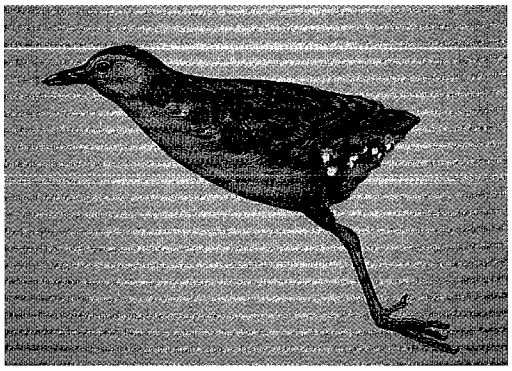
Laysan Rail

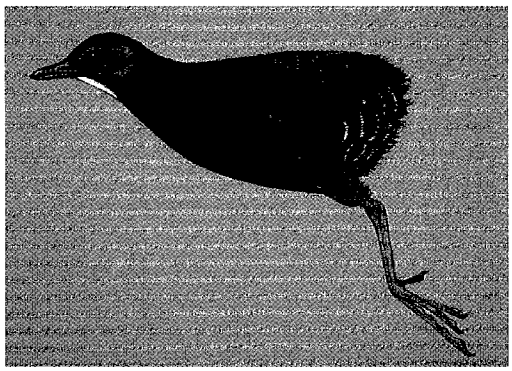
Porzana palmeri FRENCH: *Marouette de Laysan*

Hawaiian Rail

Porzana sandwichensis FRENCH: *Marouette de Hawaï*



Laysan Rail © J. Hume



Hawaiian Rail © J. Hume

Before the arrival of humans, all the main Hawaiian islands probably were populated by flightless rails, some islands having up to 3 species each. At least 12 species are known, 10 from fossil remains only (Olson and James 1991). All were short-billed "crakes" that have been referred to the genus *Porzana*. The 2 flightless species that are known to have survived into the historic period in the Hawaiian Archipelago are also now extinct, exemplifying the extreme vulnerability conferred by flightlessness. Whereas the Hawaiian Rail is known from 7 specimens only, the last taken in the mid-1800s, the Laysan Rail is abundantly represented in collections and became extinct in the mid-1940s. Both were relatively small species, although even smaller ones are known among the archipelago's fossil rails. Some of the fossil species probably persisted into the historic period; Perkins (1903: 453–454) was confident that a rail existed on Moloka'i I. in the nineteenth century.

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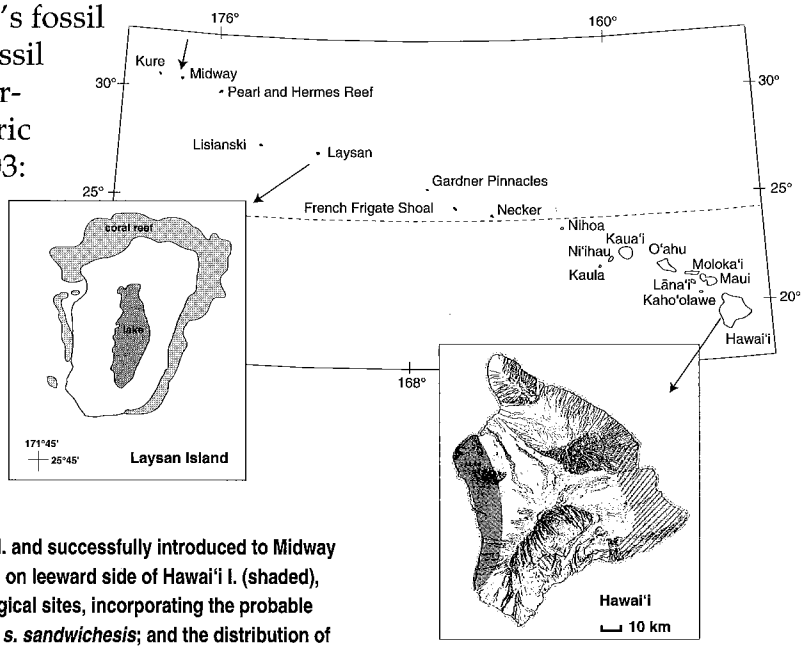

Figure 1.
Former distribution of Laysan Rail endemic to Laysan I. and successfully introduced to Midway Atoll. Approximate former distribution of Hawaiian Rail on leeward side of Hawai'i I. (shaded), so far as is known from archaeological and paleontological sites, incorporating the probable source area of the 2 mounted specimens referred to *P. s. sandwichesis*; and the distribution of *P. s. millsi* on the windward side (hatched) as reconstructed from historical accounts.

The native name *moho* for the Hawaiian Rail is the same as is used throughout Polynesia to refer to small rails of the genus *Porzana*, and it is unfortunate that Lesson (1830–1831) introduced confusion by transliterating the Hawaiian name *'o'o* as *Moho*, which has now come down to us as the generic name of most of the Hawaiian honeyeaters (Meliphagidae). English names of the rails follow American Ornithologists' Union 1998, although Taylor (1998) more consistently uses the names Laysan Crake and Hawaiian Crake instead.

Specimens and drawings of the Hawaiian Rail were among objects obtained in 1779 and brought back by ships of Captain James Cook's third and final voyage (Medway 1981). Much confusion ensued in the literature concerning the number of species of flightless rails to be recognized in the historical record of the main islands, but none of the existing evidence indicates more than one.

The Laysan Rail was first noted during the visit of the Russian ship *Moller* to Laysan I. in 1828 (Kittlitz 1834), but not until 1891 were specimens that had been brought from Laysan obtained by Henry Palmer and sent to Walter Rothschild in England. Not long thereafter, Palmer went to Laysan himself and collected many additional specimens, including live birds that made it safely back to England. For an unexplained reason, the original description of the new species, which was Rothschild's to name, was delegated to the artist F. W. Frohawk (1892); this was his only nonpictorial contribution to Hawaiian ornithology.

It is not known how many separate colonizations gave rise to the radiation of Hawaiian flightless rails, although a minimum of 3 seems likely (Olson and James 1991). Because of the differences in their plumage, the Laysan and Hawaiian rails were presumed to have descended from different ancestral species of Old World rather than New World origin, an assumption that was recently confirmed by DNA evidence. Each had once been placed in its own monotypic genus (*Porzanula* and *Pennula*, respectively) on the basis of characters associated with flightlessness that are no longer considered to be of generic value (Olson 1973a, 1973b).

The 2 species considered here are the only flightless, insular species of Rallidae to be treated in the *Birds of North America* series. Because both are extinct, few details are known about their life histories compared with extant continental North American birds. Therefore, some comments on rails in general may help fill in the gaps and bring these 2 birds into perspective.

Rails belong to a distinct family of Gruiformes not especially closely related to any other living birds. In the Tropics, many species inhabit forests, which was probably the primitive habitat, but in temperate continental areas, rails generally inhabit marshes, which are discontinuous and often ephemeral, necessitating extensive postbreeding wandering by individuals in search of more habitat. This wandering, coupled with an excellent ability for overwater dispersal, has resulted in rails' successful colonization of most oceanic islands of the world, where, in the absence of predators, they quickly become flightless (Olson 1973a). Because they are vulnerable to predation, hundreds of populations of flightless rails have probably become extinct in the period of human conquest of the oceans (Steadman 1995).

Very few rails have specialized feeding habits; most are generalized, opportunistic omnivores. They are capable of surviving under harsh conditions such as on Laysan or Ascension Is., where the birds were heavily dependent on seabird colonies (Olson 1973a). In places such as the main Hawaiian islands, rails would probably have occupied most vegetated habitats, and they may have relied to a considerable extent on land snails (Gastropoda) for food. Probably only predation, particularly of nests, causes temperate continental rails to be restricted to marshes; otherwise they might be expected in habitats as diverse as those that they occupy on oceanic islands.

The great number of flightless insular populations of rails has been produced by relatively few continental genera—mainly *Rallus*, *Gallirallus*, and *Porzana*, and to a lesser extent various gallinules. Apart from some of the rails of New Zealand and the Chatham Is., insular rails usually exhibit little morphological diversity. Other than the adaptations associated with flightlessness and the generally more robust hindlimbs associated with being more terrestrial, rails appear to require little in the way of adaptations to insular environments, so depending on the ancestral genus, flightless rails tend to differ among themselves mainly in plumage, size, and amount of reduction in the flight apparatus. Morphologically and probably behaviorally, one flightless rail is much like another and the Hawaiian species are unexceptional.

DISTINGUISHING CHARACTERISTICS

Laysan Rail. Small flightless rail; light brownish, with black streaks above, gray below. Very similar in overall size and coloration to the darker-breasted races of Baillon's Crake (*Porzana pusilla*), but bill is longer and more arched, wings are greatly reduced (with only 8 primaries), tarsi and particularly toes are shorter, tail is vestigial and decomposed, and white dorsal streaking and ventral barring are

greatly reduced. Sexes alike. Juvenile buffy rather than gray below.

Hawaiian Rail. Small flightless rail; somewhat larger than Laysan Rail; wings and tail softer and more reduced; overall coloration darker; rusty cinnamon below, dark brownish or fuscous above, with dark centers of dorsal feathers evident or obscured. Differences between sexes and age classes are unresolved.

DISTRIBUTION

HAWAIIAN ARCHIPELAGO

Laysan Rail. Natural range of the species was restricted to Laysan I. in Northwestern Hawaiian Is. (Fig. 1).

Hawaiian Rail. Restricted to Hawai'i I. (Fig. 1). Specimens described from Cook's voyage are from leeward side of the island inland from Kealakekua Bay (see Systematics: geographic variation; subspecies, below), and remains are known from midden and fossil sites along much of the leeward slope (see Fossil history, below).

On windward side of the island, all 5 extant specimens, formerly in the James Mills collection, were obtained by the bird-catcher Hawelu, who at one point ran a travelers' halfway house between Hilo and Kīlauea Volcano (Manning 1978), in the 'Ōla'a area of Puna District. Manning (1978: 89) stated that the rails "were definitely taken in 'Ōla'a between the Kīlauea crater and Hawelu's halfway house," citing Wilson and Evans (1890–1899: 173). However, Wilson and Evans only opined that "the bird may, nay probably does, still exist on the scrub-covered plains between Olaa and Kilauea," which would be northeast of the crater, yet a few lines later they specifically stated that the birds were obtained by Hawelu, from whom Wilson obtained information directly, "in the scrub-covered lava-flats about five miles [8 km] *south* [emphasis added] of the Volcano House." Wilson and Evans may not have been referring to the Volcano House at Kīlauea Crater, however, because Rothschild (1893–1900: 242) used the term "lower volcano house" evidently to refer to Hawelu's halfway house, and this may be what Wilson meant.

Henshaw (1902: 97) was told that rails once occurred along the windward coast as far as Onomea and that in the 1860s they "lived on the edge of the woods not far above the town of Hilo."

HISTORICAL CHANGES

Laysan Rail. Laysan I.: Demise of the species on Laysan I. began with introduction by Max Schlemmer of European rabbits (*Oryctolagus cuniculus*) to Laysan in 1902 or 1903 (Olson 1996). Although Dill (1912: 9) reported that Schlemmer also introduced "Belgian hares, and English hares," these names refer to rabbits and not to *Lepus lepus*. Rabbits (*Oryctolagus*) were definitely the agents of destruction on Laysan; 8 specimens from Laysan in the Smithsonian collections (National Museum of History [USNM] nos. 243829–243835 and 243862) were preserved by the *Tanager* expedition in 1923. By 1913, Bailey (1956: 89) wrote, "the vegetation of Laysan was rapidly being destroyed by the hordes of rabbits," although rails were still regarded as "abundant." Rails were still "everywhere" on the island in 1915 and 1916, and seen "often" in 1918 (Ely and Clapp 1973: 186). Yet 5 yr later, when the *Tanager* expedition arrived (in Apr 1923), the vegetation had been almost entirely eliminated and only 2 living rails were found on the entire island (Olson 1996). Rabbits were exterminated by members of the *Tanager* expedition, and 8 Laysan Rails were reintroduced from Midway on 29 Apr 1923, but at least 2 or 3 of these were found dead before the expedition departed on 14 May (A. Wetmore in Olson 1996: 184), although Grant (1947) said that "all" were found dead around the lagoon. Regardless, conditions in 1923 were not amenable to the species' survival. W. Coultas collected on Laysan I. in Dec 1936 and saw no rails (Bailey 1956: 16, 90). The species was never reestablished on Laysan.

Midway Atoll: Although the notorious Captain F. D. Walker, of the schooner *Kaalokai*, may have released Laysan Rails on Midway in 1887 (Baldwin 1945), it is known more certainly that a "pair" of Laysan Rails was released on Eastern I. of Midway Atoll on 13 Jul 1891 (Munro 1947). It is not known whether these were male and female or whether they reproduced. At the instigation of Max Schlemmer, additional rails were introduced to Eastern I. from Laysan through Captain Niblack and later Captain Piltz (T. Schlemmer in litt. to A. Wetmore; see Olson 1996: 118). These introductions would have been in the years just after 1894, when Schlemmer first went to Laysan. Additional introductions to Midway were made in 1904 or 1905 (Ely and Clapp 1973: 183). Rails were taken from Eastern I. to Sand I. about 1906, according to one source (in Olson 1996: 185), but Bartsch's (1922) implicit mention of them only on Eastern I. in Nov 1907 suggests that a 1910 date of transfer (Baldwin 1945, Munro 1947) is correct. An unknown portion, but probably more than 50, of "more than one hundred" captured on Laysan were released on Eastern I. by G. Willett and A. M. Bailey on 14 Mar 1913, although it was thought that this inoculation "probably was of no importance" (Bailey 1956: 89). Populations flourished on both islands until World War II, when rats (*Rattus rattus*) arrived at Midway, appearing first on Sand I. in Feb or Mar 1943, where the last

rail encountered was a "young" bird and an adult calling to it on 15 Nov 1943 (Baldwin 1945, Munro 1945a). Two were seen on Eastern I. in Jul 1944. An intensive search from 7 to 18 May 1945 by Fisher and Baldwin (1946) revealed none.

Lisianski I.: Although there is an ambiguous reference (quoted in Kittlitz 1834) to rails possibly having been seen on Lisianski I. in 1828, extensive excavations on the island yielded no conclusive evidence in support of a former population of rails (Olson and Ziegler 1995). Rabbits had been introduced to Lisianski sometime before 1910 and had made significant inroads on the vegetation when Willett and Bailey introduced about 45 individual rails from Laysan on 12 Mar 1913 (Clapp and Wirtz 1975). One or 2 were observed as late as Feb 1916, when no rabbits or vegetation could be seen, although rails and rabbits were certainly gone by May 1923 (Clapp and Wirtz 1975), when the *Tanager* expedition collected some bones identified as European rabbit (specimens in USNM). A single coracoid of a rail the size of that of a Laysan Rail was found in excavations on the island and is thought to have come from one of the individuals introduced by Willett and Bailey (Olson and Ziegler 1995).

Pearl and Hermes Reef: Captain William G. Anderson released 7 pairs of Laysan Rails from Sand I., Midway Atoll, onto one of the islets of this group, probably Southeast I., in Jun 1929 (Munro 1945b). Rails were not present in 1930 and are thought to have been destroyed by storms that swept the islands of most vegetation (Amerson et al. 1974.)

Islands off O'ahu: Munro (1947) reported that Laysan Rails were sent from Midway to Honolulu with the intention of introducing them to islands off windward O'ahu. Although he knew of no evidence that this was ever done, he wrote of a secondhand report of a bird on Kekepa Islet that could not fly but "jumped." If Laysan Rails were ever introduced to any of these islands, they certainly have not survived. Munro (1944: 51) also mentioned an experiment to introduce Laysan Rails "to cane fields on the main islands" that "naturally failed."

Hawaiian Rail. Recorded with certainty in historical times only inland from Kealakekua Bay in 1779 and on the windward side of Hawai'i I. from about 1859 to 1864, after which it became extinct (see Demography and populations: population status, below).

FOSSIL HISTORY

Laysan Rail. None, apart from the coracoid from Lisianski I. (see Historical changes, above).

Hawaiian Rail. This species was but 1 of 3 flightless rails that inhabited Hawai'i I. in prehistoric times; the other 2 are yet unnamed and known only from fossils (Olson and James 1991). One of these was smaller than Hawaiian Rail and was probably related to the small fossil rails *Porzana keplerorum, P. menehune,* and *P. ziegleri,* from Maui, Moloka'i, and O'ahu Is., respectively (Olson and James 1991). The other was a larger species very similar to the fossil species *P. severnsi* of Maui (Olson and James 1991). An unnamed rail of intermediate size, and thus possibly related to Hawaiian Rail, occurs rather uncommonly as a fossil on Maui.

Bones indicating a rail the size of Hawaiian Rail have been found at several sites on the leeward side of Hawai'i I. (S. L. Olson and H. F. James unpubl.), including coastal archaeological deposits from Kīholo Bay in the north to Manukā Bay in the south, and up to 500 m above Makalawena. These deposits presumably accumulated as remains of food once eaten by Hawaiians. Other naturally occurring bones of this species have been found in various caves on western slopes of Mt. Hualālai at elevations of about 1,000–1,500 m.

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

Laysan Rail. Because it was restricted to tiny Laysan I., this species showed no geographic variation.

Hawaiian Rail. Considerable confusion once existed concerning the number of species of rails to be recognized from Hawai'i I. and their nomenclature. The names *Rallus ecaudatus* Clerke (in Cook and King 1784, vol. 3: 119; the name is usually credited to King—it is preoccupied in any case [Lysaght 1953]), *Rallus sandwichensis* Gmelin (1789), *Rallus obscurus* Gmelin (1789), and *Pennula wilsoni* Finsch (1898) are all based on specimens, drawings, or descriptions from Cook's voyage and hence refer to birds from the vicinity of Kealakekua Bay, Hawai'i I., the type locality of all Hawaiian birds named from Cook's voyage (Medway 1981, Olson 1989). All these names are currently subsumed under *Porzana sandwichensis* (Gmelin).

According to Medway (1981), Joseph Banks received 2 specimens of Hawaiian Rail from Cook's voyage, and a third was once in the former Leverian Museum. Medway (1981) concluded that the specimen in the Rijksmuseum van Naturlijke Historie in Leiden, Netherlands, quite possibly originated in Cook's voyage, in which event it would be a syntype, one of several specimens upon which the original description of the species was based, of *Rallus sandwichensis* Gmelin. The specimen in Vienna appears to have been neglected in nearly all accounts of this species. On examination, it was

found to be most similar to the Leiden specimen and thus definitely referable to *P. sandwichensis* (SLO). The naturalist Leopold von Fichtel was commissioned to purchase specimens from the auction of the Leverian Museum in 1806 on behalf of the Imperial Museum in Vienna, which included specimens from Cook's voyage, but the specimen of rail was never mentioned in this connection (Pelzeln 1873). Although there is no evidence linking the Vienna specimen with Cook's voyage, there is likewise no evidence of any alternative source for it, and it and the Leiden specimen probably have a similar origin.

The remaining 5 specimens are from the collection assembled by James Mills and came from the windward side of Hawai'i I., between Hilo and Kīlauea (see Distribution, above). These specimens form the basis for the name *Pennula millsi* Dole (1878; emended from *P. millei*, a typographical error), and all 5 may be regarded as syntypes of that name (Olson 1994).

The Leiden and Vienna specimens, which came from the leeward side of Hawai'i I. (and from where all the Cook Voyage specimens are presumed to have been collected [Medway 1981, Olson 1989]), differ from those from of the windward side (Mills collection) in the lighter dorsal coloration, which emphasizes the darker centers of dorsal feathers. These light and dark forms have given rise to considerable confusion, not the least of which arose from Greenway (1958: 236), who regarded a specimen in New York as being "without question the paler *sandwichensis*." This statement must refer to American Museum of Natural History specimen no. 546232, the only specimen of the species now remaining in New York. Greenway would have compared this with specimen no. 20 from the Bernice P. Bishop Museum, Honolulu, which had long been on loan in New York but was later returned to the Bishop Museum (Manning 1982). Both specimens are from the Mills collection, however, and belong to the darker windward form. Thus, Greenway never actually saw a specimen of the paler form.

Greenway also regarded the paler plumage to be the result of immaturity. Unfortunately, this conclusion has recently been perpetuated by Taylor (1998), but it is not substantiated by examination of all 7 specimens, which suggests that immature birds were darker (see Appearance, below), as are the young of many rails. That the differences between light and dark forms might be due to geographic variation has not received attention. Pratt (1979, 1980), however, demonstrated geographic variation in the 'Elepaio (*Chasiempis sandwichensis*) within Hawai'i I., 2 of the 3 subspecies he recognized were also distributed on leeward versus windward slopes, the third on Mauna Kea. Presumably, the flightless Hawaiian Rail would have been more sedentary than the volant 'Elepaio and thus even more likely to have differentiated within the island. On the basis of the little available evidence, therefore, it seems prudent to recognize 2 subspecies of Hawaiian Rail: *P. s. sandwichensis* (Gmelin) for the lighter leeward population, and *P. s. millsi* (Dole) for the darker windward birds. This distinction also accords with the widely observed tendency for birds from more humid environments to be darker (Gloger's Rule). Rothschild's taxonomic treatment (1893–1900) was similar, except he recognized these taxa at the specific level.

RELATED SPECIES

Laysan Rail. Like most other flightless rails, Laysan Rail was originally described in a monotypic genus, *Porzanula*, but little was ventured concerning its relationships other than the implied affinity with *Porzana*. Certain American authors (e.g., Fisher 1903, Baldwin 1947) suggested a relationship to New World rails of genus *Laterallus*, particularly Black Rail (*L. jamaicensis*), but probably only through lack of familiarity with Old World species, because the plumages of the 2 species are quite different. Olson (1973a, 1973b) merged *Porzanula* with *Porzana* and pointed out the obvious similarities in plumage to the widespread Baillon's Crake, from which he suggested the Laysan bird had been derived. Interestingly, a decade earlier Schönwetter (1962: 324) had remarked on the similarity of the eggs of Laysan Rail to those of Baillon's Crake. This relationship has since been substantiated by studies of mitochondrial DNA showing that Laysan Rail differs no more from Baillon's Crake than populations of that species differ among one another (B. Slikas and R. Fleischer [National Zoological Park] unpubl.).

Laysan is a very low island; highest point is only 12 m above present sea level. The last major interglacial rise in sea level above the present level peaked about 125,000 yr ago (Harmon et al. 1983). Seas at this time were at least 5 m above present levels, on basis of the oxygen isotope record (Harmon et al. 1983), but the rock record indicates even higher levels, at about 9 m (Land et al. 1967), which is now the prevailing view (P. J. Hearty pers. comm.). At this time only a small part of Laysan would have been emergent, and that part would surely have been awash in storms. Thus, much of the terrestrial biota of Laysan, including the rail, might have colonized in <125,000 yr.

Hawaiian Rail. Olson (1973b) suggested, on basis of general similarity in coloration, that Hawaiian Rail may have been derived from Asian Ruddy Crake (*Porzana fusca*), but this relationship is

contradicted by mitochondrial-DNA evidence (B. Slikas and R. Fleischer [National Zoological Park] unpubl.), which shows Hawaiian Rail to be very closely related to Sooty Crake (*P. tabuensis*), a species widespread in sw. Pacific that appears to have given rise to many other flightless forms. Differences in plumage may be due to masking of underlying plumage patterns in Sooty Crake by increased melanization.

MIGRATION

Both species were flightless and nonmigratory.

HABITAT

Laysan Rail. Laysan is a low (12 m maximum elevation) island about 1.6×2.9 km, but with a large central hypersaline lake that considerably reduced the amount of habitat available for rails, which were confined to the vegetation between open beaches and the lagoon, an area estimated by Baldwin (1947) at 0.9 square mile (2.3 km^2). Vegetation consists of viny strand plants such as alena (*Boerhavia repens*), pōhuehue (*Ipomea pes-caprae*), and koali'awa (*I. indica*); shrubs, dominated by naupaka (*Scaevola sericea*); and sedges (Cyperaceae) and bunchgrass (*Eragrostis variabilis*), of which the last 2 were particularly important to the rails for cover and nesting material (repeated references in the literature to the importance of *Juncus* [rushes] for cover and nest-building are erroneous; *Juncus* does not occur in the Northwestern Hawaiian Is.). For more details of Laysan habitat, see Lamoureaux 1963 and Moulton and Marshall 1996. Habitat on islands of Midway Atoll was generally similar, but with less grass and sedge and more introduced plants.

Hawaiian Rail. Perkins (1903: 454) found that in the 1890s, Hawaiian Rail was well known to the oldest natives on both leeward and windward sides of Hawai'i I., from whom he may have garnered information on its habitat, which he reported to be "open country below the continuous forest, and open country covered with scrub that lies within the forest belt. Its last home on Hawaii appears to have been the rather open country which lies just outside the heavily timbered part of the Olaa district on the smooth or pahoehoe lava, and the country between the same heavy forests and the crater of Kilauea. There is little doubt that the specimens formerly in Mills' collection came from one or [the] other of these two neighbouring localities."

Wilson and Evans (1890–1899: 173) described the area from which Mills's rails came as similar to "a Scotch moor, with a short densely-growing *Vaccinium* ['ōhelo, *V. reticulatum*] in the place of heather; this is intermingled with a species of *Carex* and the Ukiuki (*Dianella ensifolia* [=*D. sandwicensis*]), a bright, silver leaved plant bearing a blue berry—the whole forming the thickest of cover. The only trees in this region are scrubby stunted ohias ['ōhi'a, *Metrosideros polymorpha*], though here and there are thickets of fern interspersed with small bushes" (Wilson and Evans 1890–1899: 173).

Under natural conditions, most of the island below the tree line, apart from recent lava flows, would have been vegetated, and rails were probably generally distributed anywhere that an invertebrate fauna was present. (See Introduction, above.)

FOOD HABITS

FEEDING

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Main foods taken. Arthropods, eggs of birds, carrion, seeds.

Microhabitat for foraging. No information.

Food capture and consumption. Laysan Rail was directly or indirectly dependent on nesting seabirds for much of its annual caloric intake. It scavenged carcasses of seabirds not only for associated maggots (larval Diptera) and beetles (Coleoptera) but also for strips of decaying flesh (Schauinsland 1899 [1966]). It was sufficiently agile to capture both flies (Diptera) and moths (Lepidoptera), of which the latter, in the form of "millers" (probably *Agrostis* spp., Noctuidae), once were particularly abundant on Laysan. Blackman (1945) described the special adeptness of rails at catching flies from petrel carcasses on Midway, but when unsuccessful, would eat small pieces of flesh from the carcass and sometimes the rail's head would be "entirely buried in the [body] cavity for a moment" (T. M. Blackman, MS HI.NH.15, Bishop Museum Archives). These rails would also dig up pupating maggots by "flipping the sand sidewise with the beak" (Baldwin 1947: 18). Presumably the dropped or regurgitated prey of seabirds would also have been consumed.

Laysan Rail was said by Schauinsland (1899 [1966]) and Fisher (1903) to be unable to open seabirds' eggs itself, although Palmer and Munro observed one opening a tern's egg (Rothschild 1893–1900, Baldwin 1947). Bailey (1956: 89) reported that the rails were easy to capture with a simple drop-trap, using as bait a "chicken-egg—which rails could not break," and that as many as a half dozen at a time would attack the egg, "jumping off the ground to give more force to the beaks' strike."

To have developed such behavior, the birds would likely have been reasonably successful at opening terns' eggs on their own. Rails were observed frequently partaking of eggs opened by Laysan Finches (*Telespiza cantans*) and probably those opened by Bristle-thighed Curlews (*Numenius tahitiensis*) and Ruddy Turnstones (*Arenaria interpres*) as well, because these were aggressive predators of seabird eggs on Laysan in 1923 (Olson 1996). A rail was once observed aggressively driving off 3 Laysan Finches from a tern's egg they had opened; it "finished the repast, dragging the embryo about in a vain attempt to swallow it" (Fisher 1903: 33). Egg-eating by Laysan Finches may be frequent only when humans disturb nesting colonies because humans flush the adult terns off nests and this leaves the eggs exposed when they typically would be covered (M. Morin pers. comm.). Egg predation by shorebirds was probably more prevalent under the denuded conditions of 1923 than before or after (J. Marks pers. comm.). On Midway, rails took advantage of trampling by humans to feed on eggs of Bonin Petrels (*Pterodroma hypoleuca*), which would normally be less accessible at the ends of burrows. Rails were also observed to run into and spend considerable time in petrel burrows, where they may have fed on eggs or insects (Blackman 1945). Bailey (1956) speculated that Laysan Rails preyed on eggs of the 3 species of passerines (Laysan Finch, Laysan Honeycreeper [*Himatione sanguinea freethi*], Laysan Millerbird [*Acrocephalus familiaris*]) on Laysan, but no direct observations of this were reported.

Observed feeding among chickens (*Gallus gallus*) on Midway in 1923 (Olson 1996), and on Laysan fed opportunistically on flesh made available during preparation of bird specimens, even being fed by hand (Schauinsland 1899 [1966]).

DIET

Laysan Rail. Insects (especially moths and flies, with caterpillars [larval Lepidoptera], beetles, and earwigs [Dermaptera] also being mentioned), spiders (Araneida), seeds, "green material," and eggs of seabirds. Repeatedly mentioned to be particularly fond of maggots in carcasses of dead seabirds, and fed on decaying flesh as well. Said to keep vegetation on Sand I., Midway Atoll, "free from caterpillars" (Baldwin 1945: 346).

Hawaiian Rail. No information.

FOOD SELECTION AND STORAGE

Neither species was reported to store food.

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING

Laysan Rail. Reported to drink frequently in captivity (Manning 1982) and from pans of water set out on Midway (Baldwin 1947). On Eastern I., Midway Atoll, where introduced rails once thrived, Munro (1947: 25) thought the birds "must have gone long periods without drinking water," and Bailey (1956) felt they did not need standing fresh water, possibly getting moisture from precipitation on vegetation.

Hawaiian Rail. No information.

SOUNDS

VOCALIZATIONS

Development. *Laysan Rail.* Two downy young "gave vent to much noise" (Dill 1912: 21).

Hawaiian Rail. No information.

Vocal array. *Laysan Rail.* Of captive birds in England, Frohawk (1892: 248–249) wrote, "During the day they keep up an incessant chirping, consisting of from one to three soft, short, and clear notes; but soon after dusk they all, as if by one given signal, strike up a most peculiar chorus, which lasts but a few seconds, and then all remain silent. I can only compare the sound to a handful or two of marbles being thrown on a glass roof and then descending in a succession of bounds." To Schauinsland (1899 [1966: 18]), "their most remarkable song . . . had a certain similarity to the clanging of the loudest sounding alarm clock," whereas to Fisher (1903: 801), the call was "a plaintive, high-keyed little rattle, which resembles remotely an alarm clock with a muffled bell." (Perhaps German alarm clocks were not as obtrusive as American ones.) Birds were reported to "chatter with a loud scolding note from cover" (A. Wetmore in Olson 1996: 185).

Hawaiian Rail. The cry was said to be "a whirring sound resembling the rising of a bevy of quail," and imitations of the call made by natives for Palmer "sounded much like that of the Laysan Rail" (Rothschild 1893–1900: 242).

Phenology. No information.

Social context and presumed functions. *Laysan Rail.* Fisher (1903: 801) saw birds standing in shade of bushes give the rattling call "with swollen throats and bills slightly opened," which may have been territorial, because he "once saw two approach each other with feathers erect, and when close together begin rattling in each other's face. Then they suddenly ceased and slunk away in opposite directions." Baldwin (1947) thought that such calling

may have been louder and more frequent in breeding season and quoted an observation of the rattling call given at a spot most frequented by a bird and its mate. On Midway, this call was heard "at all hours of the night" (Blackman 1945: 298).

Baldwin (1947) reported notes being given intermittently during foraging, which is probably the chirping call noted by Frohawk. Thus the impression is that the main vocalizations of the species may have been a chirping or peeping contact call between mated birds and a rattling territorial announcement.

Hawaiian Rail. No information.

NONVOCAL SOUNDS

No information.

BEHAVIOR

Laysan Rail. Because the species is extinct, there is little other to draw on than the accounts of the few firsthand observers to visit the remote islands of Laysan and Midway. Although it includes mild anthropomorphisms, the following sketch of the general character of the Laysan Rail given by Fisher (1903: 800) is so evocative and engaging that it bears repetition:

> The Laysan rail is a wide-awake, inquisitive little creature, with an insatiable thirst for first-hand knowledge. It is one of the most naive, unsophisticated, and wholly unsuspicious birds in the whole avian catalogue. At times it is confiding and familiar in deportment, yet at others holds aloof with some show of reserve. It will occasionally hide behind a bunch of grass, as if afraid, and then suddenly come forth with entire change of demeanor and examine the intruder with critical eye. One can never tell just how he will be received by the next rail. Often they scurry away, as if pursued by a *bête noir*, but an insect will stop them in their mad career, and having partaken of the interruption, they seem to forget their former fright and walk about stretching their necks in a highly inquisitive manner. It is evident that they are incapable of pursuing a train of thought for more than an instant. Their ideas seem to flash by in kaleidoscopic succession and within a minute they make as many false starts as a healthy monkey. One can scarcely imagine more amusing and foolish little birds than these.

All accounts reflect the restless activity, inquisitiveness, fearlessness, rapid alarm reaction, and persistence of these birds (Baldwin 1947). They were reported to be less active at midday in summer on Laysan, but little difference was noted in activity patterns through the day on Midway. Extremely active in morning hours. Not reported abroad at night, although nocturnal calling at all hours on Midway led to supposition of activity (Blackman 1945).

Figure 2. Adult Laysan Rail poised as if about to catch prey. By A. M. Bailey; photographed on Laysan I. in Dec 1912. All rights reserved, Photo Archives, Denver Museum of Natural History.

Hawaiian Rail. No information.

LOCOMOTION

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Walking, hopping, etc. Capable of running very rapidly with "mouse-like speed," or walking about with "long nervous steps," sometimes pausing with one foot held in the air (Fisher 1903, Schauinsland 1899 [1966]: 17, A. Wetmore in Olson 1996: 185). Birds might speed over the sand from one clump of grass to another or creep in and out of burrows and through vegetation, thrusting head forward and from side to side (Baldwin 1947). Tail could be held either drooping or elevated and was frequently jerked up and down (Frohawk 1892). Captives were reported to have "a habit of standing on one leg" (Manning 1982: 87).

Some observers thought these birds used their wings hardly at all; others reported the birds to flap their wings wildly when running at full speed, the motion becoming a blur. Probably the Laysan Rail used its wings in jumping, as birds were reported

to be able to leap up on a table where specimens were being prepared (Schauinsland 1899 [1996]: 18). Captives were reported to "fly up into a chair when pursued" (Manning 1982: 87), but were incapable of leaping out of a pit 1.2–1.5 m deep (Baldwin 1947).

Flight. Both species were flightless.

Swimming. Willett observed one bird "swim across the end of the freshwater pond (about twenty feet [6 m])" (Bailey 1956: 89).

SELF-MAINTENANCE

Laysan Rail. Thought to have preferred shady places to avoid direct sun. Captives were said not to roost (Manning 1982). On Midway, observed to bathe in pan of water set out for the birds (Baldwin 1947).

Hawaiian Rail. No information.

AGONISTIC BEHAVIOR

Laysan Rail. "When held in the hand they . . . bit and struck at one another viciously when two were held within striking distance. They fought when at freedom, too, and the victor drove the conquered one about from place to place chasing it for yards and yards" (A. Wetmore in Olson, 1996: 185).

Hawaiian Rail. No information.

SPACING

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Territoriality. Evidently maintained territories through vocalizations and aggressive pursuit of conspecifics (see Agonistic behavior, above), but little else known.

Individual distance. Two birds in an enclosure 2 × 4 m coexisted peacefully, but when >2 were present, fighting broke out (Baldwin 1947: 20).

SEXUAL BEHAVIOR

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Mating system and sex ratio. See below.

Pair bond. The impression given by most accounts is that adults went about in pairs. Members of a presumably mated pair were observed in turn to hold "their heads down close to the ground while the other picked among the feathers at the top of head and back of neck" (T. M. Blackman as quoted in Baldwin 1947: 17).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. See Agonistic behavior and Sexual behavior, above.

Play. No information.

Nonpredatory interspecific interaction. No information.

PREDATION

Kinds of predators. *Laysan Rail.* Great Frigatebird (*Fregata minor*) has been mentioned as potential predator, but no instance even of attempted capture was recorded. Because of the speed and alertness of Laysan Rail, it is unlikely that under normal conditions a healthy adult would ever have been taken by a frigatebird (Grant 1947), although with the island in a denuded state, such predation could have been a cause of mortality (Munro 1947). Presence of frigatebirds may have been responsible for the persistence of vigilance and fright behavior in Laysan Rail, which otherwise might have lost all antipredator responses.

Laysan was an island of egg predators. Migratory Ruddy Turnstones, Bristle-thighed Curlews, and occasionally Pacific Golden-Plovers (*Pluvialis fulva*), joined by resident Laysan Finches and the rails themselves, took eggs of seabirds, especially terns. Most of these species would have been capable of preying on eggs of any of the 5 species of landbirds that once occurred on Laysan that were placed sufficiently close to the ground and left unattended. Under normal circumstances, the rails, with well-hidden and presumably well-tended nests, would probably have suffered little egg predation. With denudation of vegetation by rabbits, however, egg predation may have become a serious cause of decline of the endemic landbirds, as hypothesized by D. R. Dickey (in Olson 1996: 129).

The disappearance of the introduced population of Laysan Rail from Midway is linked to the arrival of rats during World War II (see Distribution: historical changes, above), which assumes predation either on eggs or on adults and young as well, although no direct observations were recorded.

Hawaiian Rail. Would almost certainly have been subject to predation by Hawaiian Hawk (*Buteo solitarius*) and later perhaps by Short-eared Owl (*Asio flammeus*) after that species became established following Polynesian colonization (see discussion of natural predators on Hawai'i I. in Olson 1999). Predation by rats (*Rattus* spp.) introduced by Polynesians or later by Europeans could have been a factor in the disappearance of the species, although Hawaiian Rail was reported to coexist with "the small native rat" (Polynesian rat [*Rattus exulans*]), even hiding in rat burrows (Perkins 1903: 454). The Wake Island Rail (*Gallirallus wakensis*) lived harmoniously with the Polynesian rat (SLO), so rat predation on Hawaiian Rail may not have been important until after appearance of European rats. Henshaw (1902: 96) speculated that dogs, and especially wild cats, which "abounded in the woods from an early day," played a part in extermination of the rail. Mongooses (*Herpestes auropunctatus*)

were introduced in 1883 (Berger 1981), by which time the rail was probably already extinct.

Response to predators. *Laysan Rail.* When pursued by humans, would dart in and out of petrel burrows (Bartsch 1922, Baldwin 1947) but usually was remarkably fearless, approaching people closely.

Hawaiian Rail. Reported to hide in burrows of Polynesian rat "in times of danger" (Perkins 1903: 454).

BREEDING

PHENOLOGY

Laysan Rail. Figure 3. Extreme egg dates reported from Midway range from chicks and nests present in Mar 1940 to supposedly fresh eggs on 26 Jul of same year (Baldwin 1947). In 1941, a nest with eggs was found 20 Jun, and "chicks of all stages" were present on 18 Jul, when eggs were not present (Baldwin 1947). On Laysan I., Palmer reported rails of "every size from the egg upwards" from 17 to 25 Jun 1891, with one nest found 24 Jun with 3 eggs and another with an egg and young, the egg hatching the following day (Rothschild 1893–1900). Only adults on nest and fresh eggs were present 16–23 May 1903 (Fisher 1906), and 2 downy young were noted on 4 Jun 1911 (Dill 1912). Males with large or very large testes were collected by H. Schauinsland on 21 Jul, 8 Aug, and 27 Aug (specimen labels).

Hawaiian Rail. No information.

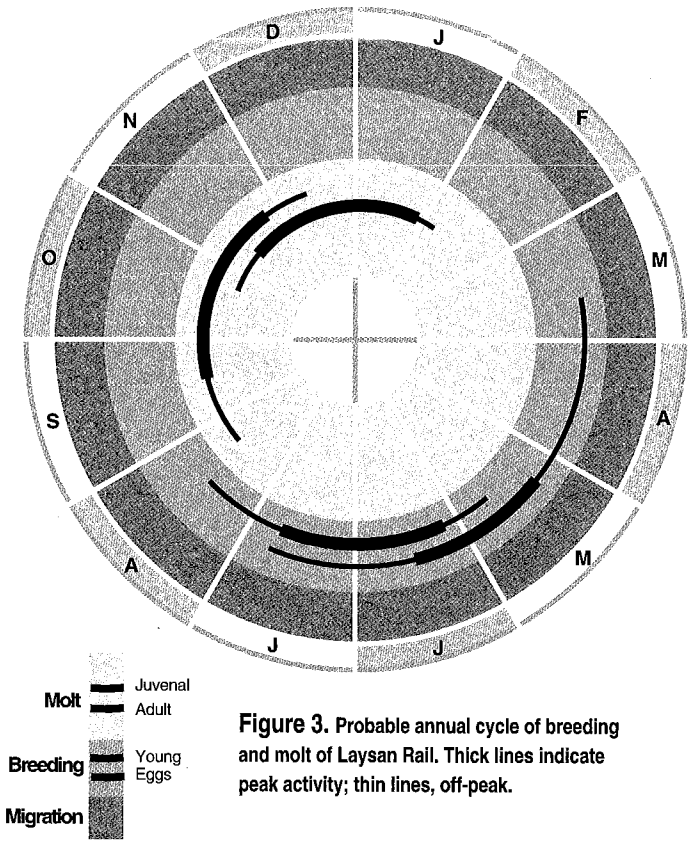

Figure 3. Probable annual cycle of breeding and molt of Laysan Rail. Thick lines indicate peak activity; thin lines, off-peak.

NEST SITE

Laysan Rail. On the ground or matted vegetation, or in tussocks of grass. On Laysan I., most abundantly found in vegetation around the lagoon.

Hawaiian Rail. From information Palmer received from natives, "its nest stood on the ground" (Rothschild 1893–1900: 242). An informant told Henshaw (1902: 97) of a nest "built in the grass close to a cane field."

NEST

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Construction process. No information.

Structure and composition. Variously described as either small or bulky, usually roofed over by vegetation, being built in sedges (makaloa [*Cyperus laevigatus*]), or those of a more "pretentious" type being placed "near the ground in big grass tussocks [*Eragrostis*]" (Fisher 1903: 802). Most nests were placed at end of cleverly camouflaged tunnel or runway about 13–15 cm long partly built into nest. Nest was hollowed out of mass of dried grass leaves and consisted of a roundish cavity lined above and on all sides with finer, soft, shredded leaves, sometimes mixed with small amount of down from young albatrosses (Fisher 1906). Material in 3 nests in USNM collections was verified by W. Wagner (Smithsonian Institution) as leaves of *Eragrostis*.

Dimensions. Eggs were deposited in bowl-shaped hollow about 10 cm in diameter (Fisher 1903). For 1 nest in USNM, outside diameter about 12 cm, inside diameter about 7 cm, and depth about 4 cm.

EGGS

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Shape. On basis of the series in USNM collections, eggs were occasionally oval but usually elliptical, varying from short elliptical to decidedly long elliptical (terminology from Palmer 1962: 13).

Size. Original measurements of specimens in USNM collection: 12 wild-taken eggs (including 1 from Midway), length 27.5–32.0 mm (mean 30.9), width 20.5–21.9 mm (mean 21.2); 27 eggs laid in captivity at Honolulu Zoo (on average smaller), length 25.5–30.1 mm (mean 27.9), width 19.7–21.7 mm (mean 19.9). Two asymmetrical runt eggs laid in captivity were 23.8 × 16.7 mm and 23.90 × 16.4 mm, respectively.

Figure 4. Nest and eggs of Laysan Rail. By Walter K. Fisher; photographed on Laysan I. in May 1902. All rights reserved, Photo Archives, Denver Museum of Natural History.

Mass. Using the formula for calculating volume from egg dimensions used by Rohwer (1988) for waterfowl, masses of 12 wild-taken eggs would have been 6.9–8.1 g (mean 7.6). Egg was noted as large for the size of the bird, and if the estimated body mass of the bird is anywhere close (see Measurements: mass, below), the mass of a single egg would have been about 23% of body mass.

Color. "Very pale creamy buff flecked with light red-brown and purplish grey, both colours being pale and somewhat indistinct, in some the colouring is much suffused and variable in depth" (Frohawk 1892: 248).

"The ground color is a pale olive buff, closely spotted with pale clay color or raw sienna, and faint lilac gray. The maculations are distributed fairly evenly over the egg, but in some specimens seem more crowded at the broader end. The clay color is brightest and seems to predominate. The specimens vary in the relative closeness and size of the spottings, the flecks being larger and more scattered in a few examples. None of our specimens present the creamy buff ground-color mentioned by Rothschild (1893–1900). Ours are distinctly greenish" (Fisher 1903: 802).

Figure 5. Laysan Rail on nest. By Walter K. Fisher; photographed on Laysan I. in May 1902. All rights reserved, Photo Archives, Denver Museum of Natural History.

These descriptions are borne out by the USNM series, which contains the specimens forming the basis for Fisher's description. The additional captive-laid series contains eggs with much lighter, cream-colored, almost white, background with mainly lilac flecks.

Surface texture. Usually smooth, occasionally slightly rough; 1 in the USNM collections is decidedly rough all over, as mentioned by Fisher (1903).

Eggshell thickness. No information.

Clutch size. Both Fisher (1906) and F. C. Hadden (in Bailey 1956: 90) gave clutch size as 2 or 3. Although a clutch of 4 was reported by W. Donagho (in Bailey 1956: 90), this occurrence was probably anomalous. Berger (1981: 82) erroneously quotes Bryan as noting a pair of rails "with a flock of five young following them"; this observation actually pertains to Laysan Duck (*Anas laysanensis*; Bryan 1912: 28).

Egg-laying. No information.

INCUBATION

No information on Hawaiian Rail; all information in this section pertains to Laysan Rail.

Onset of broodiness and incubation in relation to laying. Fisher (1906) reported one female that would permit herself to be lifted off nest and would return.

Incubation patch. No information.

Incubation period. No information.

Parental behavior. Most birds collected were males, implying that females were on nests.

HATCHING

No information.

YOUNG BIRDS

Laysan Rail. Legs and feet were so small and moved so rapidly that the young looked "like a black velvet marble rolling along the ground" (F. C. Hadden in Bailey 1956: 90). Young could run as fast as older birds at 4–5 d of age and "soon learns to find its own food" (F. C. Hadden in Bailey 1956: 90).

Hawaiian Rail. No information.

PARENTAL CARE

Laysan Rail. Young were taught to forage on their own by adults, "which carefully guard it for the first month" (F. C. Hadden in Bailey 1956: 90).

Hawaiian Rail. No information.

COOPERATIVE BREEDING

No information.

BROOD PARASITISM

No information.

FLEDGLING STAGE

No information.

IMMATURE STAGE

See Parental care, above, and Appearance, below.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

No information.

LIFE SPAN AND SURVIVORSHIP

No information.

DISEASE AND BODY PARASITES

No information.

CAUSES OF MORTALITY

See Conservation and management: effects of human activity, below.

Exposure. Severe storms causing flooding and drastic loss of vegetation cover almost certainly would have been responsible for fluctuations in numbers of Laysan population during the history of the species on the island. Rails would have been able to take shelter in petrel burrows, but those not drowned or blown away (as were the last Laysan Honeycreepers [*Himatione sanguinea freethii*]; see D. R. Dickey in Olson 1996) may have faced limited food resources and reduction in suitable nesting sites until vegetation recovered. Storms are thought to have been responsible for failure of Laysan Rail to become established after being introduced to an island of Pearl and Hermes Reef.

Starvation. At least 2 or 3, and perhaps all, of 8 Laysan Rails from Midway released on Laysan I. 29 Apr 1923 were found dead in ensuing days in May, presumably from starvation or exposure due to nearly complete lack of vegetation caused by rabbits (Olson 1996).

Predation. See Behavior: predation, above.

POPULATION STATUS

Numbers. *Laysan Rail.* No proper census was ever made, and most estimates seem like mere guesses. Given their contradictory nature, the low estimates surely are too low, and the high estimates much too high. Palmer reported that on Laysan I. in Jun 1891, the species "covers the island" (Rothschild 1893–1900). Dill (1912) estimated 2,000 birds in 1911. Even about 12 yr after introduction of rabbits, W. H. Munter estimated 5,000 rails on Laysan, in 1915 (Ely and Clapp 1973: 183). In a turgid passage, Baldwin (1945: 345) spoke of "scores of thousands of adults, limited in numbers only by space and food requirements."

Later, using Bryan's (1915: 319) statement that "almost every square rod of the grassy portion of the island has its pair of rails," Baldwin (1947: 20) somehow calculated 922 pairs, or 1,844 breeding adults, which with unpaired birds would have come close to Dill's estimate of 2,000 birds. Baldwin's calculations were far off the mark, however, as he considered the 0.9 square mile (2.3 km^2) of available habitat to be equivalent to 922 square rods, even though a square mile contains 102,400 square rods so that the available habitat would have comprised 92,160 square rods, which at 1 pair/square rod comes to 184,320 rails—which seems much too high. If we allow only 2 pairs/acre (0.4 ha) of habitat, the estimate would come to 2,304 individuals, not far off of Dill's 2,000, but probably too conservative.

On Midway, the rail was said to be "probably the most abundant bird on Eastern Island" in Nov 1907 (Bartsch 1922: 487) and as late as 1940 was reported to be "extremely abundant over the whole area of both Sand and Eastern Islands"; "they cross one's path wherever one goes at all hours of the day and run under buildings in our camp. There must be literally millions of them" (T. M. Blackman in litt. to E. H. Bryan unpubl. [Bishop Museum Archives]). Without further documentation, Berger (1981:83) mentioned an estimate of 5,000 rails on Midway in 1922, which he regarded as "probably greatly exaggerated"; a year later, E. L. Caum estimated 600 to 750 rails on Midway (Baldwin 1947:20).

Hawaiian Rail. No information.

Trends (extinction). *Laysan Rail.* The species disappeared from Laysan ultimately because of destruction of vegetation by rabbits. On Midway Atoll, extinction is attributed directly to accidental introduction of rats in 1943, when the islets were overrun with an "extreme infestation," although another contributing factor was the wartime destruction or modification of vegetation, which was reduced to smaller and more isolated clumps (Fisher and Baldwin 1946: 8).

Hawaiian Rail. Exact causes of extinction of the dozen or so species of flightless rails of the main Hawaiian islands are unknown, but all were surely anthropogenic. Because most of these extinctions took place prehistorically, it can be postulated that a combination of direct human predation, habitat destruction, and predation by the introduced Polynesian rat resulted in extermination, conceivably aided by diseases introduced along with the poultry brought by Polynesians was responsible for the disappearance of rails. The introduction of additional predators after European contact, particularly dogs, cats, and rats, would also have been a factor in extinction of Hawaiian Rail.

Specimens in the Mills collection were obtained at least as early as 1859 (Manning 1978), and the last specimen was said by Munro (1944), with no further elaboration, to have been taken in 1864. In 1887, S. B. Wilson was told by the bird-catcher Hawelu that a rail had been seen by a mail carrier within the 3 previous years (Wilson and Evans 1890–1899: 173); this dubious thirdhand report presumably was the basis for the citation of 1884 as the date of last occurrence (Berger 1981, Am. Ornithol. Union 1998). A supposed sighting along construction for the Hilo-Volcano road about 1889 was never verified, and a reward of $100 for a specimen at that time failed to find any takers (Manning 1982). In May 1892, Palmer hunted intensively for rails in Hawelu's old haunts with a specially trained dog sent for the purpose by Rothschild, but he was unsuccessful and found the area then overrun with mongooses (Rothschild 1893–1900, 1907). Thus a supposed sighting of a rail some 8 km east of Volcano House (see Distribution: Hawaiian Archipelago, above) in 1893 (Henshaw 1902) is not likely.

POPULATION REGULATION

Laysan Rail. Appears to have been heavily dependent for food on eggs, as well as carrion and carrion-feeding insects associated with breeding seabirds. Breeding season of the rail was closely linked to peak seabird breeding season, and the much more limited food resources during late fall and early winter, when few or no nonburrowing seabirds were present on the island, probably limited the number of rails.

Hawaiian Rail. No information.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Laysan Rail. There is no question that human activity was responsible for extermination of the Laysan Rail. Vegetation of its native environment was destroyed by introduced rabbits, resulting in population decline due to starvation and lack of cover to hide nests from the abundant egg predators on the island. On Midway, introduced populations of rails quickly succumbed to predation by introduced rats.

Hawaiian Rail. Extermination of Hawaiian Rail also is presumed to be due entirely to anthropogenic causes. It is said to have been hunted for sport by Hawaiian chiefs "in olden times" (Perkins 1903: 454). D. Malo (in Handy and Handy 1991: 258) noted that in Ka'ū the "rails (moho), which are not able to fly, were caught in their nesting holes and were eaten."

MANAGEMENT

Laysan Rail. The only attempts at management were the various introductions of the species to islands other than Laysan, which were successful only on Midway. The great pity is that the species was not reintroduced to Laysan in the 2 decades between 1923, when rabbits were exterminated on Laysan and the vegetation began to return, and 1943, when rats arrived on Midway and exterminated the only existing populations. Although efforts were made to encourage reintroduction to Laysan, they were thwarted by bureaucratic red tape (M. Rauzon pers. comm., based on correspondence in the Bishop Museum).

Although the Laysan Rail itself cannot be restored, it was genetically so similar to its progenitor, Baillon's Crake, that introduction of that species to Laysan can be regarded as a justifiable step in restoration of the island's ecosystem, as well as providing an extremely interesting experiment to determine how rapidly such a species would adapt behaviorally and morphologically to insular conditions.

Hawaiian Rail. No attempts at management.

APPEARANCE: LAYSAN RAIL

MOLTS AND PLUMAGES

Hatchlings. Entirely covered with black down; bill yellowish (Frohawk 1892: 248). Coal black, with

yellow bill (Dill 1912). This appearance is similar to that of Baillon's Crake, in which the downy young are all black, with "white or wax yellow" bills (Fjeldså 1977).

Juvenal plumage. "Young birds have the underparts pale buff, replacing the grey of the adult" (Frohawk 1892: 248). Throat and chin are also paler (whitish). The buffy feathers of underparts have gray bases, but of lighter color than in adults, and because the Juvenal plumage was molted quickly these feathers probably were shed before they were sufficiently worn to impart grayish appearance.

Definitive Basic plumage. Upperparts, sides, flanks, secondary- and upper-coverts, underwing-coverts, and rump light olive, sandy brown, the lightness usually accentuated by fading, presumably from exposure to high levels of solar radiation. Outer vane of primaries buff, inner vane cinereous brown. Feathers of crown, nape, and dorsum, scapulars, and tertials have broad blackish-fuscous median streak. Variable number of feathers of mantle have remnants of white lateral streaks or edges, sometimes nearly absent. Broad supercilium, cheeks, and entire underparts are medium slaty gray. Lower flanks and undertail-coverts have scattered remnants of white barring. Sexes similar.

Phenology of molt. Molt appears to have occurred in late summer and early fall. One specimen from Midway was in fresh, relatively unworn plumage on 7 Nov 1907. In first half of year, Jan birds are the least worn, May the most, with tails either worn off or molted. Jun birds taken in 1891 by Palmer and Munro may be very worn, but some appear to be in reasonably fresh plumage. In the series taken by Schauinsland, one was in fresh plumage as early as 21 Jul, but most of the unworn birds are from end of Aug and Sep, with extremely worn and faded specimens occurring through first week of Aug.

Juvenal plumage must have been very evanescent because in the extensive Jan–May series in the USNM collections ($n = 41$), only 3 taken 27–28 Feb retain a few buffy Juvenal feathers on breast and belly, although no feathers in sheath could be detected in these birds. A specimen from Midway taken 7 Nov 1907 is mainly in buffy Juvenal plumage, but a few gray feathers of Definitive plumage are beginning to appear on breast. Thus, Juvenal plumage was apparently replaced about Nov through Jan.

BARE PARTS

The best descriptions are from Frohawk (1892: 248), who was an artist and observed live birds in captivity, and from labels of specimens in the American Museum of Natural History (AMNH) collected by Schauinsland translated here from German.

Bill. *JUVENILE.* Greenish yellow or olive green (Schauinsland labels).

ADULT. "Light green, darkest and inclining to purplish at the tip and culmen" (Frohawk 1892). Olive green above, lighter below (Schauinsland labels).

Orbital ring ("eyelid"). "Pale grey-green" (Frohawk 1892).

Iris. *JUVENILE.* Light brown or gray-green (Schauinsland labels).

ADULT. Ruby or ruby red (both observers).

Legs and feet. *JUVENILE.* Dark gray-green or blackish gray (Schauinsland labels).

ADULT. Light olive grey-green (Frohawk 1892) or olive green (Schauinsland labels).

APPEARANCE: HAWAIIAN RAIL

MOLTS AND PLUMAGES

Hatchlings. No information.

Juvenal plumage. Possibly more grayish ventrally, without reddish nape or white barring on flanks and vent (see descriptions of specimens from the Naturhistorisches Museum Wien [NMW] in Vienna and the Bernice P. Bishop Museum [BBM] in Honolulu, HI, below).

Definitive Basic plumage. Because there are only 7 existing specimens of the Hawaiian Rail, each differing somewhat from any of the others, all are described briefly.

Two specimens are considered to be referable to nominate *P. s. sandwichensis*. Rijksmuseum van Naturlijke Historie [RMNH], Leiden, specimen no. 1: Dorsum and wing-coverts brownish; blackish centers on feathers of dorsum; nape not rufous as in *P. s. millsi*; underparts rich chestnut, paler on chin and throat; no white barring on posterior portions. Wings and tail blackish, outer vane of primaries brownish. Patch of darker red feathers near vent appears as if glued into place from somewhere else on body. NMW no. 50728: All dark vinaceous cinnamon below; not lighter on throat, and only the very faintest hint of barring on lower flanks. Upperparts dark brown; no reddish on nape. Dorsal feathers have darker centers, although not as conspicuously dark as in the RMNH specimen.

Of the 5 specimens from the former Mills collection that are syntypes of *P. s. millsi*, the 2 in England are in the best plumage and in the best condition. British Museum (Natural History [BMNH]) specimen no. 1939.12.9.553: Dorsum brown; more reddish on nape; throat pale; neck, breast, and sides rufous-vinaceous; lower flanks and vent fuscous, narrowly barred with whitish.

University Museum of Zoology, Cambridge, England [UMZC], specimen no. 15/Ral/38/a/1: Plumage as in BMNH specimen, but marked with reddish buff on outer web of outer primary (Rothschild 1893–1900: 241).

AMNH specimen no. 546232: Dorsum and wing-coverts dark reddish brown; slightly grayer on crown; nape not markedly more reddish; rump darker, more blackish. Chin and upper throat appear lighter, but mainly because bases of feathers are exposed. Cheeks slightly grayish. Breast rich chestnut. Flanks and vent darker, blackish vinaceous with little indication of paler barring. Almost no suggestion of dark centers of dorsal feathers. Tarsi and toes quite light (yellowish, probably orange in life).

BBM specimens nos. 20 and 21: Both specimens are in comparable plumage, and neither seems exactly like the BMNH or UMZC specimens (see above), although both appear to have been on exhibit for a considerable period and are more faded. These specimens are probably immature. They have no reddish on nape, and only the faint-est hint of barring on posterior. Dorsal feathers have blackish centers, but these are usually covered by lighter-brown edges of adjacent feathers. Lower breast and belly, particularly of specimen no. 20, appear grayish (as if juvenile), with more reddish-vinaceous feathers apparently coming in on breast and lower throat. Throats and chins are pale.

Phenology of molt. No information.

BARE PARTS

No information from living or fresh specimens. The best approximations are from Latham (1785: 236, 237; as quoted by Medway 1981: 163), who described specimens from Cook's voyage only a few years after they were collected. The descriptions are for both his "Sandwich Rail" and his "Dusky Rail," now believed to be the same species (see Medway 1981).

Bill. "Dusky ash-color" (Latham 1785: 236); "dusky black, edges of the mandibles yellowish" (Latham 1785: 237).

Orbital ring ("eyelid"). No information.

Iris. No information.

Legs and feet. "Dusky flesh-color" (Latham 1785: 236). As noted above, the legs in the AMNH specimen appear light, as though they may have been orangish in life.

MEASUREMENTS

LINEAR

In many or most rails, males are larger than females, but there is very little difference between sexes in Laysan Rail (Table 1). No specimen of Hawaiian Rail is sexed (see Table 2).

Table 1. Linear measurements (mm) of Laysan Rails from Laysan I. from specimens in USNM (n = 10, except for length of tail in males [n = 9] and in females [n = 7]). Data given as mean (range).

	Male	Female
Wing (flat)	58.4 (54.1–63.1)	58.5 (56.2–62.5)
Tail	26.1 (22.3–29.3)	26.7 (24.3–30.4)
Culmen	19.0 (17.3–20.1)	18.1 (17.3–19.4)
Tarsus	25.4 (23.1–27.2)	23.2 (22.4–25.0)
Middle toe with claw	30.2 (27.2–31.7)	29.0 (28.4–30.6)

MASS

Laysan Rail. Nothing recorded. Masses of 2 male Baillon's Crakes were 30 and 35 g, respectively (Dunning 1993), and Laysan Rails may have been similar in mass, with the more robust hindquarters being offset by reduced pectoral apparatus.

Hawaiian Rail. No information.

NUMBER, LOCATION, AND PRESERVATION OF SPECIMENS

Laysan Rail. Ely and Clapp (1973) listed 132 skins in 8 collections, but their compilation was very incomplete. SLO and H. F. James (unpubl.) surveyed Hawaiian birds in most of the world's museums and tallied a minimum of 259 specimens, including skeletons and fluid-preserved birds, in museums in the following cities: Ann Arbor, MI (15); Berkeley, CA (1); Berlin, Germany (2); Bremen, Germany (29); Cambridge, England (2); Cambridge, MA (11); Chicago (8); Greenville, DE (4); Honolulu, HI (27); Leiden, Netherlands (1); Liverpool, England (1); Los Angeles, CA (13—Los Angeles Co. Museum [5], University of California at Los Angeles [3], Western Foundation of Vertebrate Zoology [5]); New York, NY (42); Paris, France (2); Philadelphia, PA (2); Pittsburgh, PA (1); San Francisco, CA (11); Stockholm, Sweden (1); Toronto, Ontario (4); Tring, England (17); Washington, DC (65).

There are eggs in the collections of WFVZ, USNM, Museum of Vertebrate Zoology, Berkeley, CA (Kiff 1985), and BMNH (Knox and Walters 1994), probably at Bremen, and perhaps elsewhere. Rothschild (1893–1900: 306) and Schönwetter (1962: 324) mention an egg in the collection of a Dr. Studer, and Schönwetter also refers to an egg in the museum in Bern, Switzerland.

Table 2. Linear measurements in mm of the 7 extant skins of Hawaiian Rail. All are mounted, making accurate measurements, particularly of the tarsus, more difficult.

Museum[1]	RMNH	NMW	BMNH	UMZC	AMNH	BBM	BBM
Specimen no.	1	50728	1939.12.9.553	15/Ral/38/a/1	546232	20	21
Culmen from base	20.0	18.0	19.6	17.7	16.7+	19.5	19.9
Culmen from nostril	9.4	8.8	9.8	9.1	7.7+	9.9	8.8
Mandibular symphysis	8.6	8.5	9.7	8.1	7.2+	8.1	7.5
Wing (chord)	72.0	62.0	63.9		65.2	65.8	71.4
Tarsus	28.8	29.1	30.4	28.9	27.8	29.9	27.3
Distal width of tibia	4.7				4.1	4.8	4.8
Middle toe with claw	33.8	33.1	35.5	33.3	32.6	33.3	

[1]AMNH, American Museum of Natural History, New York; BBM, Bernice P. Bishop Museum, Honolulu, HI; BMNH, British Museum (Natural History), Tring, England; NMW, Naturhistorisches Museum Wien (Vienna); RMNH, Rijksmuseum van Naturlijke Historie, Leiden, Netherlands; UMZC, University Museum of Zoology, Cambridge, England.

Hawaian Rail. The 7 historic specimens are housed in 6 different museums, from Honolulu to Vienna. There has been some confusion as to the exact number (Banko 1979) because 1 of the specimens on extended loan was counted twice (Manning 1982), whereas the Vienna specimen was overlooked by both of these authors; the correct total is thus 7. A specimen in the museum in Hannover, Germany, was identified as this species (Boenigk 1978), but the accompanying photograph clearly shows it to be a mounted specimen of the White-browed Crake (*Poliolimnas cinereus*). The listing of 7 specimens in alcohol each of "*Pennula millsi*" and "*Pennula sandwichensis*" in BMNH (Blandamer and Burton 1979: 138) appears to have resulted from a combination of typographical errors (Knox and Walters 1994: 110) and perhaps confusion with specimens of Laysan Rail. There are certainly no existing fluid-preserved specimens of Hawaiian Rail. Nor are there any skeletons, although some bones have been removed from the AMNH specimens for comparison with fossils.

The 2 earliest specimens of Hawaiian Rail that are possibly from Cook's voyage in 1779 are at RMNH and NMW. The other 5 specimens of Hawaiian Rail come from the collection assembled by the amateur collector James Mills, of Hilo, HI (Manning 1978, 1979). Two of these specimens eventually were sold to Walter Rothschild (Manning 1982), one of which went with the Rothschild bequest to BMNH and the other with the sale of his bird collection to AMNH. Three others were acquired by Charles Reed Bishop for BBM, 1 of which was exchanged to Scott Wilson and is now at UMZC, the other 2 of which are still at BBM.

PRIORITIES FOR FUTURE RESEARCH

Because both species are extinct, only paleontological studies and studies involving "ancient" DNA are likely to yield much new information. It is possible that if all 7 specimens of Hawaiian Rail could be assembled and compared simultaneously, a few new insights might be derived, but because the time of year of collection of most of these specimens is unknown, such insights would be minimal. The reintroduction of Baillon's Crake to Laysan Island, if well monitored, could provide one of the most interesting modern experiments in insular evolution of birds ever devised, and it should be encouraged.

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and Helen James located caves and collected bones of Hawaiian Rails. Mark J. Rauzon supplied a manuscript incorporating material from the Bishop Museum Archives and made comments on the manuscript. Warren Wagner, Dept. of Botany, Smithsonian Institution, identified material forming nests of Laysan Rail, and Craig Ludwig kindly supplied information on specimens of rabbits in the USNM collections. I thank Helen F. James for assistance in collecting data from museum specimens. The manuscript benefited considerably from the comments of reviewers Jeff Marks, Marie Morin, and David Medway. Cover art by Julian Hume.

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