permanence below high tide level at the north end of the island. Sixty-three native species of vascular plants are known from Henderson, of which nine are endemic species or varieties. The tallest trees are screw-pines (*Pandanus tectorius*). Four introduced plants have been recorded (*Cocos nucifera, Cordyline terminalis, Aleurites moluccana*, and *Achyranthes aspera*), of which the first three are typical Polynesian associates that may have been brought to Henderson either prehistorically or by the recent inhabitants of Pitcairn. The terrestrial invertebrates of Henderson are poorly studied, but about 33% of the species of insects and gastropods thus far collected are endemic.

There are no native mammals, and of those introduced, only the Pacific rat (*Rattus exulans*) and perhaps the house mouse (*Mus musculus*) survive today. A widespread skink (*Emoia cyanura*), an unidentified species of gecko, and green sea turtles (*Chelonia mydas*) constitute the herpetofauna, which, however, has not been systematically sampled. Twelve species of seabirds certainly or probably breed on Henderson, as well as four resident species of land birds (Table 1): a flightless rail (*Porzana atra*), a fruit dove (*Ptilinopus insularis*), a parrot (*Vini stepheni*), and a sylviid warbler (*Acrocephalus taiti*). All of the land birds are considered to be endemic, although the fruit dove and warbler are often treated as endemic subspecies of more widespread taxa.

The occurrence of the commensal rodent *Rattus exulans* on Henderson suggests of itself that prehistoric Polynesians had once landed on the island. Unequivocal evidence, however, was provided by Sinoto's discovery in 1971 of evidence of Polynesian habitation in a cave and five "shelters," one of which included burials, along the north shore of Henderson (2, 4). Test pits in front of the cave exposed three cultural strata, yielding radiocarbon ages of 790 ± 110 years B.P. (charcoal; bottom of layer III; laboratory no. I-6344) and 495 ± 105 years B.P. (charcoal; top of layer II; laboratory no.

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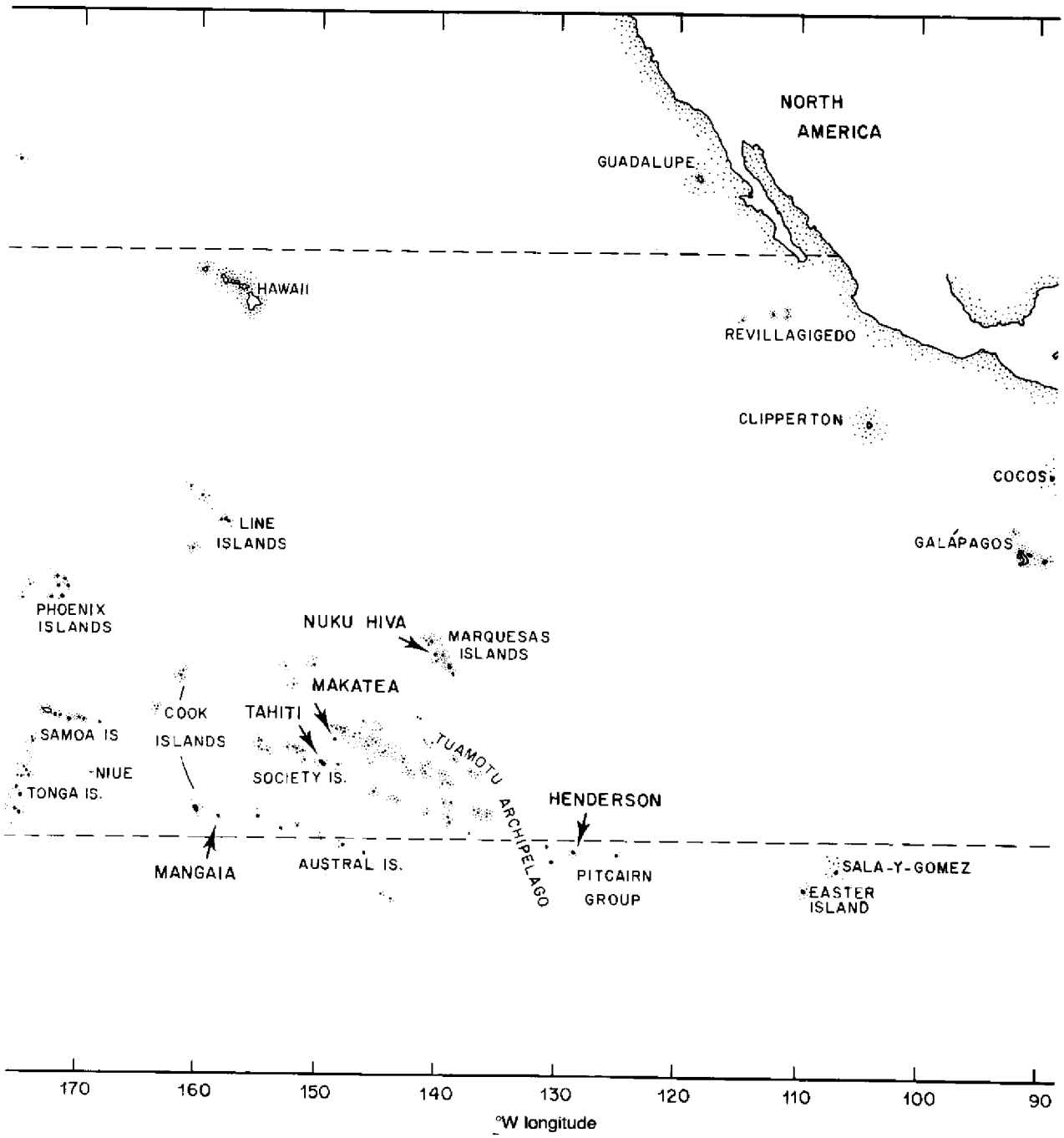

FIG. 1. The tropical eastern Pacific Ocean, showing much of Polynesia. The more important islands and island groups mentioned in the text are indicated.

I-6343). At two standard deviations these two ages overlap and therefore do not provide a certain indication of the length of time of Polynesian occupation of Henderson. The hard upper surface of layer II was paved with coral pebbles, indicating an occupational floor. A fireplace was found at the bottom of layer III, under which were noncultural sediments. The sediments of these excavations were sieved through screens of ¼-inch (6.4-mm) mesh, yielding more than 250 artifacts, including fishhooks and fishhook blanks of pearl shell, hammer shell, and oyster shell, coral abraders for making fishhooks, basalt adzes (all badly broken), pieces of volcanic glass, and adzes of fossilized *Tridacna* shells. The exogenous materials from the lower sections were interpreted by Sinoto as being of close affiliation with early Marquesan culture. Artifacts from the upper levels, however, were of local origin, having apparently been manufactured after the depletion of the material transported from other islands, such as the basalt adzes and pearl shell fishhooks, necessitated the use of inferior materials.

We studied all of the numerous bones recovered from Sinoto's excavations except those of fish, the specimens now being in the collections of the Bernice P. Bishop Museum, Honolulu. Nonavian taxa are represented by postcranial remains of rats (*Rattus* cf. *exulans*; 11 bones from at least five individuals) and sea turtles (cf. *Chelonia mydas*; 29 bones from at least one individual). Bones of juvenile individuals were recovered for six species of seabirds (Table 1) that must certainly have bred on Henderson in prehistoric times. Because we have no evidence that Polynesians had the means to obtain pelagic birds at sea and because of the unlikelihood

Table 1. Resident species of birds on Henderson Island, modern and prehistoric

Species	Recorded as breeding in historic times	Recorded from bones in archaeological site
Pterodroma ultima (Murphy's petrel)	+	—
Pterodroma neglecta (Kermadec petrel)	?	—
Pterodroma alba (Phoenix petrel)	+	165 (29)*
Pterodroma arminjoniana (Herald petrel)	+	—
Puffinus nativitatis (Christmas shearwater)	?	8 (3)*
Puffinus pacificus (Wedge-tailed shearwater)	+	—
Nesofregetta fuliginosa (White-throated storm-petrel)	—	3 (1)
Phaethon rubricauda (Red-tailed tropicbird)	+	20 (5)*
Sula dactylatra (Masked booby)	+	—
Sula sula (Red-footed booby)	?	3 (1)
Fregata minor (Great frigatebird)	+	9 (2)*
Gygis alba (White tern)	+	70 (21)*
Anous stolidus (Brown noddy)	+	4 (2)*
Procelsterna cerulea (Blue-grey noddy)	+	—
Porzana atra (Henderson Island rail)	+	8 (3)
Ptilinopus insularis (Henderson Island fruit dove)	+	1 (1)
Ducula cf. *aurorae* ("Society Islands" pigeon) or *D. pacifica* (Pacific pigeon)	—	9 (3)
Ducula cf. *galeata* ("Marquesas" pigeon)	—	3 (1)
Vini stepheni (Henderson Island parrot)	+	—
Acrocephalus taiti (Henderson Island warbler)	+	—

In the archaeological column, the first number is the total number of specimens. The number in parentheses is the minimum number of individuals represented by the specimens. The modern breeding status is taken from Williams (5) and Bourne and David (3): +, certainly breeds; ?, questionably breeds.
*Bones of juveniles represented in the sample.

of land birds being imported to such a remote locality from other sources, we have assumed that all of the species represented in the collection resided on Henderson. These remains, which were collected in direct association with abundant cultural materials, including hearths, undoubtedly represent food items of the Polynesians, for each of the species, including the rat and the sea turtle, is relished as food elsewhere in Polynesia today. Most of the bones were broken in a consistent manner that suggests standardized butchering techniques.

Among the seabirds in the sample, *Puffinus nativitatis* and *Sula sula* are not known to breed on Henderson, but have been recorded there as nonbreeding birds, with Oeno Island being the nearest breeding locality for either species. The storm-petrel *Nesofregetta fuliginosa* has not been recorded previously from Henderson or elsewhere in the Pitcairn group and now breeds no nearer than the Marquesas, more than 2000 km from Henderson, although nonbreeding birds have been recorded from the slightly closer Society and Tuamotu groups (6). Similarly, *N. fuliginosa* is now absent from Mangaia, Cook Islands, but is known there from late Holocene fossils (7). That this storm-petrel may have been exterminated on Henderson and Mangaia by early Polynesians would accord with the abundant evidence for extirpation of breeding seabird populations by humans around the world in prehistoric and historic times, although the possibility that populations of *Nesofregetta* were influenced by climatic fluctuations such as those associated with the El Niño phenomenon (8) cannot be ruled out.

Although the pelagic petrel *Pterodroma alba* was the most commonly occurring species in the deposit, suggesting heavy exploitation by Polynesians, this species nevertheless still nests on Henderson. We cannot exclude the possibility, however, that *P. alba* and perhaps other seabirds were once exterminated on Henderson and have recolonized the island since the time of human abandonment. The absence in the archaeological deposits of other species of *Pterodroma* that now occur on Henderson may indicate that this was indeed the case.

The abandonment by prehistoric man of Henderson and other relatively isolated Polynesian islands such as Pitcairn, Palmerston, Suwarrow, the Kermadecs, Norfolk, and various islands in the Phoenix and Line groups has caused Bellwood (9) to refer to these as "isolated mystery islands," and he has speculated that water shortages, lack of women, illness, homesickness, murder, or suicide might have played a role in their depopulation. The archaeological evidence from Henderson suggests another alternative. The marine resources of Henderson were limited by the lack of extensive reefs and lagoons and by the steep coastline, which allows difficult access to the sea only during calm conditions. Traditional Polynesian food items such as taro, sweet potatoes, and breadfruit were probably difficult or impossible to grow, and pigs and dogs were apparently lacking or had all been consumed before the archaeological deposits were laid down. Therefore, the human population was probably dependent upon seabirds and pigeons for food. The abandonment of Henderson and other small, unarable "isolated mystery islands" with limited marine resources can perhaps be explained by the overexploitation of the most readily available sources of protein on these islands—birds.

The two other species in the sample that have not been recorded previously on Henderson or elsewhere in the Pitcairn group are pigeons, which, being land birds, are much more likely to have been exterminated by Polynesians than by climatic fluctuations in the past 700 years. Nine incomplete specimens (five ulnae, one radius, three carpometacarpi) of a medium-large pigeon are inseparable qualitatively and in size from comparable elements of *Ducula aurorae* or *Ducula pacifica*. Only one of these specimens, a carpometacarpus, is complete enough for a measurement of total length, which, at 39.0 mm, compares closely with that of *D. pacifica* (35.0–38.0 mm; $n = 4$) and *D. aurorae* (38.6 mm; $n = 1$), as opposed to that of the much larger species *Ducula galeata* (43.7 mm; $n = 1$).

Three other bones [a partial mandibular ramus and two partial tibiotarsi (Fig. 2)] are from a very large species of columbid greatly exceeding *D. pacifica* or *D. aurorae* in size. The distal width of the best preserved tibiotarsus from Henderson is 10.2 mm, which is similar to that of *D. galeata* (10.7 mm; $n = 1$) and is much too large for *D. pacifica* (7.4–8.4 mm; $n = 4$) or *D. aurorae* (8.4 mm; $n = 1$). The three largest columbid bones from Henderson are identical qualitatively and in size to those of *D. galeata* and must be referable to that species or a very closely related representative of it.

Other species of *Ducula* compared with the fossils are: *D. oceanica*, *D. radiata*, *D. aeneus*, *D. perspicillata*, *D. pinon*,

FIG. 2. Tibiotarsus of *Ducula galeata*. Specimen A, Smithsonian Institution (USNM) 277889, modern specimen from Nuku Hiva, Marquesas. Specimen B, Bernice P. Bishop Museum (BPBM) 160267, referred archaeological specimen from Henderson Island. (Scale bar = 10 mm.)

D. badia, D. bicolor, D. luctuosa, and *D. spilorrhoa*. These species differ among themselves not only in size but in the relative proportions of individual bones and in intramembral ratios. In all of these respects, *D. pacifica* and *D. aurorae* may be segregated from all of their congeners to the west except *D. oceanica*, which is a presumed close relative of *D. pacifica* and *D. aurorae*. Thus, given that the larger bones from Henderson cannot in any way be distinguished from those of *D. galeata*, it is highly unlikely that some altogether different species lineage could be involved.

The archaeological specimens from Henderson unquestionably represent two distinct species of *Ducula* that differed from each other approximately 2-fold in weight. Such differences cannot be attributed either to sexual or individual variation within species. *D. pacifica* is about 360 mm long, weighing 360–400 g, with *D. aurorae* being of approximately similar size. In contrast, *D. galeata* is an immense pigeon about 480 mm long and weighing perhaps 800 g. There is no other columbid of comparable size known historically anywhere in the Pacific east of New Caledonia, where *Ducula goliath* resides.

The occurrence of these two species of pigeons on Henderson was not expected because *D. galeata* is supposedly endemic to the single island of Nuku Hiva in the Marquesas, more than 2000 km northwest of Henderson. *D. aurorae* is known historically only from Tahiti (Society group) and Makatea (Tuamotu group), whereas *D. pacifica* is found from the Bismark Archipelago east to the southern Cook Islands; no population of either species now occurs closer to Henderson than 2000 km. Although *D. pacifica* is common in much of its range, only about 10 individuals of *D. aurorae* now survive on Tahiti, although 500–1000 individuals are estimated to live on Makatea (10, 11, 12). Only 90–100 individuals of *D. galeata* remain on Nuku Hiva today, where they are restricted to forested mountain ridges (10, 13). Hunting and habitat destruction have been assumed to be responsible for the current rarity of both *D. aurorae* and *D. galeata*.

From the former occurrence of *Ducula* cf. *aurorae/pacifica* and *D.* cf. *galeata* on Henderson, and the probable former occurrence of *D. galeata* on Mangaia (7), we must assume that these species of pigeons, and probably other birds as well, were much more widespread in the past and have been exterminated in prehistoric times from nearly all of the islands of southeastern Polynesia.

With the benefit of hindsight, it does not seem likely that *D. galeata* would be found naturally only on one of the islands in the Marquesas and none of the others, or that *D. aurorae* should occur on Makatea (28 km^2) and on Tahiti (3700 km^2) but on none of the other Society Islands, at least five of which are larger than Makatea (14). Although it is possible that the two forms of *Ducula* on Henderson may have differentiated locally in plumage, the archeological remains show not only that two species of *Ducula* once occurred sympatrically in eastern Polynesia but also that they could do so on a small, low island completely lacking the montane forest to which *D. galeata* is now restricted on Nuku Hiva. Mayr (15) considered *D. galeata* "to be a member of the superspecies *Ducula pacifica*" whose "extreme morphological differentiation" resulted from its being "the most isolated form in the group." Our findings show, however, that *D. galeata*, or closely related forms, were more generally distributed in the Pacific, and may have been widely sympatric with smaller pigeons such as *D. pacifica* and *D. aurorae*.

The species added to the Henderson avifauna by the small archaeological sample brings the total number of land birds to at least six species, an increase of 33%. The archaeological and paleontological record of birds elsewhere in Polynesia has documented extinctions in land birds in proportions far exceeding 33%, however: e.g., New Zealand (16–18), Cook Islands (7), Hawaiian Islands (19–21). The Henderson material included only one specimen of the extant fruit dove and no remains of the extant parrot or warbler. Because the sampling technique may have biased the sample towards larger species, additional small taxa may be expected to have occurred on Henderson.

The survival of a flightless rail (*Porzana atra*) on Henderson is evidence that the fauna, although perturbed by human beings, nevertheless may be in a less altered state than that of most Pacific islands. Before human contact, one or more flightless rails probably occurred on nearly every island in the Pacific, but almost all such populations are extinct today. Nesting on the ground and being unable to fly, these rails are extremely vulnerable to the effects of man and introduced mammalian predators. The continued survival of *Porzana atra* on Henderson in spite of the presence of *Rattus exulans* may indicate that the presence of this rat by itself is not sufficient to drive flightless birds to extinction. Apparently the prehistoric absence on Henderson of Polynesian pigs, dogs, and agricultural clearing, as well as the historic absence of the Eurasian black rat *R. rattus*, has enabled *Porzana atra* to persist.

By demonstrating through fossils such as those from Henderson that the natural ranges of certain endangered species may have been much greater than has been supposed, the possibility is raised of reintroducing these species to islands that may be under less human pressure now than in prehistoric times. For instance, the pigeon *Ducula galeata* is unlikely to survive much longer on Nuku Hiva but perhaps

might be successfully restored on Henderson now that that island is no longer inhabited by human beings.

The fossil evidence from Henderson Island augments that from other islands (7, 19, 20, 22, 23) not only in casting doubt on the validity of most of the data that have been used in determining species–area relationships in island biogeographical studies but also in showing that many distributional patterns in the Pacific are not the result of natural evolutionary processes. Remote and inhospitable Henderson Island shows once again how manifestly incomplete our knowledge of island biogeography really is and further emphasizes the need for continuing paleontological and archaeological studies of insular faunas, even on supposedly uninhabited islands.

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