

and only those sites in shade and with low maximum temperatures ultimately are used to incubate eggs.

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The Gray-necked Wood-Rail: Habits, Food, Nesting, and Voice

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The large, elegant Gray-necked Wood-Rail (*Aramides cajanea*) ranges widely over all except the more arid regions of continental America, from eastern Mexico to Uruguay and northern Argentina. For many years, one or more pairs have inhabited light second-growth woods and high, dense thickets on stony land, separated by a creek from our garden and house at Los Cusingos, near Quizarrá in the valley of El General on the Pacific slope of southern Costa Rica (9°20'N, 83°38'W, altitude 740 m). About 20 years ago, a pair of these wood-rails began more frequently to approach our house, where they could be watched from windows or a porch. They have continued to remain shy, ready to run swiftly over the lawn to the nearest sheltering shrubbery when they become aware of being watched, although occasionally they appear more confident. I have never seen them in the mature rain

forest that adjoins the garden, possibly because this is mostly on a ridge, and Gray-necked Wood-Rails prefer the vicinity of water.

Throughout the year, these wood-rails live as a pair, with varying degrees of intimacy. Much of the time, one member holds its partner with threats at a distance of a few meters while eating the corn or rice that we give them. However, at certain seasons, probably when they are preparing to nest, they eat close together, or one picks up a grain in the tip of its bill, runs to the other, who may be as much as 10 m away, and passes it directly to the recipient, or lays it at this bird's feet. Probably the male feeds his consort; but the sexes are indistinguishable except by voice, and at these times they are silent.

Food.—Over the years, I have seen these rails eat a wide diversity of foods. They join White-tipped Doves

(*Leptotila verreauxi*), Gray-chested Doves (*L. cassinii*), Black-striped Sparrows (*Arremonops conirostris*), and Central American agoutis (*Dasyprocta punctata*) eating maize on the lawn at sunrise. A wood-rail and the terrestrial, largely vegetarian agouti sometimes eat only a few centimeters apart, neither paying much attention to the other. Both eat the rice, dry or cooked, that we throw from the kitchen window. They are equally fond of bananas and the fruits that drop from tall African oil palms (*Elaeis guineensis*) in the garden. To peck out fragments of the oily yellow pericarp of these plum-sized fruits, the wood-rail throws its whole body into its blows, see-sawing up and down from its legs, like a woodpecker drilling into a tree. It cannot, like sharp-toothed rodents, pierce the hard, thick, woody seed coat to extract the white embryo. Fragments or whole fruits of spiny pejibaye palms (*Bactris gasipes*), dropped from tall trees by a diversity of birds eating them, also attract the wood-rails. Unless well cooked, these widely esteemed fruits sting the human mouth, but this does not deter the birds.

I watched a wood-rail jump high to break a cluster of bright blue berries from a shrub of the coffee family. Dropping the cluster to the ground, it plucked off and swallowed the berries, one by one. Especially in wet weather, wood-rails walk over the lawn, flicking fallen leaves aside with their bills, or picking them up and tossing them, to uncover what lurks beneath. They dig into horse droppings for undigested grains of maize, or perhaps intestinal parasites.

In El Petén, Guatemala, Kilham (1979) watched a wood-rail vigorously peck and shake a 30-cm water snake for 45 min before swallowing it, still writhing feebly, on the seventh attempt. He also saw these birds take snails (*Pomacea flagellata*) from a reservoir and by several minutes of pounding on the shell open a small hole to extract the contents. These wood-rails had become as tame as domestic chickens and could be watched closely. In Panama, Wetmore (1965) found wood-rails eating small crabs in mangrove swamps. Roaches and other small invertebrates filled out their diet.

Nests and eggs.—On 15 August 1988, I found wood-rails nesting on the flat top of a massive old living fence post of maderá negra (*Gliricidia sepium*) at a corner of the garden. Surrounded by tall, leafy shoots of the repeatedly pollarded post and screened by a profuse growth of ferns (including the robust *Polypodium crassifolium* and three other species), a large bromeliad (*Pitcairnia*), a *Peperomia*, the shrub *Lycianthes synanthera*, and much moss, the nest was so well hidden that we would not have found it if a wood-rail had not flown out while we gathered oranges from a tree beside the post. I found two eggs (at a height of 3 m) on a fairly thick mat of thin twigs, bits of vines, rachises of compound leaves, and leaf blades. Most of these materials could have been found on or close beside the nest site, amid the epiphytes.

This was the fourth wood-rail nest I have found in

half a century in El General. The first three were in quite different situations, 2 to 3 m up in dense tangles of bushes and vines (in one case the scrambling, flesh-cutting *navajuela* sedge [*Scleria*]) over dry land not far from a stream. These nests were bulky, shallowly concave platforms, compactly made of coarse sticks, vines, and dead leaves, 30 to 36 cm broad, and less deep than the diameter of the eggs. Each of these earlier nests held three strongly ovate, whitish eggs, blotched and spotted with large and small marks of bright brown and pale lilac, most densely on the thicker end, sparingly over the remaining surface. Six eggs measured 50.0–54.0 by 34.9–37.3 mm ($\bar{x} = 51.8 \times 36.0$ mm).

Although it has been asserted that wood-rails abandon eggs that have been touched by human hands, the birds continued to incubate eggs that I measured. However, since handling eggs appears to increase the risk of predation, I measured only the first two sets that I found. All of these nests were so well screened by vegetation that it was difficult to glimpse more than a tiny part of the incubating bird, such as a bright red eye or a yellow-and-green bill. The four sets were laid in April, May, July, and August, the first part of the rainy season. In Trinidad, Belcher and Smooker (1935) found Gray-necked Wood-Rail eggs from May to August. Five was the usual number; sets of 3, 4, 6 or 7 were rare. The Trinidad nests were 1 to 6 m above the ground or on branches over-hanging water; they were lined with green bamboo leaves.

Incubation.—I watched the nest at the corner of the garden for 50 h during incubation. These wood-rails sat steadily for long intervals. On 20 August, when I began to watch at dawn, the bird who was sitting when daylight revealed its presence (at about 0520) incubated continuously until it became restless; it left spontaneously (at 1120) after six hours of daytime sitting, plus (apparently) a long nocturnal session. On 26 August, the bird present at dawn did not leave until 1159, 6 h and 39 min later. On 21 August (at 1015) I found a wood-rail on the nest, where it remained continuously until it left in the dusk around 1745, after a session of more than 7 h and 30 min. Other continuous sessions, not watched from beginning to end, lasted 5 h and 35 min, and 4 h and 20 min.

I could not distinguish the sexes and, until the eggs hatched, did not witness a direct changeover. However, on several occasions a bird came to incubate so soon after one had left after sitting for hours that the newcomer was probably the other partner. While they brooded nestlings, the birds changed places frequently, leaving no doubt that both sexes sat at the nest. Thus, on 22 August, the individual that had incubated since daybreak left at 0829, and one arrived 13 min later. On this day the wood-rails sat less steadily; another apparent changeover occurred when the incubating bird left at 1120 and was replaced at 1130. One bird apparently replaced the other in the drizzly

dusk (ca. 1800) on 28 August, the first time that I saw both members of the pair together while watching this nest. They were on the ground near it. While one walked away, the other flew into the mass of ferns around the nest and vanished. Except for these brief intervals when the wood-rails apparently relieved each other, the eggs were constantly covered while I watched. The change of occupancy was made at irregular hours of the forenoon and afternoon. Although one evening it occurred in the deep dusk, on others I failed to see it. Wood-rails are sometimes active at night and might changeover in darkness. In an aviary, the male incubated by day and the female at night (Ripley 1977).

These wood-rails approached their nest by walking over the ground and climbing up a leaning trunk, from which they fluttered across a narrow gap to an ascending branch of the nest tree. They walked down the ascending branch until they disappeared into the mass of epiphytes behind the nest. A few minutes later I could see (through a narrow gap in the greenery) one settle on the eggs. These secretive approaches made it difficult to time their sessions of incubation to the minute.

Unless a nearby sound made them look around, they sat immobile for long intervals, the only visible movement being the sliding of the white nictitating membrane across the bright red eye. After sitting for hours, a brief period of restless looking around and making swallowing movements presaged their departure, when they would drop to the ground and walk away. They sat tightly; shaking the nest tree or pounding on the trunk did not make them flee, but stirring the foliage around the nest with a long stick did. When I noisily set a step-ladder beside the tree and climbed up to inspect the eggs, the incubating wood-rail stuck to the nest until my head appeared above the rim, whereupon it rose up and, with a little cry, flew across the adjoining pasture to the nearest woods. At an earlier nest, 3 m up in a vine tangle in second-growth woods, the wood-rail continued to sit while a laborer, clearing land for planting, cut two small trees that fell against the supporting tangle, making the bird fly out. The wood-rail continued to incubate at the very edge of the new clearing, where preparation for planting bananas was halted to save the nest. Nevertheless, two days later the eggs had vanished, probably taken by a predator. Canny wood-rails try to save their nests by avoiding revealing departures as long as they safely can.

Early on 3 September, I heard peeps in both eggs in the maderá negra tree; one was slightly pipped. By 0715 the following morning, both had hatched, the chicks were already dry, and the shells had been removed. The incubation period was at least 20 days, which agrees with a determination made in an aviary (Ripley 1977).

The young.—The newly hatched chicks were nearly everywhere well covered with short black down. One

had a brownish head and buffy throat; on the other chick the brown was confined to the cheeks and hind-head. From the down projected many scattered, fine, crinkly whitish filaments that made the chicks appear frosted. By the following morning, these filaments, which were probably ruptured sheaths of the down, had mostly disappeared, leaving the chicks more solidly black. Except at the base, where it was dark flesh color, the bill was black, with a small white egg-tooth behind the tip of the maxilla and a minute one at the end of the lower mandible. The wide-open, dark eyes were set amid dull reddish bare skin, above which dull blue skin was visible through sparse down. The hatchlings voiced a weak *ree ree ree*, peeps like a domestic chick's, and a slight, low-pitched whistle when held in my hand.

While I examined the newborn wood-rails, the parent, who had dropped to the ground with a slight cry when driven from the nest, walked around beneath surrounding shrubbery, repeating a throaty cluck, much like that of a domestic hen calling her chicks. It joined its mate in a brief *chirincoco* duet, the first that I heard since the nest was found. One-half hour after I removed the ladder, a parent returned to the nest to brood while I watched for the remainder of the day. The chicks were already active. One climbed up on the shoulder of its parent, who continued to sit with its usual immobility. One ascended the side of the nest. Except for these brief appearances, the chicks remained out of sight for the rest of the clear morning and throughout the rainy afternoon. With one possible exception, I did not see the brooding parent feed them. As daylight faded, I heard low, soft notes when the other parent appeared on the ground near the nest. The one who had sat steadily since 0809 did not bestir itself until the newcomer reached the nest by the usual indirect approach. After looking down at the chicks, the latter settled down to brood them in the dusky nook amid the ferns.

On the chicks' second morning, the nest was much more active than on the first. After my early-morning inspection from a ladder, I watched at a distance until noon. The parents brooded alternately for seven intervals, ranging from 15 to 71 min and totalling 290. They never arrived with food held visibly, nor could I see the chicks down in the nest, but from movements of a parent's head and bill I inferred that they were fed repeatedly, with food brought inside the adult's mouth or throat. The chicks were alert and restless. When I looked at them early in the morning, they returned my gaze, then tried to hide amid dead leaves behind the nest. While a parent brooded, the chicks climbed up beside the nest, or up the adult's chest to touch its bill, without a response from the motionless brooder.

As the chick's second day ended, I found a parent brooding in the dusk. At 0800 on the next morning, the nest was empty, with no sign of disturbance. A search through nearby woods failed to reveal a parent

or young. Possibly the family had gone to more extensive woods and thickets across the creek, now with a swift current that the chicks could hardly cross without being carried. Except one fleeting glimpse, I did not see a young wood-rail until the end of September. Probably in this interval the chick(s) had slept on a "nursery nest" built for them; in Brazil, D. M. Teixeira learned that they passed the night on such a structure until they were as much as 40 days old (Ripley and Beehler 1985). Finally, on the cloudy afternoon of 29 September, both parents appeared in the garden with at least one downy grayish juvenile about half as tall as the adults. In a rainy week at October's end, a single juvenile repeatedly appeared in the garden, with both parents. Now seven weeks old, it was almost as tall as the adults and resembled them in plumage. Its eyes were less intensely red, its bill less yellow, and its legs paler red. The young wood-rail foraged almost or quite in contact with a parent, pushing fallen leaves aside and picking up things just as the adult did. The other parent remained more aloof. This wood-rail remained with its parents until at least 53 days old, then vanished.

Although the parents remained in the area, I failed to find another nest. On 20 September of the following year, one again appeared in the garden with a juvenile of unknown age. In mid-August 1990, parents brought two juveniles almost as big as themselves, but with darker bills and eyes. An adult picked maize from the open lawn, ran back to the shrubbery beneath which the young birds waited, and laid the grains, one at a time, on the ground, from which the juveniles picked them. In early July 1991, the wood-rails brought two downy chicks to the garden. Much shier than the adults, they remained at a distance while both parents picked up food and ran swiftly over the lawn, sometimes as much as 25 m, to deliver it. The chicks either picked it from the ground where a parent laid it or snatched it directly from the feeder's bill. This continued until mid-August, when the chicks were well grown. In early September, it appeared as if the adults drove them away.

Voice.—In southern Costa Rica, the Gray-necked Wood-Rail is named *chirincoco*, an excellent rendition of the opening notes of the bird's song, *chirin co chirin co chirin co co co chirin co*. This arresting performance is heard through much of the year, from January into October, but most frequently in April, May, and June, when the wood-rails are preparing to nest. I did not hear the full song while they incubated in the garden because, as Chapman (1929) learned, it is a duet; while attending a nest, the pair are rarely together. When not so-engaged, they may sing at any hour of the day, as well as by moonlight or on dark nights, but most often in wet, cloudy weather, and in the evening.

The quality of the wood-rails' performance, and the impression it makes upon the hearer, depends greatly upon circumstances, and probably also on the skill of the duetists. Heard at a distance, it is enchanting.

When the singers are near, the clear notes that carry far are often marred by an annoying undertone of weak, scratchy notes. Once, when the duetists were on different sides of me, they sang alike with perfect timing, the voices of both sounding somewhat strained or cracked. One evening, while a wood-rail beyond view sang a ringing *chirin co co co . . .*, its mate (whom I saw well) marked time by simply repeating a weaker *co co co co . . .*. These recitals may continue, with brief interruptions, for nearly a quarter of an hour.

Very different is a deep, "hollow" sound, uttered with closed bill and swelling throat, that I have rarely heard and whose significance I do not know. A similar 'oom-'oom-'oom was ascribed to the King Rail (*Rallus elegans*) by Meanley (1957). When alarmed, the wood-rails emit a harsh, stentorian cackle. One afternoon, when Gray-headed Chachalacas (*Ortalis cinereiceps*) called excitedly in the distance, a wood-rail rose to a branch about 4 m high and continued for a minute or more to repeat a loud, sharp note. Other than the chachalacas' commotion, I found no cause of this unusual behavior—wood-rails rarely perch above the ground. A wood-rail driven from its nest ran around with queer throaty grunts. To call its chicks, a parent clucks like a domestic hen. The voices of chicks were described above.

Miscellaneous observations.—To sun itself, a wood-rail stands on the ground with its back toward the sun and widely spreads its wings. Its breast and the undersides of the wings present a broad expanse of orange-rufous.

Early on a April morning, harsh cackles, suggestive of intense excitement, drew me to the stream that flows near the house. Although I had often heard such notes without finding a cause for them, this time was different. A wood-rail was walking or running ahead of a large, lumbering opossum (*Didelphis marsupialis*) along the rocky shore, and behind the marsupial walked the leading bird's mate. The trio turned into the bushes on the far side of the stream, then emerged upon the shore, to continue upstream until they vanished amid dense vegetation. It appeared that, without the usual groveling and fluttering, the leading wood-rail was engaged in a distraction display, luring the opossum away from eggs or chicks that I could not find, while its partner served as a rear guard.

In May, I found a solitary wood-rail sleeping on a platform of weed stalks, dead leaves, and other coarse bits of vegetation (30 cm in diameter and 10 cm thick) at a height of 2 m (but beneath a canopy of vines) in a shrub beside a small marshy opening in a thicket. Lacking a rim, the platform could hardly have held eggs. With one big red eye, the awakened sleeper stared into the beam of my flashlight, and nervously twitched its short, upturned tail (Skutch 1980). In Panama, Wetmore (1965) found wood-rails resting at night on branches that were sometimes exposed, 2 or 3 m above water or neighboring ground.

I have only once seen wood-rails fight. On the eve-

ning of 27 March 1991, I found two struggling at the entrance to the garden. They confronted one another like fighting roosters and attacked with their bills. At intervals one fell, but promptly regained its feet to resume the conflict, which continued until an entering car drove the birds away. While the two fought, a third wood-rail could be seen nearby, making smacking sounds.

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Interspecific Aggression by Tundra Swans Toward Snow Geese on the Sagavanirktok River Delta, Alaska

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Interspecific aggression in the Anseriformes has been reported in several studies (McKinney 1965, Kear 1972, Savard 1982, 1984, Livezey and Humphrey 1985a, b, Nuechterlein and Storer 1985a, b, Ely et al. 1987). Swans, in particular, are noted for intense aggression in captivity, but aggression by swans toward other waterfowl in the wild had been considered rare (Scott 1977, Kear 1972, Brazil 1983). Recent work from the Yukon-Kuskokwim Delta (Ely et al. 1987) and our observations from the North Slope of Alaska indicate that such aggression may be common.

During research on Lesser Snow Geese (*Chen caerulescens caerulescens*; 1985-1990), we observed frequent aggressive interactions between Tundra Swans (*Cygnus columbianus*) and the geese. The study area was located on the central Sagavanirktok River delta in an oil-development area near Prudhoe Bay, Alaska. Most of the Snow Geese that nest in Alaska occupy a small colony (150-300 pairs, nearly all white phase) on Howe Island in the outer delta. Following the hatch in late June or early July, Snow Geese are distributed in compact groups in widely-spaced brood-rearing areas along the coast, up to 25 km from Howe Island. Nonbreeders and most failed breeders undertake a molt migration (to an unidentified location), so these groups consist almost entirely of brood-rearing geese. Brood-rearing areas are discrete patches of arctic salt marsh vegetation dominated by *Carex subspathacea*, *C. ursina*, and *Puccinellia phryganodes*; the areas are shared with brood-rearing Brant (*Branta bernicla*) and other geese.

Swans, in contrast, are highly territorial throughout the breeding season and nest at relatively low densities (0.01-0.03 nests/km²) across the North Slope of Alaska. Nest densities are somewhat higher in river deltas (R. King unpubl. data) and are as high as 0.9 nests/km² in the Sagavanirktok River delta (R. J. Ritchie unpubl. data). Both Snow Geese and Tundra Swans in the study area initiate nesting in late May or, in late seasons, as soon as snow disappears from nest sites. Snow Geese usually hatch between late June and early July, whereas Tundra Swan nests hatch from early to mid-July.

Systematic observations of Snow Geese were conducted during incubation (late May-early July) and brood rearing (late June-late July) of 1985-1990. During incubation, 368 h of observations were made from a blind on the mainland about 700 m south of Howe Island. In 1988-1990, these observations included the single pair of Tundra Swans that nested on the island each year. During brood-rearing, 471 h of observations were made from blinds located near heavily used brood-rearing areas and from a vehicle on the oil field road system. Tundra Swans were observed when they approached brood-rearing Snow Geese and when Snow Geese approached an active swan nest.

During the six years of the study, we observed 38 direct attacks on Snow Geese by Tundra Swans. Attacks occurred between 30 June and at least 23 July (when observations ceased), which is early in the brood-rearing period for swans. Almost all attacks involved geese that were either unable or unwilling