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A NEW SPECIES OF RAIL FROM THE SOLOMON ISLANDS AND CONVERGENT EVOLUTION OF INSULAR FLIGHTLESSNESS

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ABSTRACT.—*Gallirallus rovianae* is an extant new species of flightless or weak-flying rail from the Solomon islands in the southwest Pacific Ocean. Within the Solomon islands it is known from New Georgia and reported from four neighboring islands, all joined at Pleistocene times of low sea level. The new species belongs to the *G. philippensis* group (*sensu* Olson 1973a) and is most similar to the widespread *G. philippensis* and to *G. owstoni* (Guam) and next most similar to *G. wakensis* (Wake). It exemplifies the phenomenon of convergent evolution in two respects. First, a volant ancestor similar to *G. philippensis* has independently given rise to flightless or weak-flying derivatives on numerous oceanic islands, including *G. rovianae, G. owstoni, G. wakensis, G. australis* (New Zealand), and others. Emphasizing the ease with which rails evolve flightlessness on islands, I note 10 other groups of rails in which insular flightlessness has evolved repeatedly. Second, I suggest that the ancestral species had boldly patterned plumage similar to that of *G. philippensis*, and that insular reduction of bold patterning has proceeded independently in *G. rovianae, G. owstoni, G. wakensis,* and several other *G. philippensis* derivatives. *Received 13 February 1990, accepted 14 February 1991.*

THE SOLOMON islands, which constitute an archipelago in the tropical southwest Pacific Ocean, harbor many localized endemic subspecies and species of birds (Mayr 1942, 1969). Ornithological exploration of the Solomon islands began in 1838 and climaxed in 1927–1930, when the Whitney South Seas Expedition made large collections on every ornithologically significant island and discovered dozens of new taxa (Mayr 1945). Between 1936 and 1980 nine additional endemic forms were described (two species and seven subspecies). Most of them were from the mountains of Guadalcanal and Bougainville, the two largest and highest Solomon islands (Danis 1938; Cain and Galbraith 1955; Hadden 1981, 1983; Ripley and Hadden 1982).

Between 1972 and 1976 I surveyed birds on most of the Solomon islands that are of ornithological interest. While I was on New Georgia and four neighboring islands, local residents repeatedly described a chickenlike, flightless or weak-flying ground bird, named "Kitikete" in the widespread Roviana language of that district. In 1977 Alisasa Bisili, a retired government officer, succeeded in collecting a specimen. It has proven to be a distinctive new species belonging to a widespread group of Pacific species that includes the volant *Gallirallus philippensis* (Buff-banded Rail), plus the flightless *G. owstoni* (Guam Rail), *G. australis* (Weka), *G. wakensis* (Wake Rail), *G. modestus* (Chatham Island Rail), and *G. sylvestris* (Lord Howe Rail) (Olson 1973a). Some characters of the new rail, however, are shared with the two species of *Nesoclopeus* (Woodford's Rail, *N. woodfordi,* and Barred-wing Rail, *N. poeciloptera*; both flightless), a genus that had not been considered close to *Gallirallus* until Olson (1973a) noted some similarities. The discovery connects *Nesoclopeus* to the *G. philippensis* group and strengthens the relationship suggested by Olson. The new species and its relatives are of interest as an example of convergent evolution, whereby rails independently evolve

FRONTISPIECE. *Gallirallus philippensis* (upper left), *G. wakensis* (upper right), *G. owstoni* (middle right), *Nesoclopeus woodfordi* (lower right), and ***G. rovianae*** (lower left). Painting by James Coe, from specimens in the American Museum of Natural History. Publication of the color plate was supported by the Donald L. Bleitz fund.

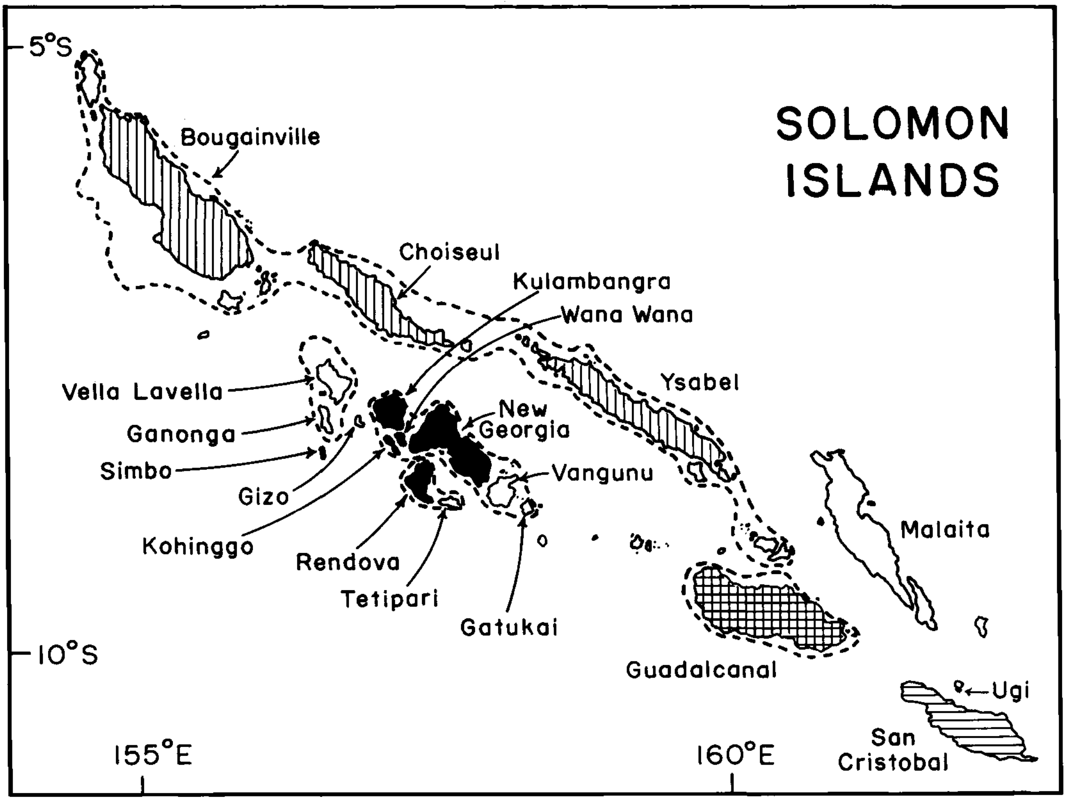

Fig. 1. Map of the Solomon islands. Dashed lines show the outlines of land during late-Pleistocene times of low sea level, as deduced from present hydrographic depth contours. Islands from which *Nesoclopeus woodfordi*, *Gallirallus philippensis*, and *G. rovianae* have been reported are marked by vertical lines, horizontal lines, and black, respectively.

flightlessness and, in some cases, similar plumage characters on widely scattered oceanic islands.

Gallirallus rovianae, sp. nov.
Roviana Rail

Holotype.—AMNH no. 826433, collected near Munda, New Georgia, the Solomon islands, in June 1977 by Alisasa Bisili. Sex unknown. The specimen was initially prepared as a mummy and then made into a study skin in New York.

Distribution.—Known only from the type specimen. Reported by villagers in the western Solomon islands to be widespread on New Georgia and to occur on the neighboring islands of Kulambangra, Kohinggo, Wana Wana, and Rendova. To be sought on the islands of Vangunu and Tetipari as well (Fig. 1).

Etymology.—From "Roviana," the name for the language spoken on New Georgia and neighboring islands, for the people occupying those islands, and for the lagoon that the islands surround.

Measurements.—See Table 1.

Diagnosis.—A medium-sized rail closest in plumage to *Gallirallus philippensis* and *G. owstoni*, and similar in body size and in bill size and shape to adults of the former, but with a much longer tarsus (Table 1). Unique among *Gallirallus* taxa in its unmarked, nearly uniform chestnut-brown upperparts. Shares boldly barred underparts with *G. philippensis* and *G. owstoni*, and shares ochraceous or rufous breast band with those two taxa plus *G. australis* and *G. wakensis*, but these characters are not shared with other *G. philippensis* relatives. *Gallirallus rovianae* is less boldly patterned than *G. philippensis* and *G. owstoni* except in the barred underparts. Specifically, there is greatly reduced wing barring, less distinct facial pattern, reduced barring of the undertail coverts, and (vs. *G. philippensis*) disrupted breast band and unmarked back. Differs further from *G. philippensis* and *G. owstoni* in that the ventral barring is not black but charcoal brown (Table 2).

Description.—The upperparts are a nearly uniform unmarked dark chestnut brown from the crown through the back to the upper tail. The color is slightly richer on the nape, continuing into a richer, slightly reddish chestnut mask through the eye. Starting at the posterior margin of each eye is an inconspicuous gray stripe that continues posteriorly almost to the nape, but there is no clear indication that this stripe continues anteriorly towards the lores. The wings agree in color with the back except for eight small white spots in the primary coverts of each wing. The chin and throat are whitish, becoming gray on the cheeks through the breast. A pinkish-tan wash on the tips of the neck and breast feathers forms a breast band. The upper abdomen, flanks, and sides of the neck and breast are barred charcoal brown and white, with the tips broadly washed with chestnut. The center of the lower abdomen is unmarked light buff; the shanks, unmarked brown. The undertail coverts are broadly barred pale buffy (washed with pinkish-tan or brick towards the tips) and black. Most of the wing is still in sheath, but the visible feathering of the underwing is unmarked dark brown except for two obscure white spots.

Soft parts.—The collector did not record colors in life. In the skin the legs and bill are dull in color.

Material examined.—Adult specimens of the following taxa in the American Museum of Natural History: 23 of the 27 currently recognized races of *Gallirallus philippensis*, plus *G. owstoni* (Guam), *G. wakensis* (Wake), *G. australis* (New Zealand), *G. modestus* (Chatham), *G. sylvestris* (Lord Howe), *G. torquatus* (Philippines and Celebes), *G. insignis* (New Britain), *G. striatus* (southeast Asia and Indonesia), *Nesoclopeus poeciloptera* (Fiji), *N. woodfordi immaculatus* (Ysabel island in the Solomon islands), and *N. w. tertius* (Bougainville island in the Solomon islands). Immature specimens of nine races of *G. philippensis*, and of *N. w. tertius*. I also compared *G. rovianae* with published descriptions of *G. okinawae* (Okinawa: Yamashina and Mano 1981), the unique type of *G. sharpei* (unknown type locality: Olson 1986) and the unique type of the remaining race of *N. woodfordi*, *N. w. woodfordi* (Guadalcanal island in the Solomon islands: Ogilvie-Grant 1889).

Discussion

Comparisons with Immatures

Because the age of the unique type is unknown, it is necessary to consider whether its distinctive characters might be marks of immaturity rather than of species status.

Alisasa Bisili, the New Georgian who collected the type, said that he was familiar with the differences between young and adult *G. rovianae* and that the type was full grown. During my 1974 and 1976 fieldwork on New Georgia, Bisili volunteered accurate information about virtually all of the 64 other resident bird species. Hence if the type is not fully adult, it is nevertheless unlikely to be much smaller than adults or much different from adults in plumage.

The primaries of the *G. rovianae* type are all in sheath. This would be compatible with its being fully adult if the adult molt of *G. rovianae* were synchronous, and would suggest an immature with primaries not fully grown if the adult molt were asynchronous. However, it is not possible to guess the adult molt pattern of *G. rovianae*, because Stresemann and Stresemann (1966) examined a single molting adult specimen each of *G. philippensis* and *N. woodfordi* and noted that the former may molt its primaries synchronously, the latter asynchronously.

The tarsus/bill ratio of 1.65 is much higher than the ratio in adults of all likely related species (1.20–1.33; Table 1). But the young of nidifugous birds quickly acquire adult-sized legs for running, and the bills do not reach adult size until later. This is true in particular of *Gallirallus philippensis* and *Nesoclopeus woodfordi*. Six immature *G. philippensis* had a tarsus length (40–45 mm) comparable to the adult value (37–47.5 mm), but a bill considerably shorter (25–29 mm vs. 27–38 mm in adults). Similarly, the single available immature *N. woodfordi* has an adult-sized (56 mm) tarsus (comparable to 53–65.5 mm for adults) but a short (36 mm) bill (41.5–44.5 mm for adults). As a result, immatures of both species have high tarsus/bill ratios (1.56 for both

TABLE 1. Measurements[a] (mm) of *Gallirallus rovianae* and its likely *Gallirallus* and *Nesoclopeus* relatives.

Species	No. of specimens ♂	No. of specimens ♀	Exposed bill length ♂	Exposed bill length ♀	Tarsus length ♂	Tarsus length ♀
G. wakensis	8		27.4 (25.0–30.0)		33.4 (32.5–35.0)	
G. philippensis	59	55	34.0 (29.5–38.0)	31.0 (27.0–36.0)	43.0 (37.0–47.5)	40.9 (37.0–46.0)
G. rovianae	1		34.5		57.0	
G. owstoni	2	2	42.0 (41.5, 42.5)	37.8 (37.5, 38.0)	50.3 (49.5, 51.0)	45.3 (45.0, 45.5)
N. woodfordi	6	2	43.4 (41.5–44.5)	42.0	56.9 (53.0–65.5)	58.7 (54.0, 63.5)
N. poeciloptera	4		47.5 (46.0–49.5)		61.9 (58.0–64.5)	

[a] Measurements are of the type of *G. rovianae* and of adult specimens of other taxa. Measurements were made to the nearest 0.5 mm and are given as the mean, followed in parentheses by the range or by individual values. Available specimens of *G. wakensis*, *G. rovianae*, and *N. poeciloptera* were not sexed.

species), similar to that of the *G. rovianae* type (1.65) but considerably higher than that of conspecific adults (1.29 for *G. philippensis*, 1.33 for *N. woodfordi*). Both the tarsus and bill lengths of the *G. rovianae* type are similar to those of the *N. woodfordi* immature.

Immatures of the nine races of *G. philippensis* examined differ from adults in the following plumage characters: rufous of the crown, nape, and mask replaced by dull dark brown; eye stripe more obscure, more washed with brown, less clear pale gray; upperparts not black with distinct white bars, but dark brown with more obscure, paler brown edges, bars, or spots; posterior throat and anterior breast mottled or barred and with some ochraceous wash, rather than clear gray; black-and-white barring of the flanks and belly more obscure and washed with brown; more extensive unbarred whitish area in the middle of the belly. The one available immature *N. woodfordi* differs in plumage from adults only in the more extensive white of the chin, and in the more brown, less gray underparts with light edges on the breast.

One of the two plumage characters by which the immature *N. woodfordi* differs from adults (the pale chin) is shared with the *G. rovianae* type, as are three of the characters by which immature *G. philippensis* differ from adults (more obscure eye stripe, reduced ventral barring, and some brown or chestnut edges ventrally). However, the *G. rovianae* type differs from immatures of both *G. philippensis* and *N. woodfordi* in its unmarked, nearly uniform chestnut-brown crown and upperparts. It differs additionally from *G. philippensis* immatures in the greatly reduced barring and spotting of the wings, the unmottled gray breast, the unspotted tail, and the lack of a large white area in the middle of the belly. It differs additionally from the *N. woodfordi* immature in its gray eye stripe contrasting with the chestnut mask, the much more marked ventral barring, the gray breast, the disrupted tan breast band, and the paleness of the anterior belly compared with the posterior belly and breast.

In short, the relatively long tarsus, short bill, and wings in sheath of the *G. rovianae* type are equivocal indicators of its age. Its plumage, however, is quite different from that of immatures as well as adults of *G. philippensis* and *N. woodfordi*. Hence its plumage distinctness indicates taxonomic distinctness.

ASSESSMENT OF RELATIONSHIPS

Olson (1973a) concluded that *Gallirallus philippensis*, *G. owstoni*, and *G. wakensis* are closely related and that *G. australis*, *G. modestus*, and *G. sylvestris* are more distant members of the same species group. Ripley's (1977) interpretation differs. As already explained (see diagnosis and Table 2), *G. rovianae* clearly is closest to the former three species, with which it shares the breast band and boldly barred underparts. However, *G. rovianae* is much less boldly patterned than any race of *G. philippensis*, especially in the absence of dorsal markings, the greatly reduced wing bars and facial pattern, the reduced barring of the undertail coverts, and the disrupted breast band. *Gallirallus owstoni*, *G. wakensis*, and *G. rovianae*, all differ from *G. philippensis* in their unmarked backs and reduced breast band, but *G. rovianae* deviates further from *G. philippensis* in its much more obscure facial pattern, and *G. rovianae* and *G. wakensis* deviate further in their greatly reduced wing markings from *G. philippensis* than does *G. owstoni*. *Gallirallus rovianae* is

TABLE 1. Extended.

Middle toe and claw length		Average tarsus/bill ratio
♂	♀	
41.7 (40.0–44.0)		1.20
46.2 (41.0–54.5)	43.3 (39.0–48.0)	1.29
53.0		1.65
50.5 (50.0, 51.0)	47.0 (47.0, 47.0)	1.30
59.9 (57.0–63.5)	60.0 (56.0, 64.0)	1.33
54.0		1.26

unique in its uniformly dark chestnut-brown dorsal coloration. Thus, reduction of patterning has proceeded the least in *G. owstoni*, further in *G. wakensis*, still further in *G. rovianae*, and furthest in the fairly monotonously plumaged *G. modestus* and *G. sylvestris*.

Of these seven species, *G. philippensis* has by far the widest geographic distribution, from the Philippines and Indonesia east to Samoa. The other species are each confined to single remote Pacific islands or island groups and are variously flightless or weak of flight. One conceivable interpretation of the plumage differences is that the ancestral condition was a relatively unpatterned plumage, that most taxa other than *G. philippensis* represent an earlier expansion wave retaining the ancestral pattern, and that the bold pattern of the now-expanding *G. philippensis* is a newly evolved character. This interpretation is unlikely, however, because the various species of the *G. philippensis* group cover the whole spectrum from the most (*G. philippensis*) to the least (*G. modestus*, *G. sylvestris*) patterned, with *G. owstoni* sharing most of the bold features of *G. philippensis* and with *G. wakensis* and *G. rovianae* sharing some (but fewer) of those features. It is much more likely that the ancestor was boldly patterned. Presumably the widespread *G. philippensis*, which still shares much of its range with numerous sympatric rail species, retained the pattern because it serves the function of species recognition. The other taxa are in the process of independently losing their patterns as a result of reaching islands with few or no other rail species. Under this interpretation the resemblances between *G. rovianae*, *G. wakensis*, and *G. owstoni*—each living on an island 2,500–3,200 km from the other two—would be due to parallelism.

The two species of *Nesoclopeus* are also flightless endemics on remote Pacific islands. *Nesoclopeus* has traditionally not been associated with the *G. philippensis* group. Olson (1973a), however, noted three similarities: a tenuous nasal bar, variably barred underwing, and obscure facial pattern. I noted several other *philippensis*-like features of some *Nesoclopeus* taxa. These include the few white spots in the upperwing and the obscure ventral barring of *N. w. woodfordi* and *N. w. tertius*, the slightly barred undertail coverts of *N. w. tertius*, the paler throat of all *Nesoclopeus* taxa except *N. w. woodfordi*, and the slightly paler belly of *N. w. tertius* and *N. poeciloptera*. Any one of these characters alone would carry little weight, but collectively they suggest that *Nesoclopeus* may be derived from the *G. philippensis* group.

Gallirallus rovianae resembles *Nesoclopeus* (especially *N. woodfordi*) and differs from *G. philippensis* in the long tarsus, unmarked back, lack of contrast between back and crown, unspotted upper tail, obscure facial pattern, few obscure white spots in the upperwing, reduced or absent barring of the underwing, and reduced barring of the undertail coverts. These similarities between *G. rovianae* and *N. woodfordi* could be convergent, as I interpret the similarity of *G. rovianae* to *G. wakensis* and *G. owstoni* to be. Alternatively, because *G. rovianae* and *N. woodfordi* are both from the Solomon islands, their resemblance could reflect relationship.

REPORTS OF *GALLIRALLUS ROVIANAE*

Most information about *G. rovianae* in life comes from reports of Solomon islanders in 1974 and 1976. On each island visited, I asked islanders (especially the older men) to describe all birds known to them. The questioning was done in such a way as to avoid leading questions and to test reliability. I asked people to describe birds they knew rather than to respond to particular questions. When it was necessary to raise the subject of a particular species, I provided just enough details to identify the species and then asked the informant to provide further details. I absolutely avoided yes/no questions (Diamond 1989). In most cases the islanders gave names (in their local language) and clearly recognizable detailed descriptions (including accounts of breeding, diet, and seasonal movements) that encompassed almost all species recorded previously for that island by European collectors, plus some species not yet recorded.

Islanders on New Georgia, Wana Wana, Ko-

TABLE 2. Character variation in species of *Gallirallus* (*philippensis, owstoni, wakensis, rovianae, sylvestris, modestus, sharpei,* and *australis*) and *Nesoclopeus* (*woodfordi* and *poeciloptera*). The last five rows grade characters from most distinct or contrasting (2, 3, 4) to absent (0).

	G. phil.	*G. ows.*	*G. wake.*	*G. rov.*	*N. wood.*	*N. poec.*	*G. sylv.*	*G. mod.*	*G. shar.*	*G. aust.*
Markings on back and rump[a]	white bars and spots, olive edges	none	none	none	none	none	none	obscure fine white bars	white spots	streaked (orange-brown margins)
Color of back and rump[a]	blackish	brown	brown	dark chestnut brown	brownish black[b]	brown	brown	brown	brownish black	blackish
Underparts[c]	bold bars	bold bars	medium light gray	bold bars	blackish	medium dark gray	brown	slightly brownish gray	dark brownish gray	medium gray
Upperwing pattern	bold white bars and spots	bold white bars and spots	a few obscure white bars	a few obscure white spots	a few obscure white spots[d]	unmarked	a few obscure white bars	obscure fine whitish bars	bold white bars and spots	orange-brown margins
Distinct underwing barring?	3	3	1	1 or 0[e]	0–2[e]	3	3	1	3	3
Distinct facial pattern?[f]	4	4	3	2	1	2	0	0	0	2
Distinct breast band?	0–3[g]	1	1	2	0	0	0	0	0	2
Undertail coverts barred?[h]	2	2	2	1	0–1	0	2	2	0	2
Paler posterior belly?	3	2	3	3	0–1	1	0	0	0	0

[a] The crown's markings and color are the same as those of the back and rump in all taxa except *G. philippensis* (crown chestnut with coarse black streaks contrasting with the white-marked blackish back), *G. australis* (streaked chestnut contrasting with the olive-brown back), and *G. sharpei* (brownish gray much as the back, but without the white spots). In *G. rovianae* the crown is unstreaked chestnut as in *G. owstoni*, but the back is the same color.

[b] Blackish in *Nesoclopeus woodfordi immaculatus*.

[c] The underparts are unbarred and almost uniformly colored in most taxa other than the boldly barred *G. philippensis, G. owstoni,* and *G. rovianae*. Exceptions are as follows: the posterior belly is paler than the anterior belly and breast in some taxa (Table's last row); the chin and throat are paler than the breast in most taxa, but barely so in *N. woodfordi tertius* and *G. modestus* and not so in *G. australis* and *G. sharpei*; and the barring on the lower breast, belly, and flanks is present though not conspicuous in *G. wakensis*, faint and fine in *G. modestus*, and obscure to negligible in *N. woodfordi tertius*.

[d] Unmarked in *N. w. intermedius*.

[e] Barring rather conspicuous in the race *tertius*, less so in *woodfordi*, and nearly absent in *intermedius*. Most primaries of *G. rovianae* are still in sheath, but the visible feathering indicates that barring is at least greatly reduced and possibly absent.

hinggo, and Rendova islands independently described a chickenlike ground bird, called "Kitikete" in the Roviana language shared among these islands. A similar bird on Kulambangra island was called "Keremete," and bilingual islanders said that it was the same as the bird called "Kitikete" in the Roviana language. The Kitikete (alias Keremete) was said to differ from other chickenlike ground birds, which were readily identified as *Amaurornis olivaceus* (Pyu-Peyo), *Porphyrio porphyrio* (Balikuhu), and *Megapodius freycinet* (Eo) (Roviana names in parentheses). All accounts emphasized that the Kitikete ran very fast, zigzagged, could be caught only with dogs, and was flightless or nearly so. One informant said that it could flutter but never more than half-a-meter above the ground. Its habitat was described as forest and especially second growth, where young trees grew on abandoned garden sites. The call was said to be a rapidly repeated high-pitched note, which gave rise to its Roviana name, Kitikete. Additional details were provided by my most knowledgeable informant, Teu Zinghite of Kulambangra. Zinghite described the diet as omnivorous (e.g. worms, seeds, coconut shoots, potatoes and taro from gardens, and small crabs) and the nest as a depression on the ground lined with debris, containing two or three eggs, and built in the dry season (June), when rainwater on the forest floor was not a problem for a ground bird.

When informants on the other major islands near New Georgia (Gatukai, Simbo, Ganonga, Vella Lavella, Gizo) volunteered descriptions of birds known to them, they did not include the Kitikete or any bird suggestive of it. I specifically discussed the Kitikete (as described by people from New Georgia, etc.) with informants on Vella Lavella and Gizo, and they denied that the Kitikete occurred on their own islands. No local information was obtained for Tetipari island, which lacks a village, or for Vangunu island, where I did not visit a village. Thus, the reported range of the Kitikete consists of New Georgia, Wana Wana, Kohinggo, Rendova, and Kulambangra; and it is still to be sought on Tetipari and Vangunu. It was in response to my request for a specimen of a Kitikete that Bisili collected the type of *G. rovianae* and identified it as the Kitikete.

There are three possible reports of *G. rovianae* by western observers. First, when I was on Kohinggo island on 19 September 1976, I heard a

[f] *Gallirallus philippensis* has the most distinct facial pattern, namely a chestnut mask separated from the chestnut crown by a pale stripe from the lores through the superciliary almost to the nape, shading from whitish anteriorly to pale gray posteriorly. The pattern is similar in *G. owstoni*, except the chestnut color is duller. The pattern is slightly less conspicuous in *G. wakensis*, where the chestnut is replaced by dull brown. The pattern is quite obscure in *G. australis*, with a dull chestnut mask and crown but only a thin whitish loral line becoming obscurely gray posterior to the eye; in *N. poeciloptera*, with only a faint and individually variable trace of a mask and gray stripe posterior to the eye; and in *G. rovianae*, with a chestnut mask lighter than the crown and an obscure gray stripe posterior to the eye. In *N. woodfordi* the pattern is scarcely detectable (a blackish stripe posterior to the eye, barely differing from the dull dark feathering through the eye), and the pattern is absent in *G. modestus*, *G. sharpei*, and *G. sylvestris* in which the whole head is virtually uniform in color.

[g] An ochraceous or rufous breast band is well developed in all available specimens of the races *anachoretae* (Anchorites) and *praedo* (Skoki). It varies individually from fairly well developed to virtually absent in *pelewensis* (Palau), *swindellsi* (New Caledonia), *tounelieri* (Loyalties), *sethsmithi* (Fiji), and *goodsoni* (Samoa); and is reduced, obscure, or absent in *reductus* (Long and northeast New Guinea), *christophori* (eastern Solomon islands), *ecaudata* (Tonga), and *philippensis* (Philippines).

[h] The tail (virtually lacking in *G. owstoni* and *G. modestus*) has dorsal obscure white spots in *G. philippensis* and is unspotted in the other taxa.

soft, very rapidly repeated call like "kitiketekitiketekitikete..." etc. from dense second growth 3-m tall at the edge of a garden. My Roviana-speaking guide identified the caller as the Kitikete.

Second, Blaber (1990) observed on New Georgia a group of three rails that he identified as *G. philippensis*, based on his experience with that species on Guadalcanal and Australia. He noted them as similar in size to *G. philippensis* of Guadalcanal and perhaps smaller than Australian birds. He did not record plumage details except for noting that the ochre breast band familiar to him from Guadalcanal and Australian birds was narrow and "ragged" in the New Georgia birds. His description may correspond to what I describe as the disrupted pinkish-tan breast band in the type of *G. rovianae.*

Finally, in a dictionary of the Roviana language (Waterhouse 1949: 169) a list of Roviana names for plants and animals and of their English identifications includes the entry *"kitikete,* a dark, very nimble bird. [Hypotaenidia sp.]." *Gallirallus philippensis* was often placed in the genus *Hypotaenidia* when the dictionary was written in 1928. It is unknown how Waterhouse was able to associate the Kitikete correctly with *G. philippensis,* but he may have used Roviana informants familiar with the islands of Guadalcanal and San Cristobal, where *G. philippensis* is a common roadside bird.

DISTRIBUTIONS IN THE SOLOMON ISLANDS

Distributions of rails of the *G. philippensis* group and of *Nesoclopeus* in the Solomon islands are summarized in Figure 1.

The five islands of the New Georgia group from which *G. rovianae* has been reported were joined at Pleistocene times of low sea level until approximately 10,000 yr ago (Diamond and Mayr 1976). The nearby islands of Vella Lavella and Gizo, whose inhabitants reported *G. rovianae* as not present, were not joined to New Georgia and its neighbors. Thus, the present distribution of *G. rovianae* is a legacy of Pleistocene land bridges.

Nesoclopeus woodfordi has been collected on Bougainville, Ysabel, and Guadalcanal (Mayr 1949) and observed on Choiseul (H. Hamlin *in* the unpubl. journal of the Whitney South Seas Expedition; my unpubl. obs.). Sight observations of large dark rails suggestive of *N. woodfordi* have been obtained from New Georgia (Sibley 1951, Blaber 1990) and Kulambangra (Finch 1985). Bougainville, Choiseul, Ysabel, and possibly Guadalcanal were joined by Pleistocene land bridges. *Nesoclopeus woodfordi* is still extant on Ysabel and Choiseul but apparently became extinct many decades ago on Bougainville and Guadalcanal (Diamond 1987).

Finally, in the eastern Solomon islands the volant *G. philippensis* occurs on San Cristobal, Ugi, and Guadalcanal, which lacked recent land connections to each other. The colonization of Guadalcanal may be recent, postdating the extinction there of *N. woodfordi.*

Thus, rails of the *G. philippensis* group or *Nesoclopeus* probably occur on many central Solomon islands. The presence of *N. woodfordi* and the discovery of *G. rovianae* may explain the otherwise puzzling restriction of *G. philippensis* in the Solomon islands to the eastern islands, despite the superior colonizing ability that has permitted it to occupy a range extending from Indonesia to Samoa (>8,000 km).

REPEATED INDEPENDENT EVOLUTION OF FLIGHTLESSNESS IN ISLAND RAILS

Gallirallus rovianae adds one more to the growing list of flightless or weak-flying derivatives of *G. philippensis* stock endemic to oceanic islands. At least eight are now known (Table 3), ranging from *G. p. dieffenbachii* (so similar to *G. philippensis* that it is now usually considered conspecific) through *G. rovianae* and *G. owstoni,* whose specific distinctness is clear but whose relationship to *G. philippensis* is equally clear, to strongly modified derivatives such as *G. australis, G. sylvestris,* and *G. wakensis.* Because none of the islands involved were connected by land to each other, they must have been colonized independently by a volant ancestor, and the colonists must have evolved independently towards flightlessness. Reduction in patterning of plumage has also evolved independently in most of these taxa.

At least 10 other groups of rails show independent evolution of multiple flightless or weak-flying derivatives on oceanic islands (Table 3). Evidently, as discussed by Olson (1973b), insular rails not only evolve flightlessness easily, but they are also under strong pressure to do so. Olson noted that evolution of flightlessness may involve only few genetic changes, for instance in genes controlling relative growth rates of different body parts. The selective force

TABLE 3. Convergent evolution of flightlessness in island rails.[a] Asterisks denote extinct taxa.

Volant relative[b]	Flightless or weak-flying taxa (range)[c]
Fulica atra	**F. c. chathamensis* (Chatham), **F. c. prisca* (New Zealand)
Gallinula chloropus	*G. comeri* (Gough), **G. nesiotis* (Tristan de Cunha)
Gallinula ventralis	**G. hodgeni* (New Zealand), *G. mortieri* (Tasmania)
Gallirallus philippensis	**G. p. dieffenbachii* (Chatham), *G. australis* (New Zealand), **G. modestus* (Chatham), *G. owstoni* (Guam), **G. pacificus* (Societies), *G. rovianae* (Solomons), *G. sylvestris* (Lord Howe), **G. wakensis* (Wake)
Gallirallus torquatus	*G. insignis* (New Britain), *G. okinawae* (Okinawa)
Porphyrio porphyrio	**P. albus* (Lord Howe), **P. kukwiedei* (New Caledonia), *P. mantelli* (New Zealand), **P. paepae* (Marquesas)
Porzana pusilla	**P. astrictocarpus* (St. Helena), **P. palmeri* (Laysan)
Porzana tabuensis	*P. atra* (Henderson), **P. monasa* (Kusaie)
Dryolimnas pectoralis?	**Atlantisia elpenor* (Ascension), **A. podarces* (St. Helena), *A. rogersi* (Inaccessible)
Gallirallus	**Nesoclopeus poeciloptera* (Fiji), *N. woodfordi* (Solomons)
?	**Pareudiastes pacificus* (Samoa), *P. silvestris* (Solomons)

[a] From Olson (1973a, b, 1975), Steadman (1986, 1988, 1989), Balouet and Olson (1989), and references cited therein.

[b] The most closely related volant species.

[c] Rails that are endemic to different oceanic islands and that appear to have evolved to or towards flightlessness independently. Not listed are other *Porzana* taxa from the Cooks, Societies, and Hawaii for which it is uncertain whether *P. pusilla* or *P. tabuensis* is the closest volant relative, and other *Gallirallus* taxa from the Cooks, Marquesas, and Societies for which it is uncertain whether *G. philippensis*, *G. torquatus*, or another congener is the closest volant relative.

is surely the energetic (and weight) burden of flight muscle. Muscle is doubly costly because of high initial investment of biosynthetic energy, plus the continuing maintenance expense due to its high metabolic rate. On extensive land masses with predators, these costs are balanced by the benefits of dispersal and of escape from predators. But on oceanic islands free of mammalian predators, reduction of flight muscle brings great energy savings with little penalty.

Convergent evolution of flightless insular rails is probably much more frequent than indicated. Of the flightless or weak-flying taxa listed (Table 3), half of those that were extant at the time of European discovery have subsequently become extinct, and at least half of the survivors are now endangered—victims especially of introduced mammalian predators. Even more such taxa must have gone extinct before European discovery and soon after the first human colonization of remote Pacific islands by Polynesians and Melanesians, who brought rats, pigs, and dogs. Subfossil remains of extinct flightless or weak-flying rails have now been found on most paleontologically explored Pacific islands (Steadman 1989, Olson 1989). Many more surely await discovery as subfossils. The example of *Gallirallus rovianae* shows that some may also await discovery as living birds.

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