

THE ENDEMIC LAND BIRDS OF HENDERSON ISLAND, SOUTHEASTERN POLYNESIA: NOTES ON NATURAL HISTORY AND CONSERVATION

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ABSTRACT.—New data are presented on the foraging ecology, behavior, vocalizations, body masses, and soft part colors of the endemic land birds of Henderson Island (128°20'W, 24°20'S), southeastern Polynesia. Population estimates of species range from 720–1820 for Stephen's Lorikeet (*Vini stepheni*), 3240 ± for Henderson Island Crake (*Porzana atra*), 3420 ± for Henderson Island Fruit-Dove (*Ptilonopus insularis*), to 10,800 ± for Henderson Island Reed-Warbler (*Acrocephalus taiti*). Conservation issues and translocation of species are discussed. Received 12 April 1991, accepted 5 Aug. 1991.

Henderson Island (128°20'W, 24°20'S; Fig. 1), a small elevated coral atoll in the Pitcairn Island group some 2300 km southeast of Tahiti, was colonized and abandoned by Polynesians before it was discovered by Europeans in 1606 (Sinoto 1983, Fosberg et al. 1983). Henderson's four species of endemic landbirds, Henderson Island Crake (*Porzana atra*), Henderson Island Fruit-Dove (*Ptilonopus insularis*), Stephen's Lorikeet (*Vini stepheni*), and Henderson Island Reed-Warbler (*Acrocephalus taiti*), were discovered early this century by phosphate prospectors and described from a few specimens by North (1908) and Ogilvie-Grant (1913). Recent archaeological excavations revealed that at least three additional species of pigeons (*Gallicolumba* sp., two *Ducula* sp.) became extinct during the Polynesian occupation of the island (Steadman and Olson 1985, Steadman 1989). Virtually all that is known about the natural history of the surviving species is contained in the unpublished field notes of Ernest H. Quayle, who collected landbirds on Henderson Island, 12–20 March and 1–13 April 1922, for the Whitney South Seas Expedition of the American Museum of Natural History. Quayle's notes have been liberally paraphrased by Bourne and David (1983).

During 12–22 May 1987, I made natural history observations, conducted censuses, and collected specimens of the landbirds on Henderson Island. The purpose of this paper is to present (1) new natural history observations, (2) population estimates, (3) preliminary descriptions of vocalizations, and (4) specimen data for the endemic land birds. Finally, I discuss the conservation of Henderson's avifauna.

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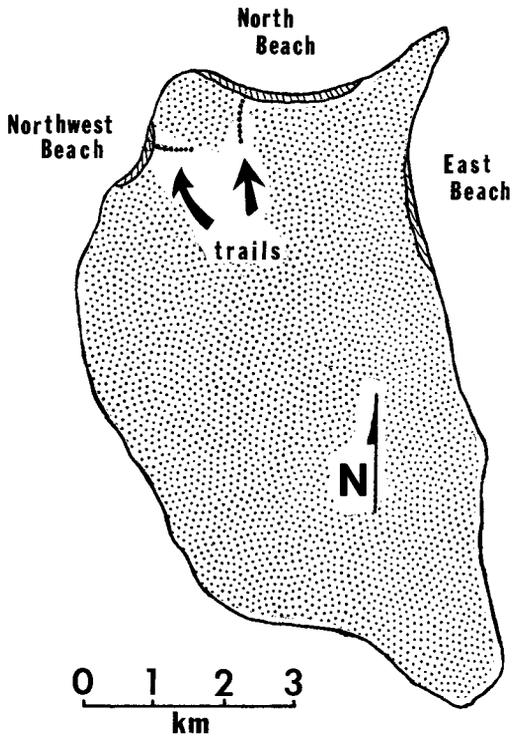


FIG. 1. Henderson Island, southeastern Polynesia, is completely forested. The border of the former ancient lagoon, which begins 400–600 m inland on the north end of the island, has not been mapped. Width of beaches is exaggerated.

HENDERSON ISLAND

Detailed accounts of the physiography, vegetation, and scientific history of Henderson Island are given by Fosberg et al. (1983), Spencer and Paulay (1989), and Paulay and Spencer (1989), from which the following description is partly derived. Henderson Island is an ancient coral reef and lagoon that has been thrust 30 m above sea level by lithospheric flexure under the weight of Pitcairn Island (200 km WSW of Henderson). Henderson Island, which appears flat-topped from a distance, has maximum dimensions of 9.6×5.1 km and an area of 36 km². Its shoreline is characterized by vertical cliffs (15–30 m) interrupted by three narrow beaches (Northwest, North, and East) on the northern end of the island. Wave action is unusually intense and landings are treacherous. From high vantage points along the northwest coast, surf spray may be seen through binoculars on the south side of the island some 7–8 km away. The entire island appears to be heavily forested. With the exception of introduced coconut palms (*Cocos nucifera*) and four other adventive species along the beaches, the vegetation of Henderson Island is undisturbed; miro (*Thespesia populnea*) and sandalwood (*Santalum hendersonense*) are occasionally harvested by Pitcairners. Away from cliff edges,

the interior of the island is covered with a low (4–9 m), tangled, nearly impenetrable forest. Except in the central area formerly occupied by a lagoon, passage is hampered by exceptionally rough terrain of jagged limestone pinnacles, fossil coral rubble, and small sink holes. Understory vegetation may be lush in well-lit exposures, but a thick layer of leaf litter is found in taller forest with a closed canopy. Permanent sources of fresh water in the island's interior are unknown. Dominant trees on Henderson include *Cocos nucifera*, *Pandanus tectorius*, *Thespesia populnea*, *Tournefortia argentea*, *Cordia subcordata*, *Guettarda speciosa*, *Pisonia grandis*, *Geniostoma hendersonense*, *Nesoluma st-johnianum*, *Hernandia stokesii*, *Myrsine hosakae*, and *Celtis* sp.

METHODS

Most observations were made in the narrow strip of forest behind Northwest Beach (700 × 30 m = 2.1 ha) and along an 875 m trail into the island's interior, cut roughly perpendicular to the shoreline (Fig. 1). Censuses along the beach (N = 8 days; 10.75 h) and trail (N = 6 days; 19.75 h) were made by walking slowly and mapping all birds seen or heard in relation to trail markers. Because the few species present were tame and responded readily to "squeaks" and tape playbacks of their vocalizations, the location of nearly all individuals along the census route was determined. Detection distances for vocalizations of each species were estimated from repeated observations in beach front forest and in the island's interior away from surf noise.

A narrow strip of forest behind North Beach (750 × 35 m = 2.63 ha; 3.5 h) and a previously cut trail (ca 1 km; 1.5 h) perpendicular to North Beach were censused by the same methods on 20 May. North Beach censuses are less reliable because of their short duration.

Vocalizations were recorded with a Sony TCM-5000 cassette recorder and condenser microphone and analyzed on a Uniscan II real-time spectral display analyzer (Multigon Industries).

Stomach contents of specimens collected for genetic and anatomical studies were preserved in alcohol. Body masses of males and females were compared with two-tailed *t*-tests. All specimens are deposited in the National Museum of Natural History, Smithsonian Institution.

SPECIES ACCOUNTS

Henderson Island Crane. — This is the last surviving species of flightless rail in Polynesia (see Steadman 1989). It was common in the interior of the island and along the bases of cliffs above the beaches. This small black-plumaged crane is rather tame and inquisitive, approaching stationary observers to within 2 m. Its preferred habitat is shady understory of low dense forest carpeted with a thick layer of leaf litter. Foraging birds obtained food items, most too small to identify through binoculars, by scratching and flicking aside leaves with their feet and bill. Stomachs (N = 2) contained small land snails and insect parts.

Pairs of crakes often foraged together, usually within 10 m of one another, and maintained contact with a frog-like callnote, "kwa." Rapid series of similar notes were given by agitated crakes in response to playback of vocalizations (Fig. 2). Birds were especially vocal in early morning

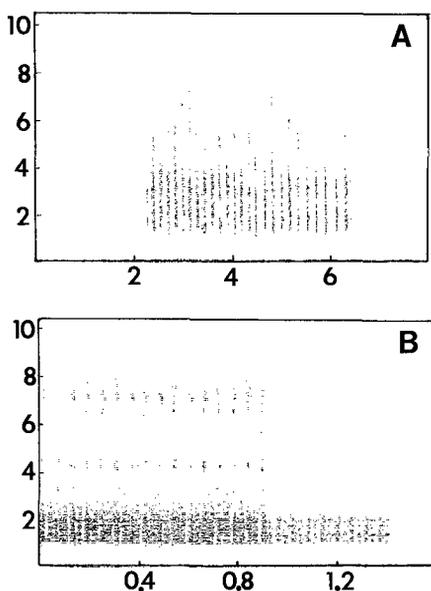


FIG. 2. Spectrograms of vocalizations of the Henderson Island Crake (*Porzana atra*). A: rapid callnotes given by crake in response to playback. B: terminal portion of duet where one crake of pair ceased calling. X-axis of all sonograms in seconds; Y-axis in kHz.

and at dusk. Twice I observed duetting displays of pairs. In each instance one crake began calling and running rapidly, with slightly raised wings and lowered head, through the undergrowth to its presumed mate. The pair commenced duetting (3.7–4.1 sec) as soon as they were in physical contact. Pairs often engaged in bouts (0.25–2.0 min) of allopreening after the duetting ceased. On a third occasion, I observed a pair of foraging adults followed by a full-sized subadult; when the adults began duetting, the subadult joined them, and all three called simultaneously.

Population estimates were based on sight and vocal records. In the island interior away from the surf, crake vocalizations could be heard from a distance of 75 m. However, within 300 m of the beach, I had difficulty hearing vocalizations more than 50 m away. Therefore, I estimate that I censused a transect with average dimensions of 875×133 m along the Northwest Beach and 1000×135 m along the North Beach trail. A minimum of six pairs were present along the Northwest Beach trail, two pairs below the cliffs on Northwest Beach, seven pairs along the North Beach trail, and four pairs below the cliffs at North Beach. Based on these data, the density of crakes along the beach fronts, where every

bird could be located, ranged from 0.95 pairs/ha to 1.53 pairs/ha. Assuming home ranges were non-overlapping, completely packed, and randomly sampled, crane densities in the island's interior were estimated to be 0.52 pairs/ha on both transects. Using an arbitrary conservative figure of 0.45 pairs/ha, the total population of *Porzana atra* was estimated to be $3240 \pm$ individuals.

Gonads of collected specimens were not reproductively active. Body masses of males ($N = 3$, 78–82 g, $\bar{x} = 80.3 \pm 2.1$) and females ($N = 6$, 76–88 g, $\bar{x} = 79.0 \pm 4.8$), including subadults of both sexes, were statistically indistinguishable ($t = 0.45$, $P > 0.05$). Sexes cannot be identified under field conditions. Soft parts are vividly colored: iris, red; eyering, orange; feet and legs, reddish-orange; bill, black, base of culmen green. Subadult birds, similar in size to adults, were identified by dusky tarsi and dark orbital skin.

Henderson Island Fruit-Dove.—Low-pitched advertising calls of *P. insularis* were a conspicuous feature of the interior forest on Henderson (Fig. 3). Fruit-doves were fairly tame and approached observers to within 3 m in response to "squeaking." They frequently flew over the forest canopy for 100–200 m but appeared to be territorial and responded to playbacks of their calls. Most calling was done from the vicinity of fruiting trees. Although cooing notes may be given occasionally by females, I assumed that series of calls were given by males. Cooing fruit-doves could be detected from a distance of about 75 m in the island interior and 50 m within 300 m of the surf. I found a minimum of 12 doves along the Northwest Beach trail, six below the cliffs at Northwest Beach, 10 along the North Beach trail, and six below the cliffs of North Beach. Densities of individuals varied from 2.29 to 2.86 doves/ha along beach fronts and from 0.74 to 1.03 doves/ha in the island's interior. Because fruit-dove censuses along the Northwest Beach trail were repeated on six different days, I believe the density estimate from this location was the most accurate. Using an arbitrary conservative figure of 0.95 fruit-doves/ha, the total population of *Ptilonopus insularis* was estimated to be $3420 \pm$ individuals.

Specimens had moderately enlarged gonads (i.e., thickened oviducts and enlarged testes). Stomachs ($N = 3$) contained fruit pulp and intact fruits (*Nesoluma st-johnianum*, *Ixora fragrans*, and another unidentified species). Soft part colors of sexes were similar: iris, orange becoming yellower near pupil; bill, greenish-yellow becoming yellower at base; orbital skin, bluish-gray; eyering, pale yellow; legs and feet, coral red; toe pads, pale yellow. Juveniles lack the purplish-crimson crown of adults. Body masses ranged from 102–105 g in males ($N = 2$) and from 95–105 g in females ($N = 3$).

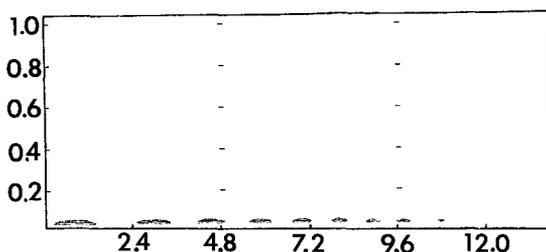


FIG. 3. Spectrograms of advertising song of Henderson Island Fruit-Dove (*Ptilonopus insularis*).

Stephen's Lorikeet.—Stephen's Lorikeets were a conspicuous feature of our encampment on Northwest Beach where they fed on coconut (*Cocos nucifera*) nectar. They were seen frequently in small flocks of 3–5 (possibly family groups) flying 20–40 m over the forest canopy. Despite their brilliant red, green, and yellow plumage, they were difficult to locate once they alighted in foliage. Feeding birds were often detected by their soft twittering calls. Flight calls were louder and could be detected at a distance of 100 m, away from the surf (Fig. 4). Because lorikeets made relatively large daily movements, I estimated their local abundance by recording the number of lorikeets observed along the beach and interior forest trails during a continuous census, taking into account the location of flocks and the destination of flying birds. Single census maxima of 14 and 11 individuals were observed, respectively, at Northwest Beach and North Beach. Estimates of total population size were difficult to make because coconut groves along the beach attract lorikeets from the island's interior. However, I speculate that lorikeet density falls between 0.2 and 0.5 individuals/ha, a total population size of 720 to 1820 individuals.

Of five specimens collected, one female had a greatly enlarged ovary and thickened oviduct, but the others had quiescent gonads. Body masses varied from 42–51 g for females ($N = 4$) to 55 g for a single male. Subcutaneous fat was moderate to heavy. Soft part colors of *V. stephensi* reported by Ogilvie-Grant (1913) were based on faded specimens. Colors of freshly collected specimens were as follows: iris, pale to medium orange; feet and legs, orange; bill, orange with dusky markings at tip of upper mandible.

Henderson Island Reed-Warbler.—This abundant reed-warbler occurs throughout the island, and possibly outnumbers the combined populations of the other three endemic species. Typically, pairs of adults were accompanied by one or two fully grown subadults. Warblers foraged on all substrates (i.e., foliage, twigs, branches, bark crevices, etc.) from ground

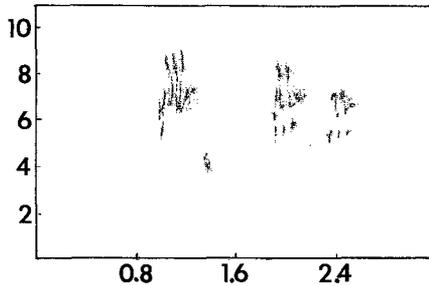


FIG. 4. Spectrograms of flight calls of Stephen's Lorikeet (*Vini stephensi*).

level to the upper fronds of the tallest coconut palms. Field observations, supplemented by stomach contents, showed that Henderson Island Reed-Warblers have catholic diets that include several species of land snails (1–3 mm), ants, flies, beetles, cockroaches, large wasps, seeds, and fruit pulp.

The closely related Pitcairn Reed-Warbler (*Acrocephalus vaughani*), of Pitcairn Island, rarely forages near ground level and is much warier than *A. taiti* of Henderson. This behavioral difference may be related to the presence of cats and humans on Pitcairn. Henderson Island Reed-Warblers (*Acrocephalus taiti*), as well as reed-warblers from Pitcairn Island and Rimitara (*A. rimitarae*) in the Austral Islands, were reported by Holyoak (1978) to give a variety of chirping calls but no song. Holyoak's data on Henderson Island Reed-Warblers were taken from Quayle's field notes. My observations suggest that the lack of song may be a matter of interpretation. Most vocalizations of *A. taiti* are high pitched (4–8 kHz) single notes of short duration (<0.13 sec). However, series of thin, longer notes (1–5 sec) given by adult territorial birds, albeit in an unknown context, resemble song (Fig. 5). These vocalizations can be clearly heard at 25 m above the white noise of wind and surf (both predominately 0–3 kHz) along the beaches, and probably function in interterritorial communication, given the small territory size of *A. taiti*.

Henderson Island Reed-Warblers apparently breed during the austral summer and none of the specimens collected was in breeding condition. One family group, consisting of an adult pair and a warbler in subadult plumage that begged for food, attended a recently built nest and occasionally added nesting material. On several days, I observed an adult sitting on the nest, as though incubating. However, periodic checks of the nest with a mirror between 12 and 20 May revealed no eggs. A brief

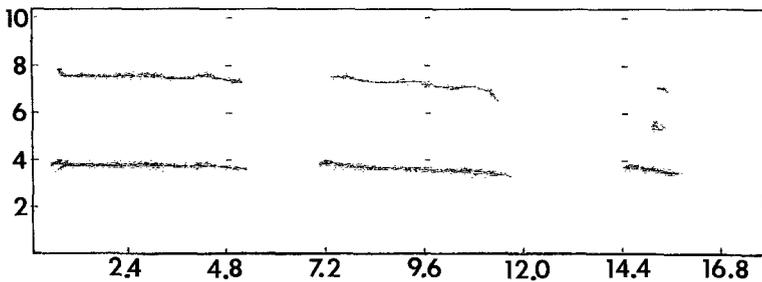


FIG. 5. Spectrograms of vocalizations, possibly song, of Henderson Island Reed-Warbler (*Acrocephalus taiti*).

account of the previously undescribed nest of *A. taiti* follows. The nest was built in a fork of a thin and nearly horizontal lower branch of *Thespesia argentea*, 4 m above ground level, in the lower canopy of relatively tall forest (7 m) below the cliffs of North Beach. The bulky nest was composed of thin rootlets and *Cocos* fibers and lined with finer material. Outside dimensions were 210 × 200 mm wide and 80 mm deep; the nest cup was 55 mm in diameter and 45 mm deep. A second weathered nest found nearby was constructed with similar materials.

Holyoak (1978) speculated that the conspicuous plumage leucism of *Acrocephalus* from Rimitara, Pitcairn, and Henderson islands was somehow correlated with the loss of song. The pattern of leucism is strikingly different among these taxa (Graves, in prep.), affecting primarily the anterior body plumage, secondaries, and rectrices of *A. taiti*, the primaries, secondaries, and rectrices of *A. vaughani*, and scattered parts of the plumage of *A. rimitarae*. In all three taxa, leucism appears to progress with age in both sexes. Specimens of *A. taiti* (N = 7) with crania less than 75% pneumatized lack leucistic feathers. Holyoak (1978) suggested that the occurrence of leucism may allow individuals to recognize each other and facilitate territorial defense. Although leucistic reed-warbler plumage may function as a signal in dominance hierarchies, plumage patterns are unstable and may change at every molt for several years before converging in the "typical" Henderson Island pattern. This argues against behavioral selection of plumage pattern for individual recognition. In any event, there is no evidence that leucism is a consequence of songlessness or vice versa.

Fundamental differences in the sequence and pattern of leucistic plumages among the reed-warblers of Rimitara, Pitcairn, and Henderson suggest substantial genetic differentiation at the species level. This idea is

supported by differences in subadult plumages and the color of mouth-linings on Pitcairn (orange) and Henderson (pinkish-orange or "peach"). Because populations of reed-warblers on all three islands are relatively small and separated by great distances of open ocean, gene flow among islands is probably infinitesimal. Lumping the three taxa on the basis of superficial appearance (Murphy and Mathews 1929) is clearly unwarranted. Until contradictory information becomes available, I consider the three populations of "leucistic" reed-warblers as separate species.

Reed-warbler populations were censused by vocalizations, sight records, and selective collecting. Chipping notes and song-like phrases could be heard up to 50 m away under windless conditions inland and about 30 m away within 50 m of the surf. Territories were small, and available habitat appeared to be saturated. A minimum of 10 reed-warblers (including subadults) occurred along Northwest Beach, 25 along the Northwest Beach trail, 27 along North Beach, and 12 (thought to be an underestimate) along North Beach trail. Estimated densities varied from 1.36 reed-warblers/ha on the North Beach trail to 10.29 reed-warblers/ha along North Beach. I believe censuses along the Northwest Beach trail (3.31 reed-warblers/ha) more accurately reflect reed-warbler densities in the island's interior. Using an arbitrary conservative estimate of 3.0 reed-warblers/ha, I estimated that the total population of Henderson Island Reed-Warblers was 10,800 \pm .

Soft parts of warbler specimens were as follows: iris, brown; feet and legs, medium gray; upper mandible, dark grayish-brown; lower mandible, silvery-flesh with a dusky tip. Subcutaneous fat was moderate to heavy. Body masses of males ($N = 21$, 22.5–30.5 g, $\bar{x} = 25.8 \pm 2.0$) were significantly greater than those of females ($N = 19$, 21.0–25.0 g, $\bar{x} = 22.8 \pm 1.11$) ($t = 5.89$, $P < 0.0001$).

CONSERVATION

The accumulating knowledge of prehistoric avifaunas in southeastern Polynesia (reviewed in Steadman 1989) indicates that most, if not all, flighted species were more widespread in the past, and most flightless species are extinct. These data have important implications for conservation strategies. For instance, Henderson once supported as many as four species of pigeons ranging in size from the surviving fruit dove (105 g) to two large species of *Ducula* with estimated body masses of 400 g and 800 g, respectively (see Steadman and Olson 1985). Historically, the nearest occurrences of *Ducula* pigeons to Henderson Island have been in the Society and Marquesas islands more than 2000 km distant. Strong-

flying pigeons as well as the Stephen's Lorikeet (*Vini stepheni*) probably occurred on Pitcairn Island as well, although fossil evidence of their residency has not yet been discovered. In other words, avifaunas throughout Polynesia have been drastically altered by man and may now bear little resemblance to their primeval condition. It is probable that nearly every vegetated island in southeastern Polynesia the size of Henderson or larger once supported a flightless rail, one or more pigeons, a lorikeet, and a reed-warbler.

Current predation on the eggs, nestlings, and adults of Henderson's land birds is probably limited to the Pacific rat (*Rattus exulans*), introduced by the Polynesians, and a large terrestrial hermit crab. Crabs are ubiquitous nocturnal scavengers in beach front forest but were uncommon in the island's elevated interior. *Rattus exulans*, however, occurred commonly in all habitats and was observed in the upper branches of trees. The surviving land birds on Henderson Island apparently have adapted to the presence of *R. exulans*, or at least are able to co-exist with it. Present levels of wood-cutting by Pitcairners pose little threat to the island's avifauna, while the introduction of the coconut palm may actually have benefited the Stephen's Lorikeet.

The greatest potential danger for Henderson's birds is the possible introduction of other mammalian predators, especially the black rat (*R. rattus*) (see Atkinson 1985). Release of domestic cats or a second species of rat by visiting yachts or disabled ships would probably cause the rapid extinction of Henderson's crane and perhaps other species (Greenway 1958, Ripley 1977, Atkinson 1985). Undisputable evidence (e.g., rubbish, charcoal) of past landings was seen on both Northwest and North Beach areas. The introduction of mosquitoes and avian malaria is perhaps less of a threat because of the lack of fresh water on Henderson. Mosquito ovipositing sites would be restricted to small temporary pools of rainwater on karst surfaces and in sparsely distributed tree holes. Mosquitos were abundant on nearby Pitcairn (*Aedes aegypti*, *Culex quinquefasciatus*: Mathis 1989) which has permanent sources of fresh water. The latter species is a vector of avian malaria in Hawaii (Warner 1968, van Riper et al. 1986). Another potentially devastating disease for which Henderson's endemic birds may have no immunity is avian pox (see Warner 1968). Unfortunately, avian pox is transmitted by hippoboscids and other biting flies, which are already present on Henderson, as well as by mosquitoes.

Available data indicate that land bird populations on Henderson Island are relatively stable. Yet, despite the island's great isolation, accidental introduction of predators, disease vectors, and diseases is probably inevitable because of unauthorized landings of yachts. Clearly, other con-

servation measures should be considered in addition to legislating the inviolability of Henderson's biota.

One potential conservation tool is the establishment of populations of Henderson's endemic land birds on "bird-less" islands in southeastern Polynesia. Establishment of viable populations on the islands would be an important hedge against extinction in the event of catastrophic mortality on Henderson. Unfortunately, translocation is often a strategy of last resort in conservation biology. In fact, Diamond (1985) suggested that translocation be used only for those species for which there is no realistic hope of survival in the wild on their native islands. However, translocation efforts are much more successful when larger numbers of individuals are transplanted (Griffith et al. 1989). Ironically, by the time a species is recognized as threatened or endangered, populations are often so small that translocation efforts have a low probability of success. Thus, translocation or captive propagation of Henderson's endemic species as well as many other Polynesian endemics should be implemented in the near future while populations are still high. Why wait for another Guam-like faunal debacle?

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LITERATURE CITED

- ATKINSON, I. A. E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. ICBP Tech. Publ. No. 3:35-81.
- BOURNE, W. R. P. AND A. C. F. DAVID. 1983. Henderson Island, central south Pacific, and its birds. *Notornis* 30:233-252.
- DIAMOND, A. W. 1985. The conservation of landbirds on islands in the tropical Indian Ocean. ICBP Tech. Publ. No. 3:85-100.
- FOSBERG, F. R., M.-H. SACHET, AND D. R. STODDART. 1983. Henderson Island (South-eastern Polynesia): summary of current knowledge. *Atoll Res. Bull.* 272:1-47.
- GREENWAY, J. 1958. Extinct and vanishing birds of the world. *Amer. Com. Int. Wildl. Prot. Spec. Pub.* 13.
- GRIFFITH, B., J. M. SCOTT, J. W. CARPENTER, AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477-480.

- HOLYOAK, D. T. 1978. Variable albinism of the flight feathers as an adaptation for recognition of individual birds in some Polynesian populations of *Acrocephalus* warblers. *Ardea* 66:112-117.
- MATHIS, W. N. 1989. Diptera (Insecta) or true flies of the Pitcairn Group (Ducie, Henderson, Oeno, and Pitcairn Islands). *Atoll Res. Bull.* 327:1-15.
- MURPHY, R. C. AND G. M. MATHEWS. 1929. Birds collected during the Whitney South Sea expedition. VI. *Amer. Mus. Novitates* 350:1-21.
- NORTH, A. J. 1908. On three apparently undescribed birds from Henderson or Elizabeth Island. *Rec. Aust. Mus.* 7:29-32.
- OGILVIE-GRANT, W. R. 1913. Remarks on a small collection of birds from Henderson Island, South Pacific, collected and presented to the British Museum by Messrs. D. R. Tait and J. R. Jamieson. *Bull. Brit. Ornith. Cl.* 31:58-61.
- PAULAY, G. AND T. SPENCER. 1989. Vegetation of Henderson Island. *Atoll Res. Bull.* 328:1-19.
- RIPLEY, S. D. 1977. *Rails of the world*. Godine, Boston, Massachusetts.
- SINOTO, Y. H. 1983. An analysis of Polynesian migrations based on archaeological assessments. *J. Soc. Oceanistes* 39:57-67.
- SPENCER, T. AND G. PAULAY. 1989. Geology and geomorphology of Henderson Island. *Atoll Res. Bull.* 323:1-50.
- STEADMAN, D. W. 1989. Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific island groups. *J. Archaeol. Sci.* 16:177-205.
- AND S. L. OLSON. 1985. Bird remains from an archaeological site on Henderson Island, South Pacific: man-caused extinctions on an "uninhabited" island. *Proc. Nat. Acad. Sci.* 82:6191-6195.
- VAN RIPER, C., III, S. G. VAN RIPER, M. L. GOFF, AND M. LAIRD. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Mon.* 56:327-344.
- WARNER, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101-120.