LIFE HISTORY OF THE RUFOUS-TAILED JACAMAR *GALBULA RUFICAUDA* IN COSTA RICA

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In 1937 I published a life history of the Black-chinned Jacamar *Galbula melanogenia*. This bird, the only representative of the Neotropical family Galbulidae that ranges north of Costa Rica, is now held to be conspecific with the Rufous-tailed Jacamar *G. ruficauda*, widespread in tropical South America. My first paper on the jacamar was based on the study of two nests which I found in the Motagua Valley of Guatemala in 1932. Three years later I came to Costa Rica, where I have found ten additional nests of the Rufous-tailed Jacamar and made the observations that are reported in the present paper.

Imagine a small, glittering hummingbird enlarged to the size of a Starling, with no loss of daintiness or brilliance. Such a bird is the Rufous-tailed Jacamar, which after years of familiarity I find one of the most exciting birds to meet, as it seems to be even more highly charged with energy than most feathered creatures; it gives the impression of being electrified with a high voltage. All its upper parts, including the four central feathers of its long tail, are glittering metallic green, with blue, golden, and coppery glints. A broad band of the same shining green crosses the breast, posterior to which the under plumage, including the lateral tail feathers, is rufous-tawny or cinnamon. The male's throat is pure white, whereas that of the female is buffy, and her abdomen is sometimes paler than his; otherwise, the sexes are alike. The long, straight, sharp, black bill is usually held with a jaunty upward tilt. The legs are short and each foot has two toes directed backward, as in other families of the order Piciformes.

In Central America, the Rufous-tailed Jacamar inhabits humid lowlands. On the Pacific slope of southern Costa Rica it is found occasionally as high as 3,000 feet, and most of the nests reported in this paper were situated at about 2,500 feet above sea level. On the opposite or Caribbean slope, Carriker (1910) also found this bird occasionally at 3,000 feet. In the Caribbean lowlands, I met jacamars chiefly in the heavier second-growth woods, often amid such tangled vegetation that a man could hardly advance without cutting his way with a machete. I also found them in the primary forest, especially where the canopy had been thinned by lumbering and the undergrowth was therefore dense. But here in the valley of El General on the Pacific slope, I have found jacamars chiefly in tall forest which has been little disturbed by man. In such forest they were not rare on this farm when I settled here in 1941, and they continued to breed here until 1949. Since then, with the steady increase of the human population of the district and the continual disturbance of our forest by trespassers and their dogs, the jacamar has disappeared as a breeding resident, along with several other of the larger or more spectacular birds. At long intervals a jacamar arrives and proclaims its presence with stirring calls, but in the last dozen years none has, to my knowledge, stayed to nest.

Rufous-tailed Jacamars subsist largely, if not wholly, on flying insects, which they catch in their slender bills on spectacular darts into the air. Between forays they rest, incessantly turning their heads as they keep a sharp watch for prey, on a perch which is usually horizontal and in the lower half of the woodland, but well above a man's head. Frequently the branch which serves as their lookout projects over a pathway or a narrow stream, which permits them to perform their aerial manoeuvres with less encumbrance

than amid the surrounding dense vegetation. Jacamars are especially fond of large, spectacular butterflies, such as morphos with sky-blue satiny wings and swallow-tails of varied colours. They also catch many large dragonflies, and beetles with glittering shards. Seized with an audible snap of the bird's long bill, the prey is carried back to the lookout perch, against which, if it be large, it is vigorously beaten, often until its wings break loose and flutter to the ground. The wingless body is then swallowed.

The jacamar's voice, freely used, is in keeping with the bird's appearance and helps to create the impression of a creature keyed up to the highest pitch of excitement. When I first came to El General, I noticed a difference between the utterances of the local jacamars and those I had known not long before in northern Central America. A common note of the northern birds was a sharp, not unpleasant, squeak or squeal. A more elaborate performance consisted of modified squeaks delivered in a long series in which the notes, at first rather widely spaced, were repeated with accelerated tempo until a climax was reached, after which they were again more widely spaced. The notes also rose in pitch from beginning to end of the series. The calls of the jacamars which I studied here in El General seemed to be less sharp and more mellow, so that they could hardly be called squeaks. Although I frequently heard accelerated series of notes, the increase in tempo was preserved to the end of the performance and there was no final retardation.

On 13 November 1936, while wandering through the forest on a ridge above the valley of El General at an altitude of about 3,000 feet, I found three jacamars perching in a fairly open space, about mid-height of the great trees. There were a female and two males, who appeared to be competing for her. The males sang again and again, so splendidly that few true songbirds (Oscines) could surpass them. Their rapid trills were long-drawn, clear and soft, delivered with ascending pitch until they reached a very high note. As a variation, these jacamars sometimes delivered a dry rather than a liquid trill. Their call notes were whistles rather than squeaks. From time to time one of the males darted toward his rival, but I saw no actual clashes. After the singing had continued for many minutes, the birds moved off through the forest, whose thick undergrowth made it impossible for me to keep up with them. Although I passed two nesting seasons in this locality, I did not find jacamars breeding so high above sea level.

At a nest which I watched for many hours, the female, whose under plumage was decidedly paler than that of her mate, had also a distinctly weaker voice. Her trill was rather dry or reedy, never so clear and sweet as the male's. Her call notes were so like the mellow piping of the Royal Flycatcher *Onychorhynchus mexicanus* that on hearing them I sometimes looked for the latter. The sharper calls of the male jacamar could hardly be mistaken for the flycatcher's notes. The male and female of other pairs of jacamars are more similar in voice and plumage.

THE NEST

In El General, the Rufous-tailed Jacamars begin to look for nest-sites, and sometimes even to dig their burrows, about the middle of February, in the midst of the dry season. Almost any vertical or steeply inclined surface of bare earth may be chosen as the burrow's site. Often it is a bank beside a woodland road or trail. The bank need not be high, and I have known jacamars to breed successfully in a cut-bank only one foot high, beside a little-used cart-road. One burrow was in the vertical wall of a narrow gully at the forest's edge, beside an old rice field overgrown with tall, dense weeds. The gully was about five feet deep and the mouth of the tunnel was about halfway up its side. The top of this bank was overhung by root-bound earth, and the whole gully was screened above by overarching vegetation. Of all the jacamars' burrows that I have seen, this was in the most secluded site. Usually the tunnel's mouth is far more exposed.

Five of the nests found on this farm were in masses of clay adhering to the roots of fallen trees. When a large tree growing on the heavy red clay of the uplands is overthrown by wind, it frequently raises a great quantity of earth whose originally lower surface may form a vertical wall, higher than a tall man's head, two or three yards long, and several feet thick. This wall provides sites for burrow-nesting birds in the midst of forest where no stream banks, road cuttings, or other escarpments are available. In addition to jacamars, I have known an ovenbird, the Scaly-throated Leaftosser *Sclerurus guatemalensis*, to nest in these walls of root-bound clay; and a pair of Blue-diademed Motmots *Momotus momota* started a burrow in such a site but did not finish it, probably because it was not adequate for the very long tunnels which they prefer. These three species were attracted by a single root-mass, that belonging to a tall campana tree *Laplacea semiserrata* that was overturned by a windstorm in our forest. The jacamars' burrows that I have seen in such sites were from 28 inches to five feet above the bottom of the shallow depression in the ground made by the uprooted tree. Accordingly they were higher, and apparently more difficult for a snake or small mammal to reach, than most of the nests that I have seen in banks.

Both the jacamars' burrows that I found in Guatemala were in steep, nearly bare slopes amid second-growth woods rather than in vertical banks, but I have seen no similar sites in Costa Rica. In Trinidad, Belcher & Smooker (1936) found Rufous-tailed Jacamars nesting in low, sandy banks. In Venezuela, this jacamar nested in the cut banks of gullies, in the sides of a pit from which earth had been removed for building, and once in an excavation in a termitarium situated at the base of a tree (Medina Padilla 1957). In Surinam, Haverschmidt (1958) found a nestling of the jacamar *Galbula leucogastra* in a chamber in the midst of a large arboreal termitary that was still occupied by the termites, although they were absent from the nest cavity itself. It is not known whether the nest chamber was carved by the jacamars themselves or by some other bird. The long, slender bills of jacamars seem to be less appropriate for carving into the hard, laminated material of a termitary than are the thick bills of parrots and trogons, which have been observed digging their nest cavities in such structures. But jacamars' bills also seem too delicate for digging a tunnel in the ground, which nevertheless they commonly do.

Seven burrows of the Rufous-tailed Jacamar that I measured in Costa Rica varied from 11½ to 16 inches in length; five of these burrows were from 12 to 13 inches long. Just inside the mouth these tunnels were about 1¾ inches in diameter. Often there was no significant difference between the horizontal and vertical diameters, but sometimes the tube was a little wider than high; one was 1⅞ inches in width by 1½ inches in height. Often the tunnels were nearly straight throughout their length. Five which showed more or less curvature all inclined to the right (of an observer facing the entrance) but none bent to the left. Only one tunnel had a pronounced flexure; in this case the jacamars, burrowing into a mass of root-bound clay, struck a root 8½ inches from the mouth and turned sharply to the right. At its inner end the jacamar's burrow expands into a low-vaulted chamber where the eggs are laid on the bare earth, for no lining of any kind is carried in.

My two Guatemalan burrows of the Rufous-tailed Jacamar were 13¼ and 16½ inches long, and the former was 2 inches wide by 1¾ inches high at the mouth. The burrows measured by Belcher & Smooker (1936) in Trinidad varied from 12 to 18 inches in length. They remarked that a jacamar's burrow could be distinguished from that of any other bird by its rectangular entrance, with vertical sides. (A burrow of the Blue-throated Jacamar *Galbula tombacea* that I found at an altitude of 4,500 feet in the Pastaza Valley of Ecuador was 14½ inches long and 2 inches in diameter at the mouth. On 25 October 1939 it contained two pure white eggs that were evidently being incubated.)

Rufous-tailed Jacamars may use the same burrow in successive years. A burrow in a very low bank, from which the last nestling departed on 4 July 1943, was re-claimed by

the jacamars at the end of the following February. They threw out a little earth, especially from the bottom of the nest chamber, but they did not appreciably lengthen their excavation; and a month after their return the female began to lay in it. In the middle of February 1945, I again found the pair of jacamars in front of this burrow, and the male repeatedly clung in the entrance. Possibly the pair would have nested in this same burrow for the third year, but before it was time to lay some mammal dug into the low bank just below the tunnel, which was then abandoned by the birds.

In the above-mentioned mass of clay surrounding the roots of the fallen campana tree, a pair of jacamars dug a burrow in February and March of 1945 and hatched two nestlings, which on 18 May were lost in consequence of interference by a trespasser. By 8 June the birds had about completed a new burrow higher in the same root-mass, in which they again hatched two nestlings and lost them prematurely. In 1949 a pair of jacamars dug a third burrow in this same mass of clay, and this time they reared two fledglings.

In Guatemala I watched a pair of jacamars dig a burrow. At first the female did all the work, while her mate perched nearby, sang, and fed her repeatedly. Little by little he warmed up to the task, until finally he dug almost as much as she did, the two alternating in the burrow for spells of work which usually lasted only from two to four minutes, and rarely as much as ten minutes. Still the male continued to give butterflies, dragonflies, and beetles to his mate (Skutch 1937).

Although I repeatedly watched burrows that were being excavated in Costa Rica, I never seemed to choose the right time for seeing the jacamars at work. When, on 14 February 1945, the jacamars returned to the burrow in which a brood had been reared in each of the two preceding years, the male was clearly more eager to start operations than his mate was at this early date. When I came in view of this burrow in the roadside bank, the male was perching on low bushes nearby, calling and trilling, while the female answered from the distance. Once he clung in front of the nearly closed entrance to the burrow in the low bank. After about a quarter of an hour, the female arrived and was given a small insect, which her mate passed to her while they perched side by side on a twig. Several times more he went to cling at the tunnel's entrance. The female watched, caught insects, and called, but she did not go to the burrow and after about five minutes she flew off toward the neighbouring forest. The male lingered a few minutes longer, went once more to the entrance, then followed his mate. It was obvious from the burrow's condition that the work of renovating it had not yet begun.

In Venezuela, Gilliard (1959) saw a male Rufous-tailed Jacamar give a butterfly to his mate on 26 April. Thus nuptial feeding has been observed in this species at points as widely separated as Guatemala, Costa Rica, and Venezuela. The Venezuelan jacamars drove away Rough-winged Swallows *Stelgidopteryx ruficollis* that evidently coveted their burrow. In this same locality, this swallow was found nesting in a jacamar's burrow; but whether it had dispossessed the diggers of the tunnel or waited until it was abandoned, could no longer be learned.

THE EGGS

The jacamars begin to prepare their burrow long before they will lay. On 29 February 1944, I found the pair cleaning out the burrow in which they had successfully nested in the preceding year. The renovation was finished by 8 March, but the first egg was not laid until 26 March. In the six days preceding laying, the tunnel had not been entered, as was evident from the fact that the twigs which I set in its mouth remained upright. A burrow that was begun in the root-mass of the fallen campana tree about 24 February 1945 did not contain an egg until 8 April. The burrow made in this same site in 1949 seemed finished by 17 May and the first egg was laid on 26 or 27 May. About 10 days seems to be the usual interval between the completion of a new burrow and the start of

laying. The pair of jacamars that I watched dig their burrow in Guatemala worked with such concentration that I was sure the female had urgent need of a receptacle for her developing eggs, yet about two weeks elapsed before she and her mate began to incubate.

In sets of two or three eggs, two or more days may elapse between the deposition of successive eggs. In an unusually early nest, the first egg was laid on 26 March and the second, which completed the set, did not appear until 30 March. Possibly another egg was laid and one was lost in this interval, but there was no evidence of this. The persistence with which the jacamars often stay in their burrows during the laying period makes it difficult to learn just when the eggs are deposited. When one throws a torchlight beam into the tunnel and looks in, they usually remain within. I have hesitated to urge the female to leave, because she might have been laying; but sometimes I stamped heavily on the ground near the burrow to send forth the male, yet he would not fly out and expose the eggs. Even pushing a lighted electric bulb into the burrow did not send him forth. In one case, my desire to count the eggs was thwarted for as long as two days by the jacamars' stubborn refusal to co-operate.

Of the nine occupied burrows that I have examined in Costa Rica, four contained 2 eggs and five held 3 eggs or nestlings. In Guatemala, about six degrees farther north, both of my nests held sets of four. Several other birds lay larger sets in Guatemala than in Costa Rica, and this seems to be an example of the " latitude effect ". In Trinidad, which is slightly north of southern Costa Rica where my observations were made, the Rufous-tailed Jacamar lays 2 to 4 eggs, which average $22{\cdot}5 \times 19{\cdot}5$ mm. (Belcher & Smooker 1936). Since I did not open any Costa Rican nests to reach the eggs, I shall give here measurements that I made in Guatemala. The four eggs of a set measured $22{\cdot}2 \times 19{\cdot}1$, $22{\cdot}2 \times 19{\cdot}1$, $22{\cdot}2 \times 19{\cdot}4$, and $23 \times 19{\cdot}8$ mm. The Rufous-tailed Jacamar's eggs are pure white and nearly round.

In nine nests in Costa Rica, eggs were laid as follows: March, one; April, four; May, two; June, two. All these nests were in the valley of El General at about 2,500 feet, except one April nest which was on the opposite or Caribbean slope at about the same altitude. My earliest date for the beginning of laying is 26 March; my latest, about 20 June. This latest nest replaced one from which two-week-old nestlings were lost on 18 May. The other nest where eggs were laid in June may well have been the second brood of the pair which laid the earliest set. This pair brought forth two fledglings on 12 May; and in what I believe to be their second nest, 200 or 300 yards from the successful early one, laying began about 1 June. Second clutches, as opposed to replacement clutches, if they actually occur, appear to be exceptional, at least near the upper limit of the jacamar's altitudinal range in El General.

INCUBATION

The female is in charge of the nest during the night, and by day she and her mate sit alternately on the eggs. As has already been noticed, at some nests incubation begins before the last egg has been laid and the parents, especially the male, already stick to their nest with great steadfastness. After the routine of incubation is well established, the female habitually leaves the burrow in the dim light of dawn, often before her mate's arrival. At the nest in the low roadside bank, the time of the female's departure on seven mornings varied from 5.03 to 5.26. Her latest departure was recorded on a darkly clouded morning. On only one morning, 4 June, did she stay with her eggs until her mate came to call her forth, at 5.21. This was his earliest arrival that I witnessed, and her latest departure, with the exception of the dark and gloomy dawn. On six other mornings, the male arrived from 6 to 26 minutes after the female flew from the burrow. He was even more regular in coming than she in leaving; on seven mornings the extreme variation was only 14 minutes, or from 5.21 to 5.35. He appeared latest on the gloomy morning when the female left latest.

After his arrival near the burrow, the male delayed a while, calling, before he entered. One morning, when I watched from a hide, this delay amounted to only three minutes. On other mornings, when I watched from imperfect concealment, my presence may have delayed his entry. As the date of hatching approached, I took advantage of the interval between the female's departure and her mate's arrival to examine the eggs by throwing a beam of light into the burrow, and I had not always completed my inspection when the male's sharp calls announced his approach. Since the male began his turn on the eggs long before sunrise, he had little time to feed himself and must often have begun to sit with a rather empty stomach.

I spent most of 26 May 1943 watching this burrow in the low bank from a hide. A transcript, slightly abbreviated, of the record I then made will provide a picture of how a pair of incubating jacamars spend their day. After one of the partners entered the burrow, I always set a little twig upright in the entrance. Since a jacamar could neither enter nor leave without upsetting this sentinel, its continuing erectness assured me that I had not missed a movement in a moment of inattention.

4.55 I enter the hide as the day dawns.
5.03 The female? (not clearly identified in the dim light) spontaneously leaves the burrow.
5.22 The male arrives, alights on a low branch across the road from the burrow and calls many times.
5.25 He enters the burrow.
6.55 The female returns, calls much, alights on a branch opposite the entrance and continues to call; but the male does not emerge. She lingers near the nest, calling loudly from time to time, until at
7.18 her mate responds, comes down the tunnel to the entrance, seizes my twig in his bill and carries it out. The female trills as he approaches her. He alights beside her on a *Piper* bush and trills in turn. She enters the burrow; he flies away.
8.41 The male arrives, calls.
8.42 The female leaves. One of the pair trills.
8.44 The male enters the burrow.
10.34 The female arrives, calls.
10.36 The male leaves the burrow. They perch side by side and trill. The female then goes to a perch in front of the entrance, darts out to catch a small dragonfly, calls, answering her mate in the distance.
10.41 She enters. I set up the sentinel twig and leave.

12.35 I return. The twig is down, I reset it.
14.18 The female returns through the woods and calls.
14.21 The male leaves the burrow, carrying away my twig.
14.23 The female enters. I set up a new twig.
16.03 The male returns, calls loudly as usual.
16.04 The female leaves, knocking out the twig with her body. The male calls loudly and trills.
16.05 He enters. Soon a light rain begins.
17.45 The female arrives, calls; the male leaves; she enters. The light is fading rapidly and I go.

From the foregoing record, it is evident that in the course of the day the male took at least four turns on the eggs, the female at least three in addition to her long nocturnal session. The male's three sessions that I timed in full lasted 113, 112, and 100 minutes, and another session exceeded 106 minutes. The two diurnal sessions of the female that were timed lasted 84 and 101 minutes. In the early morning, the eggs were left alone for 22 minutes before the male entered to begin his first session of the day, but thereafter they were never left uncovered for more than five minutes when a change-over occurred. The eggs were incubated for 95% of the nearly 11 hours that I watched.

As the female habitually left the burrow very early in the morning, so she began her night session late in the afternoon. The male did not always stay with the eggs until she arrived. When she came at 17.43 on 30 May, she called in vain for him to come forth, and three minutes later she entered the unoccupied burrow. On 31 May, the male left between 17.10 and 17.18, as my sentinel twig showed; the female arrived at 17.28 and entered at 17.39. On 5 June, the male flew from the burrow at 17.28 and called in

the distance. Arriving at 17.53, the female called much, then entered at 17.56. When, as on the day that I spent in the hide, the male remained at his post until his mate called him forth in the evening, he again had little time for feeding himself, as the light was already fading.

The pair of jacamars whose incubation habits I had studied in Guatemala 11 years earlier followed a pattern which was essentially the same. Here, too, the female left the nest in the dim light of dawn, sometimes in response to her mate's calls, and she began her nocturnal session late in the afternoon; but the sessions of these Guatemalan jacamars were sometimes longer than any that I timed in Costa Rica. In the forenoon both the male and the female were observed to incubate for somewhat over two hours at a stretch, and once in the afternoon the male was with the eggs for three hours or more without a break.

While incubating, the jacamars regurgitate the indigestible chitinous parts of the insects which they have eaten. As these remains accumulate, they form a pavement on which the eggs rest, or in which they are partly imbedded. Conspicuous in this litter are the glittering shards of numerous brightly coloured beetles.

The incubation period is rather variable. At a nest which I studied in 1949, the third and last egg was laid between 11.30 hours on 30 May and 7.15 hours on 31 May. All three eggs hatched between 7.30 and 17.30 hours on 19 June, probably near the later hour, as at 17.30 hours the nestlings were not yet dry. The incubation period, counting from the laying of the last egg to its hatching, was accordingly between 19 days and 20¼ days. At three other nests, it was 20 or 21 days, 22 days, and about 23 days.

For a small piciform bird, the jacamar has a remarkably long incubation period. Recorded incubation periods of woodpeckers range from 11 to 18 or 19 days, the longer periods being for the bigger members of the family, which are considerably larger than the jacamar. The eggs of the Blue-throated Toucanet *Aulacorhynchus caeruleogularis* hatch in 16 days and those of the Prong-billed Barbet *Semnornis frantzii*, a bird of about the same size as the Rufous-tailed Jacamar, in 13 days. All these woodpeckers, toucans, and barbets commonly nest in holes in trees rather than in burrows. The incubation period of the jacamar is about the same as that of certain burrow-nesting kingfishers, motmots, and bee-eaters, all belonging to the Coraciiformes. This agreement suggests that ecological factors, especially the site of the nest, influence the length of incubation more strongly than does taxonomic position (Skutch 1945).

THE NESTLINGS

APPEARANCE AND DEVELOPMENT

In striking contrast to most piciform birds, which are hatched quite naked, the jacamars emerge from the shell with plentiful natal down over much of the body. After drying, the long, soft, white filaments stand out prominently from the pink skin, which they fail to conceal (see Skutch 1937, Plate 7). The tufts of down are especially conspicuous on the chin and throat, where they suggest a long beard. The nestling's tightly closed eyes form dark protuberances on the sides of its head. The lower mandible of the short bill projects slightly beyond the upper mandible, as in a number of newly hatched kingfishers, woodpeckers, and other birds. All four of the nestling's toes are at first directed forward, although in adults the outer and inner toes are turned back. The heel is covered with a prominent oval pad that is considerably broader than the tarsus, but is nearly smooth rather than strongly tuberculate as in woodpeckers, toucans, and barbets. This pad of callous protects the heel joint from abrasion as the nestlings shuffle around on the hard, unlined floor of their nursery. Soon after they hatch, the young jacamars can stand erect, supporting their weight on their heels, and they already peep softly.

In my earlier paper (1937), I described in some detail the development of the nestlings, which I periodically removed from their specially prepared burrow. None of my Costa Rican nests was opened to make the young accessible, and I limited myself to recording such points as could be noticed by looking in at the burrow's mouth, while the interior was illuminated by an electric bulb. When the nestlings were six days old, their pinfeathers were becoming prominent. The development of the young in the late nest, to which I gave most attention, was slow, and their expanding plumage did not entirely cover them until they were about 18 days old. As soon as they are feathered, the white-throated males can be distinguished from the buff-throated females.

VOICE

These nestlings soon became very loquacious. When they were only six days old and still had closed eyes, their little calls attracted attention as one passed along the roadway in front of the burrow. At the age of two weeks, when their eyes were open and their pinfeathers had grown long, these voluble youngsters called through much of the day. Their favourite utterance was a little whistle that was at first repeated in a low voice at measured intervals. Soon the notes followed each other with increasing rapidity, each a trifle louder and higher in pitch than its predecessor, until the whistles ran together into a near-trill, or sometimes a true trill much like that of the parents.

Their mother had now ceased to brood these nestlings whose only covering was the horny pinfeathers, and in the evening they continued their vocal excercises after all other diurnal birds had become silent. Before they fell quiet, the roadway in front of the burrow was nearly dark, and the light in their earth-walled chamber must have become exceedingly dim. Even after these nestlings had become silent, overcome by drowsiness, I could incite a renewed outburst of loud notes by directing the beam of an electric torch into their burrow. When the light was extinguished, their voices gradually died away once more. Likewise, if my torchlight beam fell upon the nestlings toward the end of the night, when they were sleeping soundly, they would awake and immediately begin to call. Even if undisturbed, they would raise their voices as soon as the first dim rays of the new day penetrated into their subterranean nursery, and they continued to call in low tones until their parents arrived with food.

During the nestlings' third week, the trill which terminated their song became sweet and long-continued—a most musical utterance. From a slow, deliberate beginning, the whistles would rise and rise in pitch, at the same time following each other more rapidly, until they became a trill that tapered off into a fine, slender point. The young jacamars seemed to be practising the musical scale. Now, instead of sounding their voices indiscriminately all day long, they used them with more purpose. They called less continuously, reserving their songs to respond to their parents whose approaching notes they heard, and for the times when they were very hungry. The nestlings' voices were now clearly audible at a distance of seventy feet from the burrow's mouth, even above the loud clamour of the broad mountain torrent that flowed not far away. Since at about their sixteenth day the nestlings began to grow wary and shrank back in their burrow when I illuminated it, my visits henceforth induced silence instead of stimulating renewed vocal activity, as when they were younger.

Although the nestlings that I studied in Guatemala first accelerated, then retarded, their sequence of notes, these Costa Rican nestlings continued to repeat their notes more rapidly to the end of the series, even if it did not become a trill—as it usually did after they were older. I never noticed any decrease in tempo at the end of a song. The same difference in the utterances of the adult jacamars of the two countries has already been noticed.

One might suppose that the sounds which continually issued from the jacamars' burrow would soon betray the nestlings to an enemy, with disastrous consequences.

Surprisingly enough, many nesting birds of the tropical forest, including a number whose nests are open cups placed amid vegetation, are far from silent. Even when approaching their nest with excessive caution, the parents may call loudly—an incongruity which strikes the observer as absurd—and the nestlings may be noisy at mealtimes. These facts suggest the conclusion that the principal enemies of these nestlings hunt by sight or scent rather than by ear; probably they are snakes (Skutch 1954 : 58–59, 182). In the case of the jacamars, however, I was able to observe the behaviour of a mammalian predator, whose hearing is evidently keen, when it came within range of the nestlings' voices. While I watched the nest on the morning of 30 June, a coatimundi *Nasua narica*, a long-snouted, practically omnivorous relative of the raccoon that is certainly not above eating young birds, crossed the roadway between me and the burrow. It passed only about ten feet from the tunnel's mouth, whence the songs of the young jacamars were then issuing, but it took as little notice of them as of me, sitting unconcealed in the roadway. Without pausing, it cut obliquely across the road and vanished amid the bushes on the farther side. As it passed almost directly beneath the nestlings' father, who happened to be perching in front of the burrow, he remained motionless and silent. I have little doubt that the coati could have reached the nestlings in their shallow burrow, if it had become aware of them.

FOOD

At this nest in the low roadside bank, the parents caught much of the nestlings' food in the vicinity of the burrow, giving me an excellent opportunity to watch their foraging procedures and to identify their prey, as well as this could be done without having it in my hand. As far as I saw, insects comprised the whole diet of the young jacamars. These insects were invariably caught in the air, often after a long, dashing foray from the exposed perch where the parents kept watch. Butterflies entered largely into the nestlings' meals. Many of these had the stout bodies and hooked antennae of skippers (Hesperioidea). Swallow-tails *Papilio* were occasionally caught in my presence; but heliconians, even when they flew close to the jacamars, were quite ignored, evidently because they are unpalatable to birds. I did not see the parents catch a single morpho, or bring one to the nest in recognizable condition, doubtless because these big, spectacular butterflies were rare here at this season, for elsewhere I have seen jacamars capture them. The largest swallow-tails were served to the nestlings after the wings had been knocked off by beating them against the perch. Other butterflies, even those of a considerable size, might be delivered with or without wings—the parents were not at all consistent in this matter. The young, as I could see after they left the nest, gulped down attached wings along with the body and seemed not to be inconvenienced by them.

Large dragonflies with filmy wings were occasionally taken into the burrow. Other insects were more difficult to identify. Many seemed to be beetles, large diptera, and bees. I definitely recognized a shining green, long-tongued euglossid bee in the female's bill. This bee, about the size of a horse-fly, was among the smallest insects taken into the nest. Those of still smaller size, if caught by a parent, were swallowed at once, as though not worth the effort to carry them into the burrow. The amount of beating against the perch that an insect received depended on its size and consistency. Small, soft insects might receive one or two knocks; large, hard ones were pounded long and loudly. Not infrequently an insect, especially a slippery-shelled beetle, would slip from between the bird's slender mandibles and fly away. Often it was retrieved by the jacamar's swift dart, but at times it made good its escape. These birds never attempted to add insect to insect in their bills, in the manner of many flycatching passerines when feeding their nestlings. The structure of the jacamar's long, slender bill, and doubtless also the larger size of the prey, evidently precluded multiple captures. Hence a single item was taken to the nestlings at each parental visit.

After capturing and preparing an insect, the parents invariably took it to a low dead branch across the roadway from the burrow and about ten feet in front of its mouth. Here they would call and frequently also trill. If both members of the pair happened to be present, they were almost sure to trill with food in their bills. Answering calls and trills came from the young inside the burrow. The manner of delivering the food changed as the nestlings grew older. While they were still small and naked, each parent would remain to brood after delivering a meal, and when finally it emerged it came out head-foremost. At a later period, the parent would stay inside only long enough to deliver the food and then back out tail-first. I noticed this mode of departure for the first time when the nestlings were eight days old and in pinfeathers. Gradually the young birds formed the habit of advancing down the tunnel to receive their meals, so that the parents were not obliged to go all the way in. Their rump and tail would often remain exposed while they delivered the food, and in a moment they would back out and fly away.

When the nestlings were 20 days old, the parents merely alighted momentarily in the burrow's mouth to deliver the food. Apparently each was aware that with its head in the tunnel so that it could not see an approaching enemy and most of its body exposed, it was in a peculiarly precarious situation. If a nestling did not take the food promptly, the parent would dart away still holding it. Usually the parent would not delay in the burrow's mouth more than a second or two, but rarely it would remain as long as eight or ten seconds. Leaving the burrow with the undelivered food, it would fly to its customary perch across the road, and after a variable interval return to present the insect once more. Usually the food was taken by a nestling at the second or third offering. Once, however, when the male parent brought a butterfly, he made 16 visits to the burrow's mouth before a nestling took it. At times he started to fly from the burrow but after proceeding only a foot or two he turned around in mid-air, with a deftness worthy of a hummingbird, and returned to the entrance. If I had counted each of these quick returns as a separate visit, the number made with the same insect would have been greater than 16.

From 28 June, when the two surviving nestlings were 20 days old, until the first to leave passed beyond my view on 3 July, I spent a total of 25¼ hours watching the parents attend them. The male delivered food 88 times and the female 34 times, making a total of 122 meals. Thus the feathered nestlings were fed at the rate of 2·4 times each per hour. The male was their chief provider, bringing food two and a half times as often as the female. On each of the eight days when I watched the nest at dawn, the male was the first to arrive with food, always early, while the light was still dim. On 8 June, he appeared with a tiny morsel for the newly hatched nestlings at 5.11, and this was the earliest feeding that I recorded. The latest hour at which he brought the day's first meal was 5.30 on 2 July, a dark, threatening morning. The next-to-latest feeding was at 5.23 on 1 July, also a dull, overcast morning. In the evening, sometimes the male, sometimes the female, brought the day's last meal.

During the first two hours of the morning of 1 July, the female twice appeared near the nest with food, delayed a while, then swallowed her insect and departed without having offered it to a nestling. On the following morning, which was heavily overcast, she first arrived at 5.55, bearing a moth in her bill. For eight minutes she lingered near the nest, holding it, then swallowed it and flew away. By 8.30 she had not returned. Although when the male came with food he habitually took it into the burrow more promptly, after delivering it he did not fly away as soon as the female usually did. He spent much time in view of the burrow, catching his own food from a lofty perch above the roadway even when he was not actively feeding the nestlings. Sometimes he would remain in sight for an hour at a stretch.

The number of meals brought in a single hour by both parents ranged from none to ten. In two-hour periods, the number of meals which the nestlings received varied

from 3 to 13; on each of three days, 13 meals were brought in a two-hour interval. The number of feedings by the male in a single hour ranged from none to seven; by the female, from none to five. In only one of the 25 hours that I watched did the male fail to bring at least one meal, but the female so failed in nine hours. Once she brought nothing in two consecutive hours; and on the day before the first nestling left, she did not deliver food during the first three hours of the morning. If the male had been as negligent as the female, they would have fared badly indeed; but the emergence from the burrow of the first fledgling stimulated her to greater activity. In the first hour after his departure she fed him twice and a fledgling inside once. In the following hour, she fed him at least twice and the stay-at-home thrice, establishing the maximum rate, five times in an hour, that I recorded for her. At a nest which I studied in Guatemala in 1932, the male seemed to be bringing food to older nestlings more often than the female did. At least, he was far more in evidence at the burrow, although I made no count of feedings.

DEPARTURE

At the burrow in the low roadside bank in 1943, the two young, both males, remained inside unusually long. Early in the foggy morning of 3 July, these nestlings were unusually slow in taking their food. It was then that I noticed the greatest number of repeated offerings of the same item: 16 times by the male on his first visit of the day, eight times on the second. Meanwhile, the female had come with a small insect, but after four unsuccessful attempts to deliver it she carried it away. When the male again brought food at 6.20, he called and trilled much from his usual perch in front of the burrow. Soon the answering trills from within the earth grew louder, and presently a nestling's head appeared in the entrance—the first time that I saw one there. At this point the female arrived with a very small insect, and all three—parents and youngster—trilled back and forth. The male now flew to the burrow and delivered the meal to the nestling in an instant. A few minutes later, the female delivered her offering without delay.

During the next two hours, one or the other of the nestlings appeared several times in the doorway, and a number of meals were delivered to them. Then, at 8.20, when both parents were in front of the burrow, a nestling stuck his head and breast through the doorway and peered all around—his first good look at the outside world, I believe. While he was in this position, the female came with an insect and hovered before and somewhat above him. She flew off without attempting to deliver her offering, but soon she returned with it and behaved as before. Doubtless some observers would say that she withheld food in an effort to entice the young jacamar into the open; but it seemed to me that she did not deliver the food simply because, with the young bird occupying the burrow's mouth, she had no place to alight within reach of him.

A minute or two later, the nestling hopped down to the bare roadway, a drop of about six inches. His first attempt to fly took him only a few inches, and he alighted on an exposed root. Whistling and trilling delightfully, he gradually worked across the roadway and flew into the light woods between it and the river. Here I found him resting on a fallen twig, half an inch above the ground. Much down adhered in long, pappus-like tufts to his wonderfully iridescent plumage, especially on the sides of his head and his breast, where he could not reach to preen, but also a little on his wing-coverts and tail-coverts. His tail was still stubby. Quite fearless of me, he continued to perch on the loose twig while I picked it up. While I held him so he even trilled, his whole body vibrating with the effort. He looked around brightly while I smoothed his plumage with a finger tip. After I set him on a branch beside the roadway, he flew about 20 feet, on a slightly descending course, and this seemed to be about the limit of his ability. Starting from level ground, he could with difficulty rise and fly two or three feet.

Although I repeatedly placed the young jacamar on a perch, he persisted in flying or falling to the ground. Here his parents hesitated to feed him, although once the male alighted on the ground beside him and gave him an insect. Once the female offered him a meal while he was in the midst of one of his long trills, which he would not interrupt in order to take food. On another occasion, however, he received and swallowed a small insect while he continued, with hardly a break, to sing. In the three hours following his departure, the fledgling was fed six times by the male and four or five times by the female. In the same interval the nestling still in the burrow was fed twice by the male and four times by the female. It did not appear that the parents were withholding food from the stay-at-home to make him come out. Sometimes they flew close by the fledgling in the open to feed the one in the nest.

On the following morning, 4 July, the male fed the nestling in the burrow five times between 5.15 and 6.26, then stayed out of sight for two hours. Possibly in this interval he attended the fledgling who had left on the preceding day and was now out of sight. Since dawn, the female had brought no food to the burrow. Returning at 8.27, the male perched high above the road and trilled. The answering trills of the nestling grew louder as he advanced down the tunnel toward the doorway. Finally he appeared in the opening, hesitated, and drew back. Soon he appeared again, pushed out his head, then his breast and shoulders, and looked with evident interest from side to side, up into the trees and down into the roadway. He trilled much, while his father answered from his perch high above the road, where it was doubtful whether the young bird could see him. Then, at 8.34, the young jacamar half jumped, half tumbled, into the roadway. He hopped over the bare ground, trilling loudly and often. When I advanced to within six feet of him, he took wing and flew about 30 feet, alighting in a vine-covered bush in the lower ground toward the river. Soon he dropped into the midst of the *Selaginella* and other low herbage that covered the ground, where I could not find him until at length he called. He seemed as fearless of me as the other had been. I set him on a perch, where both parents fed him.

At intervals through the morning, I had heard the calls of the first fledgling, out of sight among the bushes. After the second fledgling's departure, I searched for and found the first, standing on a fallen leaf about 40 feet from the burrow. The accumulation of droppings indicated that he had been in the same spot for a long while. After another night, his second in the open, I found him on fallen leaves in almost the same spot. He was as fearless of me as when he first left the burrow two days earlier. This was my last meeting with either of the young jacamars.

Although these young jacamars remained in the burrow several days longer than is usual with their kind, the parents did not appear to urge them to leave, and certainly they did nothing effective to bring them out. Much calling and trilling by the parents preceded and accompanied the nestlings' departure; but this was no new development at the nest, for these jacamars used their voices very freely at all times. Moreover, they continued to call and trill even after both their offspring were in the open, although this seemed most imprudent in view of the vulnerability of the young birds on or near the ground.

Both nestlings severed contact with the burrow at a time when they could see or hear a parent or both of them; but the parents' presence seemed to be only an accessory stimulus, reinforcing what was essentially an autonomous movement. That the young departed in response to an inner impulse seems to be attested by the fact that both left at almost the same hour—8.23 and 8.34 on successive days. Similarly, two young Black-hooded Antshrikes *Thamnophilus bridgesi* hopped from their open nest at 6.51 and 6.20 on successive days; and three young Black-crowned Tityras *Tityra inquisitor* flew from their hole high in a dead tree at 7.44, 7.08 and 7.48 on three successive mornings, after

the second two had clung pertinaciously to their high nest despite considerable parental urging to follow the first into the open. Nearly all the many altricial young that I have watched leaving their nests have done so spontaneously; and with a few expections, the parents seemed not to care whether they stayed at home or left. This seemed to be true also of the parent jacamars, for instead of promptly rewarding the first fledgling when he emerged from the burrow, they ignored him to take food repeatedly to the stay-at-home, who just then did not seem to be hungry (Skutch 1961).

NESTLING PERIOD

These two young jacamars left the nest when 25 and 26 days old. In the following year, 1944, the two nestlings reared in this same burrow left spontaneously when only 21 and 22 days old, yet they were then more alert, and seemed more developed, than their predecessors of 1943 when four days older. A day or less after she left the burrow, I found a female fledgling of the 1944 brood resting about 20 feet up, and when I shook the tree in which she perched, she flew easily to another—behaviour which contrasted strongly with that of the fledglings of the preceding year, who rested on or near the ground and were indifferent to my approach. In 1944 the nestlings left the burrow on 12 May, whereas in 1943 they did so on 3 and 4 July, nearly two months later. Both broods were reared in wet weather, when almost daily rains saturated the ground; but since the soil in which this burrow was situated was light, porous, and well drained, this did not seem to incommode the nestlings. In April and May, however, the big butterflies and dragonflies which enter so largely into the jacamars' diet seem to be more abundant than later in the wet season, which suggests that the brood of 1944 developed more rapidly because it was better nourished. Yet often the nestlings of 1943 did not seem to be hungry, at least as the time for their departure approached; for, as has been told, on many occasions the parents found it necessary to offer food repeatedly before it was taken. There is additional evidence that late broods develop more slowly: two young which left their nest on 14 July 1949 were both 24 days old.

At the Guatemalan nest which I studied most carefully in 1932, two young left on 19 June at the age of 20 days, when they could fly better, and were more alert, than the brood of 1943 at the age of 25 and 26 days. The plumage of the 20-day-old Guatemalan nestlings was about as far advanced as that of the older Costa Rican nestlings. In the lower Motagua Valley in Guatemala in 1932 the rainy season did not begin until the end of May; so that these Guatemalan nestlings were raised even earlier, in relation to the beginning of the rains, than the Costa Rican brood of 1944.

To sum up, at four nests the nestling period of the Rufous-tailed Jacamar ranged from 20 to 26 days, and it was longest for late broods. Just as the jacamar's incubation period is unusually long for a piciform bird, so its nestling period is unusually short. Whereas in woodpeckers, toucans, and barbets the nestling period is frequently twice or even three times as long as the incubation period, in the jacamar the two periods are of nearly equal length. As far as I know, the only other piciform birds whose nestling period is as short as the jacamar's are a few small northern woodpeckers, including the Wryneck *Jynx torquilla* and species of *Dendrocopos*, and a tropical puffbird, the White-whiskered Soft-wing *Malacoptila panamensis*. Young soft-wings leave their short burrow in the forest floor at the age of 20 days (Skutch 1958). The similarity of the nestling periods of these two burrow-nesting piciform birds of different families, and their pronounced difference from those of tree-nesting members of the order Piciformes, especially the tropical species, suggest that ecological factors strongly influence the length of the nestling period, as they do that of the incubation period.

MISCELLANEOUS OBSERVATIONS

Jacamars give no attention to the sanitation of their nests. The many indigestible parts of insects that they regurgitate while incubating accumulate on the burrow's unlined floor to such a depth that the eggs are sometimes partly imbedded in them. After hatching, the empty shells remain in the chamber for several days and then vanish, probably being broken up and trampled down into the debris that covers the floor. To this debris the nestlings add their droppings and regurgitated fragments. Many maggots fatten on this refuse. Yet, since the nestlings stand rather than lie in the nest, their new plumage remains remarkably clean, and when they emerge it glitters with metallic reflections, like that of their parents. Tree-nesting piciform birds, including woodpeckers, toucans, and barbets, remove waste from their holes and in some species keep them scrupulously clean; but at least one puffbird, the White-whiskered Soft-wing, neglects the sanitation of its burrow in the ground.

Jacamars are strongly attached to their nests. Often they cannot be driven out by heavy stamping on the ground just far enough from the burrow to avoid causing its collapse. Sometimes a parent has remained within while I inserted a lighted electric bulb and a mirror to examine the eggs or young. Yet I have never seen a jacamar threaten an intruder or give a distraction display. Even when, as earlier recounted, a coatimundi passed near the burrow while the male was watching, he made no attempt to deflect it. If such an animal had come so close to the eggs or young of a ground-nester like the Pauraque *Nyctidromus albicollis*, the parents would doubtless have grovelled in front of it in an effort to lure it away, as I saw a pair do when an opossum approached their eggs. In their failure to attempt either to drive or to lure an intruder from their nest or their fledglings, jacamars agree with the other burrow-nesting birds that I have studied. In the whole order Piciformes, distraction displays have rarely been recorded and are perhaps never well developed.

SUMMARY

In Costa Rica, the Rufous-tailed Jacamar inhabits both humid second-growth and primary rain forest, from sea level up to about 3,000 feet. It subsists upon insects, including many large butterflies and dragonflies as well as numerous glittering beetles, all of which it catches on the wing.

The search for nest-sites begins in the dry month of February; eggs are laid from late March until June; and the latest young fledge in July. Both sexes dig the nest burrow in a roadside bank, side of a gully, or the vertical wall of clay raised up by a great uprooted tree. At this time the male often feeds his mate. Burrows range from about 12 to 16 inches in length, are straight or curve more or less to the right, and dilate at the inner end to form a low, unlined nest chamber. The same burrow may be used in successive years.

About ten days elapse between the completion of a burrow and the start of laying. The pure white eggs are deposited at intervals of two or more days. In Costa Rica sets of two or three are laid, but farther north in Guatemala two sets of four were found.

The female incubates each night. The male replaces her before sunrise, and throughout the day they change places at intervals of 1½ to 2 hours, sometimes more. The incubation period is 19–23 days.

The nestlings hatch with abundant, long, white down. They are prognathous and have well-developed heel pads. They are very loquacious, calling from an early age and soon delivering beautiful, long trills much like those of the adults. Both parents bring them insects, one at a time; no other food was noticed. The male parent fed feathered nestlings about 2½ times as often as the female. In 25 hours, two nestlings were fed at the average rate of 2·4 times each per hour, but there were great hourly fluctuations. Two young who remained in the nest unusually long finally left spontaneously, without parental urging. The nestling period varies from 20 to 26 days and is longest for late broods.

Jacamars wholly neglect the sanitation of their nests. They fail to give threat or distraction displays when a man or a small native mammal approaches their burrow.

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