

LIFE HISTORY OF THE KEEL-BILLED TOUCAN

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TOUCANS are among the most characteristic birds of tropical America, and for well over a century they have probably been depicted, in drawings and words, more frequently than any other neotropical family except hummingbirds. Yet even today there is a dearth of information about their habits, especially their nesting. Beebe (Beebe et al., 1917) described the nests, eggs, or nestlings of several toucans of British Guiana. Van Tyne (1929) made a careful study of the breeding habits of the Keel-billed Toucan (*Ramphastos sulphuratus*) in Panama, but his observations were cut short by the destruction of the nestlings. Wagner (1944) published notes on the breeding of the Emerald Toucanet (*Aulacorhynchus prasinus*) in southern Mexico. Apparently the earliest account of all stages in the nesting of a toucan, from laying to the departure of the nestlings, was my life history of the Blue-throated Toucanet (*A. caeruleocularis*) (Skutch, 1944). Important details of the nesting of this small highland toucan were added in a later account (Skutch, 1967). Observations on the breeding and general behavior of two species of middle-sized araçari toucans were recorded in another paper (Skutch, 1958).

The present contribution to the natural history of toucans is based largely upon studies made at Finca "La Selva" in 1967 and 1968. This property, largely covered by primeval rain forest but with extensive river-side plantations of cacao, lies along the left bank of the Río Puerto Viejo just above its confluence with the Río Sarapiquí, a tributary of the Río San Juan in the Caribbean lowlands of northern Costa Rica. Slud (1960) has well described the lofty, epiphyte-burdened forest with an undergrowth consisting largely of small palms, and given an account of its avifauna remarkably rich in species.

Including their enormous bills, adult Keel-billed Toucans (which in other writings I have called Rainbow-billed Toucans) range from about 17 to 22 inches in length. Even without the many-hued bill, this toucan with contrasting areas of white, yellow, red, and black would be a spectacular bird; attached to a boldly patterned body, the delicately tinted bill makes it one of the most colorful inhabitants of the Central American forests. In the southern race (*R. s. brevicarinatus*), the greater part of the swollen upper mandible is yellowish green; there is an elongated patch of bright orange along the basal half of its cutting edge; and the terminal fifth (approximately) is dull red. The lower mandible is green at the base, then light blue, then dull red on approximately the terminal eighth. Both man-

dibles are marked with a few short, widely spaced, dark, vertical bars. A narrow black border outlines the whole bill at the base. The bare skin surrounding the dark eye is pale green. The legs and toes are blue-gray. Males average larger than females, especially in the size of the bill, but their measurements overlap. While in some pairs the difference in size is great enough to permit their recognition in the field, in the pair whose nesting we followed (and to which the above description of the colors of the featherless parts applies) we detected no difference between the sexes.

The Keel-billed Toucan ranges from southern Mexico to northern Colombia and extreme northwestern Venezuela. An inhabitant of humid forests, in Central America it occurs chiefly on the wetter Caribbean side. In northern Costa Rica, where the continental divide is low, it is found in the forests of the Pacific side, where the dry season is severe, especially if these forests are kept verdant by a high water table. But in the southern part of the Pacific slope of Costa Rica, separated from the Caribbean littoral by the high Talamancan range, this toucan was absent from the heavy evergreen forests that until recently covered most of the Térraba Valley and the Golfo Dulce region. Yet 30 years ago these forests supported a flourishing population of the Chestnut-mandibled Toucan (*Ramphastos swainsonii*), whose requirements are much the same. That competition from its slightly larger congener was not the cause of the Keel-bill's absence from this region is attested by the fact that on the Caribbean side of Costa Rica and Panama the two species live in harmony, sometimes nesting close together. Altitudinally the Keel-billed Toucan ranges from sea level up to about 4,000 feet in Costa Rica and to 5,000 feet in the Santa Marta region of Colombia (Todd and Carriker, 1922: 233).

From the forests that are their true home, Keel-billed Toucans venture into neighboring areas with scattered tall trees—shaded plantations of cacao or coffee, pastures, second-growth woods—to forage and sometimes even to nest. On these excursions one has opportunities to study their social organization and manner of flight such as he seldom enjoys in the midst of the forest. They travel in small parties of up to a dozen individuals, rarely more, that exhibit none of the closely coordinated maneuvers of a flock of parrots or pigeons. When one takes wing, its companions linger behind, as though debating with themselves whether to follow. Then, one after another, they straggle along, single-file, behind the leader. Each takes a number of rapid wingbeats, then completely closes its wings, whereupon it begins to fall, as though borne downward by its great, forward-pointing beak. Immediately the black wings are spread widely again, converting the fall into a glide with a slight downward inclination, which is followed by a series of rapid beats that recover the lost altitude. Thus

the toucan traces an undulatory course from treetop to treetop. The sudden opening of the wings imparts to the toucan's flight its peculiar character, in keeping with the whole aspect and behavior of the bird, not so much grotesque and ungainly as unexpected, an artist's fantasy come to life in flesh and feathers. Clumsy in appearance, something of the avian clown, the toucan is sufficiently agile to meet all the demands of its arboreal life, hardly impeded, and perhaps often aided, by its seemingly heavy bill, which is actually a light hollow shell of horn strengthened by an interior network of thin bony rods.

On Barro Colorado Island in the Canal Zone, where this toucan was abundant, Van Tyne (1929: 16) found four breeding pairs resident in an area of one-sixteenth of a square mile.

FOOD

Toucans are among the most frugivorous arboreal birds of the tropical American forests. In addition to a number of unidentified fruits, I have seen the Keel-bill eat the green fruiting spikes of *Cecropia*; white objects that were probably seeds of *Inga* or *Protium* enclosed in soft coats; and the little hard seeds of *Alchornea costaricensis*, thinly covered by a digestible red aril. These last it shared with at least 23 other kinds of birds, including oropendolas, trogons, woodpeckers, tityras, flycatchers large and small, colorful little honeycreepers, and a variety of tanagers and finches. Van Tyne (1929: 21) gave a list of eight species that he believed included most of the important food plants of this toucan on Barro Colorado Island. Among them are two palms, *Astrocaryum polystachyum* and *Iriarteia exorrhiza*; a fig, *Ficus* sp.; the trees *Virola panamensis*, *Protium sessiliflorum* and *Cupania Seemanni*; and the liana *Cnestidium rufescens*. The palms and the fig provide edible fruits, but the other three trees and the vine have capsulate fruits with arillate seeds, which alone would supply nourishment to the toucans, as in the case of *Alchornea*. On the same inland island, Chapman (1929: 50-53) watched Keel-billed Toucans eating many of the small, hard berries of the mangabé (*Didymopanax morototoni*), a tall tree of the aralia family.

Keel-billed Toucans supplement their frugivorous diet with a small amount of animal proteins in the form of insects, spiders, and an occasional small lizard or snake. Doubtless, like others members of their family, they are not above devouring the nestlings of other birds on occasion. While I have not such definite evidence for this as I have in the case of certain other toucans, I once watched a Keel-bill behave in a most incriminating fashion. The bird clung to the twig from which a Royal Flycatcher's (*Onychorhynchus mexicanus*) nest hung above a wood-

land stream in Guatemala and pulled at the long, pensile structure as though searching for something. But the nest was already empty.

Although a long bill may help a bird to reach food, it creates a problem when it comes to swallowing, as is true of birds so diverse as tiny, slender-billed hummingbirds and big, swollen-billed toucans. The latter solve the problem by seizing the food in the tip of their bill, then giving the head an upward jerk and at the same instant opening their mouths, thereby tossing the berry or other item back between the parted mandibles into the throat. Once, while watching a nest, I witnessed an amusing display of this habit. A parent arrived with a white seed for its nestling in the tip of its bill but hesitated to deliver it in my presence. Perching nearby, it threw the seed back into its throat, probably swallowing it, then immediately brought it up into the tip of its bill again. It repeated this whole performance 23 times more, then flew away visibly carrying the seed.

On another occasion, a parent hesitating to take a large insect to the nest alternately held it beneath a foot and took it back into its bill, the whole while calling loudly. Holding things beneath a foot is, of course, a habit witnessed in only a minority of arboreal birds, but it seems to be general in the toucan family. I have watched a Fiery-billed Araçari (*Pteroglossus frantzii*) hold food in this manner while pulling off small pieces.

One morning in April on Barro Colorado Island, I watched a pair of Keel-bills in the top of a high tree. One held a bright red fruit in the tip of his multihued bill and offered it to his companion. The latter, evidently not hungry, moved away without accepting it, but the first followed and persisted in presenting it. Finally the second toucan took the berry in her bill, apparently only to free herself of the importunities of the first, for in a minute she dropped the brilliant object to the ground. This was apparently an instance of nuptial feeding, which I have seen also in the Chestnut-mandibled Toucan, the Fiery-billed Araçari, and the Blue-throated Toucanet.

VOICE

Toucans as a family are far from being melodious, and the present species is no exception. Even when compared with some of the trogons, motmots, and jacamars, it is a poor vocalist. Its harsh notes, which have been compared to the croak of a frog, are often repeated so rapidly that they seem mechanical; the sound effect is much like that produced by winding a cheap clock. Years ago, I tried to paraphrase the notes of some Keel-bills that I heard "singing" in the forested foothills of northern Honduras. "Quenk quenk quok quok" they began, the notes sometimes so guttural that they resembled the croaking of a distant bullfrog, at other times higher-pitched and shriller. Little by little the toucans warmed up

to a continuous "quenky quenky quenky quok quok quok," achieving a certain elementary rhythm and winning admiration for their whole-hearted effort if not for their voices. At a distance, a chorus of toucans reminded me strongly of a spring chorus of frogs in a woodland pond in the North.

The Keel-bills' vocabulary is extremely limited. In Costa Rica I could detect no difference between the notes they poured out interminably, protesting our intrusion at their nest, and those they used when "singing" unperturbed. While calling or singing, they throw their heads and great brilliant bills up and down and from side to side, restlessly bowing and turning. Aside from the croak, this toucan's only utterance appears to be a short, castanetlike rattle, which one immediately assumes to be produced by clacking the mandibles rapidly together, although actually it is a vocal rather than a mechanical sound.

NEST AND EGGS

The first Keel-bills' nest I ever saw was called to my attention by Gordon Orians, who noticed it while making a census of birds on a forested ridge at La Selva. The nest hole, 20 feet up in a smooth, branchless trunk of a living *Pentaclethra macroleoba* tree of moderate size, was evidently created by the decay of a knot rather than made by a woodpecker or any other bird. From an opening only 2% inches in diameter, the roughly cylindrical cavity extended straight downward for about 14 inches. Its nearly smooth walls were almost constantly wet. Fifty feet away, in a trunk of a somewhat larger *Pentaclethra* tree, was another cavity that, outwardly at least, had much the same aspect. Here a pair of Chestnut-mandibled Toucans nested simultaneously with the Keel-bills in both the years we studied them.

When first examined on 5 May 1967, the Keel-bills' nest held a single nestling with pinfeathers just sprouting. This nestling was successfully reared. On 20 March of the following year, this same cavity held four white, roundish eggs, which rested on a mosaic of seeds of various sizes, shapes, and colors, regurgitated by the toucans while sitting. Such a hard substratum for their eggs is characteristic of toucans, which seem never to carry any soft lining into their nest holes. This nest with four eggs was the one that we chiefly studied.

Later at La Selva we found another Keel-bills' nest that was not in the forest, but several hundred yards distant from it among the scattered trees of a cacao plantation. The nest was in the massive trunk of a living burio (*Heliocarpus* sp.) tree, in a cavity evidently resulting from the enlargement by decay of a knot hole in the smooth side of the trunk. The opening was 23 feet up, and the cavity so deep and irregular that only part of the bottom was visible in a mirror when a lighted electric bulb was

lowered inside. On 17 May 1968 this nest contained one or more naked nestlings, probably no more than 2 weeks old.

The only other nests of the Keel-billed Toucan of which I have information are five Van Tyne (1929) found on forested Barro Colorado Island. All were in cavities resulting from decay in large trees, with openings at heights ranging from 9–90 feet above the ground. In the lowest nest, the hollow extended 6 feet below the doorway, so that the eggs rested only 3 feet above ground level—surprisingly low for a toucan. The other four nest holes were 3–16 inches deep. The openings of three of these cavities were only 3¼ inches in diameter, but those of the other two nests were about twice as large. Three accessible nests contained, respectively, 1, 3, and 4 eggs. Van Tyne described the eggs as dull white, “curiously sculptured with irregular pitted grooves extending lengthwise along the egg and becoming most prominent at the large end.” These eggs measured 38–40.5 mm in length by 28–30 mm in transverse diameter. The only date given by Van Tyne is for his first set, which was found on 4 April 1926 and hatched the next day; but he states that on Barro Colorado this toucan breeds only in the dry season. However, nestlings hatched in April would not leave the nest until May, or later; and May is usually a rainy month on Barro Colorado, although rarely so wet as the latter part of the year. At La Selva, where the dry season is uncertain and at best short, Keel-bills must often nest in very wet weather.

Since toucans have very limited ability to carve into even rotting wood, they are dependent upon ready-made holes for their nests. Small and middle-sized species often occupy the nest cavities of woodpeckers, sometimes dispossessing the birds who laboriously carved them. The big species of *Ramphastos* seem to find the holes of even the largest woodpeckers in their territory too small for them and nearly always use natural cavities in living trees. If the cavity has solid walls of living wood, an opening just large enough for the toucans to squeeze through, and sufficient depth, its contents may be inaccessible to large and medium-sized arboreal mammals, such as ocelots, tayras, coatimundis, raccoons, and most monkeys; while squirrels and other quadrupeds small enough to enter may be held aloof by the toucans themselves. Cavities that meet all these requirements are by no means plentiful in the forest, and their scarcity may, as Van Tyne suggested, limit the population of the larger toucans. Once found, a first-class nest cavity appears to be occupied year after year. A month, or even 6 weeks before laying begins, the toucans take possession of it, remain close to it much of the day although they do not sleep in it, clean out the rotten wood and debris that have accumulated in the bottom, and almost daily carry in small green leaves, which are removed when they

wither (Van Tyne, 1929: 26). Doubtless it is thanks to the possession of a first-class cavity that our pair of Keel-bills succeeded in rearing young in both seasons we watched them.

INCUBATION

At La Selva, where the birds had little experience of man and his destructive habits, most kinds, from antbirds, tanagers, and finches that nested in trees to motmots and nunbirds that raised their families underground, could be watched carrying on their domestic activities without concealing themselves. An outstanding exception was the toucans, whose nests seemed safest of all; to watch them a blind was indispensable. Indeed, even this was not adequate, and we found it advisable to camouflage the brown cloth of the blind with palm fronds. Despite this precaution, the Keel-bills were distrustful, probably because they detected the lenses of our binoculars shining through the narrow aperture in the cloth. As the nestling grew up, the parents became increasingly reluctant to approach their nest in front of the blind; our repeated visits of inspection seemed to have made them more than ordinarily shy and suspicious. Finally we abandoned the attempt to watch the parents attend the nestling. The blind had been set on the ground about 25 feet from the nest; if we had placed it farther off, which was desirable for observation through field glasses, it would have been necessary to cut away much of the foliage that screened and protected the nest in order to have a satisfactory view of it.

On 28 March 1968, a day of intermittent showers and little sunshine, such as was typical of the weather at this period, we watched this nest from 06:10 until 17:10, when the light in the forest was growing dim beneath a heavily clouded, menacing sky. In this interval of 11 hours we timed 14 full sessions, by both parents, ranging from 4 to 86 minutes and averaging 32.9 minutes. The 12 intervals of neglect that were timed in full ranged from 2 to 44 minutes and averaged 14.7 minutes. The longest sessions, 86 and 60 minutes, came in the early afternoon; the longest interval of neglect, 44 minutes, in the early morning. The eggs were attended for 70 per cent of the 11 hours.

The toucan coming for a turn on the eggs arrived through the treetops. Alighting high above the nest, it usually called for a while, then climbed down a stout liana that hung in a loop beside the trunk of the nest tree. The horizontal portion of the loop passed a few inches in front of the doorway and provided a convenient perch for entering. Resting here, the toucan would turn its head from side to side, looking suspiciously all around. Then it would stick its great beak and head through the doorway, peering into the dark cavity, only to withdraw them and look around again. Often the wary bird did this repeatedly. Sometimes, for no apparent reason,

unless it were distrust of the innocuous blind, the bird would fly away again, but often it would enter after one or more of these inspections. It could barely squeeze through the narrow aperture.

Sometimes, after sitting for a while, the toucan would stick its head through the doorway, look out for a few minutes, then go down inside again. Once, after incubating for only 6 minutes, the parent left the hole, returned 4 minutes later, remained with the eggs another 4 minutes, then emerged and disappeared. This was the only time that we saw the same bird take two consecutive turns on the eggs; but it may have happened on other occasions, when both partners were out of sight between sessions. Sometimes a parent came, looked into the hole, found its mate sitting there, then went away, leaving the other within. Once the incubating bird left when its partner looked in, and then the latter, instead of taking its turn on the eggs, flew away, too. We witnessed only two changeovers in the course of the day, and both times the sitting partner came out of the hole before the other entered; the two were never within together. The departing bird would climb up the liana until lost to view amid the foliage, then fly away. One session was ended when a troupe of white-faced monkeys (*Cebus capucinus*), foraging noisily 50 yards from the nest, knocked down a dead branch that fell with a loud crash. After vanishing, this toucan or its mate came into view and scolded the monkeys with its usual clock-winding sequence of croaks.

On the following morning, when the eggs were on the point of hatching, watch was kept from 05:50 until 09:45. The toucans appeared even more nervous and suspicious than on the preceding morning, and neither entered until 06:41, when one went in and sat for 109 minutes. After its departure, the eggs were neglected for only 8 minutes, then a parent entered and was still within when the watch was ended 67 minutes later.

Although these Keel-bills appeared distrustful of the blind during the early hours of 28 March, for the rest of the day they seemed to ignore it, and the record we made doubtless gives a true picture of their mode of incubation. Nervous and restless, toucans are for their size surprisingly inconstant sitters. Many a far smaller bird, including those as tiny as manakins, takes longer sessions and, alone, keeps its eggs much more constantly covered than a pair of toucans sitting alternately. Van Tyne (1929: 28) found Keel-bills taking sessions of from 20 minutes to an hour. The session of 109 minutes (nearly 2 hours) on the morning of 29 March is the longest that I have recorded for any toucan. The next longest was a session of 102 minutes by a Fiery-billed Araçari (Skutch, 1958); the third longest the 86-minute session of a Keel-bill; and the fourth longest an 81-minute session by a Blue-throated Toucanet (Skutch, 1944). This

pair of toucanets kept their eggs covered for 73.9 per cent of 6 hours, and a different pair for 78 per cent of 13½ hours (Skutch, 1967: 56). A pair of Fiery-billed Araçaris did so for 63.6 per cent of 8 hours. The record of our pair of Keel-bills, 70 per cent of 11 hours, is about normal for a toucan.

The incubation period of the Keel-bill is unknown. The only determination of the incubation period of any toucan I know of is one that I made long ago for the Blue-throated Toucanet. In this small toucan incubation took 16 days.

THE NESTLINGS

When we looked into the Keel-bills' nest on the afternoon of 30 March, three nestlings had hatched since the morning of the preceding day. They greatly resembled newly hatched woodpeckers. Their pink skin was utterly naked. Their eyes were tightly closed. The lower mandible of their short bill was slightly longer than the upper mandible. Around each heel joint was a ring of light-colored projections, which fitted over, and seemed to grasp, some of the smaller seeds in the pebbly floor beneath the nestlings. They kept up an almost continuous, sharp, squeaky buzz, much like that of recently hatched woodpeckers. While their nest was electrically lighted, they moved around a good deal. At times one tumbled on its back, legs waving in the air, but it promptly righted itself. The empty shells had already been removed.

The following afternoon, despite our intentionally noisy approach, a brooding parent stayed in the nest until we set a ladder against the trunk. Before the eggs hatched, the incubating toucan, always alert, would leave before we reached the base of the tree with the ladder. After abandoning its nestlings, the parent flew silently away and remained out of sight the whole time we were present, neither protesting our intrusion nor making feints of attack, as many a smaller bird has done in similar circumstances. When we looked into the hole, the nestlings, without interrupting their squeaky buzz, stretched up their open mouths, revealing an interior colored just like the outside of the body. After this exhausting effort, they sank down huddled together. Their prominent uropygium served as a third point of support, along with their spiked heels. Their weak feet appeared to be useless appendages of the relatively stout legs terminating in well-developed heels (the joint between the tibiotarsus and the tarsometatarsus).

The fourth egg failed to hatch, and after remaining in the nest for more than 10 days it disappeared, probably removed by a parent toucan. Before they were 4 days old, two of the nestlings vanished without a trace. Perhaps the parents had been unable to attend them adequately in the very wet weather that had prevailed since they hatched. In the preceding year,

also, there had been only a single nestling when we first looked into the hole after a rainy period. Van Tyne (1929: 29) recorded that the unusually rainy season finally destroyed the nests that he had under observation in 1927.

Development.—As long as it remained in the nest, we continued to visit the surviving nestling at intervals of 3–5 days, making notes on its development. Our examinations were made by lowering into the cavity an electric bulb attached by a cord to a flashlight and inserting a mirror through the doorway. Although by this procedure we doubtless missed details that would have been evident had we taken the nestling in hand, I did not wish to jeopardize it by enlarging the narrow doorway or cutting a replaceable slab from the wall of the nest. Above all I wanted to learn the full length of the nestling period, which seemed never to have been done for any of the larger toucans. Perhaps I can best convey the extremely slow development of the young toucan by giving a selection of the notes made after each examination:

7 April. 8 days old. Except that it is bigger, the nestling has changed little since it hatched.

10 April. 11 days old. Except that it is much bigger, the blind, naked nestling looks much as it did when newly hatched. Its abdomen has become relatively enormous. The only feather rudiments I can detect are those of the rectrices, which project possibly one millimeter from the long uropygium. The nestling seems to lie much of the time with its head on the floor, sideways. (At this age, many small passerine birds are feathered and leave the nest.)

13 April. 14 days old. The nestling grows rapidly but is still quite pink and naked. The rudiments of the rectrices are a little longer, and a darkening on the wings appears to be caused by the buds of the flight feathers. The eyes are still closed. The bill is becoming big, and the upper mandible is now as long as the lower.

16 April. 17 days old. The nestling's eyes are partly open (but see under 29 April, beyond). The rudiments of body feathers are visible as dark points beneath the pink skin. The young toucan seems to lie most uncomfortably on its pebbly bed of decaying seeds, its head fallen over to one side. It still makes a squeaky buzz, which at times increases to a loud cry, somewhat like the wail of a human baby. It is especially likely to wail as the electric light is withdrawn from the nest (which might simulate the darkening of the hole as a parent coming with food fills the doorway). There is no accumulation of excrement, but an unpleasant odor of decay emanates from the damp cavity. (At this age the smaller trogons, which are also hole-nesting birds, are ready to fly or have already taken wing.)

21 April. 22 days old. The nestling is still naked, but its skin has darkened. The pins of its body and wing feathers barely project from it. The bill, a light horn-color, is at least as long as the head, and the round nostrils on its base, at the top, are conspicuous. The legs and toes have become dusky. It rests upright with less difficulty than formerly, on its heels and abdomen, with its long, prominent uropygium turned upward. The nestling kept its eyes closed the whole time its nest was illuminated.

25 April. 26 days old. The pins of the nestling's contour feathers project a few millimeters. Those of the remiges have become conspicuously long and are leaden blue

in color. The young toucan kept its eyes closed while its nest was electrically illuminated. At intervals, especially when we moved the light or made a noise, it moved abruptly, making loud, hollow thuds by striking its heels against the floor of the nest, on which the moldering seeds and other debris appear to have become compacted into a solid layer. Might not these knocks serve to frighten an intruder, like the hisses of titmice and certain other hole-nesters? (At this age even the larger trogons have flown from their holes, and the smaller motmots from their deep burrows.)

29 April. 30 days old. For the first time, the nestling had its eyes wide open, and kept them so the whole time that I looked into its lighted nest. It crouched down as though in fear. On its wings both the remiges and coverts are rapidly expanding from the ends of their sheaths. The body is still largely naked, the dorsal feathers just protruding from the ends of their short sheaths. There is a crest of pinfeathers along the top of the head, but the rest of the head is quite naked. The pale bill has become conspicuously keeled. The nestling moved with a thumping sound only once, and could not be induced to repeat this. It seemed to be intimidated by the electric light and perhaps the sight of my eyes reflected from the mirror above it. (At this age the larger motmots are ready to fly from their burrows, and many woodpeckers to leave their holes.)

2 May. 33 days old. The nestling is at last becoming feathered. It is largely black above, and yellow is appearing on its breast. The feathers on its crown are expanding, but its cheeks are widely bare. The bill is becoming darker, with an orange tip. The feet are now blackish. The nestling seemed curious rather than afraid, looking up at the mirror with wide-open eyes. At times it moved with the thumping sound.

6 May. 37 days old. The nestling is now decently clad. The red border between the yellow chest and black abdomen has become visible, and white is appearing on the rump. The rectrices, which were the first feathers to break through the skin, are at last expanding, after most of the others. The nestling made no vocal sound while we were at the nest, but sometimes it moved noisily. (At this age even the big Ringed Kingfisher (*Ceryle torquata*) has flown from its deep burrow.)

9 May. 40 days old. The nestling remained silent while we looked in. Its tail was turned up, and we could see that its under tail coverts were red, as in adults.

12 May. 43 days old. Our last visit to the nestling in its hole found it still within. To avoid causing premature departure, we did not again climb to the nest until after the young bird had flown.

15 May. 46 days old. For the first time, the nestling was seen looking through the doorway. It was shy and drew back inside when it found itself observed.

17 May. At dawn the nest was empty. The young toucan had evidently flown during the preceding afternoon, at the age of 47 days. (This is the age at which Common Potoos (*Nyctibius griseus*) first fly from the end of the exposed stub where they hatched.) On the bottom of the nest hole were decaying seeds and rotting fragments of wood, but no droppings and no maggots—in sharp contrast to the nests of trogons and motmots and puffbirds when their young leave. Parent toucans carry billfuls of waste from their nests.

The single nestling raised in this nest in the preceding year stayed within to a still more advanced age. When first seen on 5 May, its pinfeathers were sprouting, which would make it no less than 20 days old, according to the schedule of development just given. It left on 9 or 10 June, when, according to this reckoning, it was about 55 days old. Al-

though in 1968 the nestling was first seen looking through the doorway only the day before it left, in the preceding year the young toucan was seen looking out 4 or 5 days before it flew. Unlike its successor, it was not shy and remained with its head and shoulders projecting from the orifice while I approached and stood below it, in full view. It looked down at me with apparent interest. During the few minutes that I watched, the young toucan regurgitated four large seeds, apparently of *Virola*, letting them fall outside the nest. Each act of regurgitation was preceded by opening and closing the bill several times. As a parent approached with food, the young bird repeated a whining note, then withdrew into the cavity. Its bill, approaching that of the adults in size, was pale greenish yellow, narrowly tipped with orange. The bare skin around its brown eyes was pale green. Its head looked much too big for its neck, and its crown feathers were still partly ensheathed.

The brood of Keel-billed Toucans Van Tyne studied was taken from the nest by some predator when 36 days old. From their known rate of growth and the measurements of young collected immediately after leaving the nest, he estimated that his brood would have remained in the nest 10 days longer, to leave at the age of about 45 days. I believe that even 47 days must be regarded as a minimum nestling period for this big toucan. When I approached the nest tree on the second young toucan's last afternoon in the cavity, the parents, as usual, became greatly excited, and possibly they were responsible for its departure after I walked away. In the preceding year, when we climbed to the nest only once, before the nestling was feathered, and all other observations were made from the ground, the parents had fewer alarming experiences of us. Probably for this reason they permitted their nestling to remain longer. The nestling period of the much smaller Blue-throated Toucanet is 43 days; and Collared Araçaris (*Pteroglossus torquatus*), intermediate in size, remain in the nest for about 43 to 46 days.

Parental care.—On the rainy morning of 4 April, when the single surviving nestling was 5 days old, we watched from the blind from 05:53 until 11:22. The naked nestling was brooded only three times, by both parents, for intervals of 38, 13, and 41 minutes. Six times the parents came with food visible in their bills. Five of the items were fruits or arillate seeds, and the sixth was an insect. Probably on these visits additional pieces were carried in the throat or deeper inside, to be brought up after the article in the bill had been delivered to the nestling. It was evident, however, that already fruits and seeds had become the nestling's principal fare, as they continued to be throughout the nestling period.

After another 2 weeks, the parents had become so distrustful that they

could no longer be profitably watched from the blind. Whenever, arriving with food, they found us standing near the nest, or on the ladder looking in, they perched in the treetops high above us and continued interminably to complain—"winding their clocks," as my young helper said. Sometimes it was evident that the voice of one was pitched higher than that of its mate. I have already told how sometimes, in these circumstances, the parent would alternately swallow and disgorge a seed many times over, or restlessly shift an insect between its bill and a foot. Never did one come near to threaten us by clacking its great bill, or dart menacingly past us. Although they seemed greatly distressed when their nest was disturbed, they did not once jeopardize themselves to protect their young: self-preservation came first. Even after we walked away, they would sometimes continue for many minutes to complain, their voices carrying far beyond any possible range of vision in the thick forest. They had such keen eyesight and were so wary that they would never go to their nest even when, screened by the undergrowth, I watched at a distance of 50 yards.

Although daytime brooding was soon abandoned, a single parent spent the night with the nestling for most, if not all, of its stay in the nest. On the morning of 9 May, the parent slept late. When no adult had appeared in the doorway by 05:20, when the avian world was generally astir, I supposed that the nestling was alone. To make sure, I clapped my hands, but still no great bill was thrust through the doorway. Even light tapping, and scratching on the trunk, brought no response from this shy bird; but when I hammered hard with the butt of my machete, an adult squeezed out and flew silently away. Undoubtedly I had interrupted its sleep. On our next visit to the nest by moonlight, on 17 May, it was unoccupied, the nestling having flown on the preceding afternoon. Thus a single parent accompanied the young toucan at night until it was at least 40 days old and well-feathered. After its departure, neither parent nor young returned to sleep in the nest.

SLEEPING

The sleeping posture of toucans has often been described from observations on captive birds. They turn back the bill and lay it along the back, bring the tail forward until it covers the bill, and fluffing out their plumage transform their angular bodies into round balls of feathers. Thus they greatly reduce the space they occupy, and it has been widely assumed that this is an arrangement for sleeping in holes in trees. Van Tyne (1929: 20) suspected that *Ramphastos* toucans roost in small flocks in hollow trees, but the only evidence for such a habit that he could adduce referred to *Pteroglossus* (araçaris) rather than to *Ramphastos*. It is certain

that slender araquaris sleep in small groups in holes in trees (Skutch, 1958), but long ago I expressed my doubt that this habit prevails throughout the family (Skutch, 1944). Subsequent observations, including those recorded above, have served only to strengthen my scepticism. In at least two species of araquaris, both parents sleep with the nestlings, and sometimes helpers as well. After the young fly, they and the parents return to roost in the nest cavity. In the Keel-billed Toucan, as in the Blue-throated Toucanet, a single parent sleeps with the nestlings, and after the young take wing the hole is unoccupied. An ounce of positive evidence is worth a ton of negative evidence, but all of the latter that is available to me points to the conclusion that *Ramphastos*, like *Aulacorhynchus*, roosts amid the foliage.

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SUMMARY

The Keel-billed Toucan inhabits the forest, from the lowlands up to 4,000 or 5,000 feet above sea level, and makes frequent excursions into nearby clearings and plantations with scattered tall trees. It travels in small, straggling parties, tracing an undulatory course in flight.

This toucan varies its largely frugivorous diet with insects, spiders, and an occasional small lizard or snake. The food, seized in the tip of the long, brightly-colored bill, is thrown back into the throat by an upward toss of the head. Food is sometimes held beneath a foot while it is pulled apart. At times a toucan feeds its mate.

The toucan's call, or song, is a froglike croak which it delivers while tossing its head simultaneously up and down and from side to side. With a very limited vocabulary, the toucan protests intrusion at its nest with notes hardly distinguishable from its "song." A castanetlike rattle, that seems to be produced by clacking the great mandibles together, is actually a vocal sound.

In northeastern Costa Rica, this toucan was found nesting from March to June, in weather that was often very wet. The nest chiefly studied was 20 feet up in a smooth, branchless trunk of a living tree in the midst

of the forest. The nest chamber, apparently formed by the decay of a knothole, was a roughly cylindrical cavity 14 inches deep, with a doorway barely wide enough for the parents to squeeze through. A single nestling flew from this cavity on 10 June 1967, and in mid-March of the following year it again held eggs. Another nest was 23 feet up in the branchless trunk of a shade tree in a cacao plantation several hundred yards from the forest.

The Keel-billed Toucan lays three or four, dull white, unmarked, lustreless eggs, which rest on a bed of regurgitated seeds.

Both parents incubate, sitting very impatiently and often leaving their eggs unattended. Fifteen sessions ranged from 4 to 109 minutes, but those longer than three quarters of an hour were rare. One pair, watched nearly all day, kept their eggs covered for only 70 per cent of 11 hours.

In the nest chiefly studied, three of the four eggs hatched, but after four days only one nestling remained. Possibly the other two succumbed in consequence of very wet weather.

Newly hatched nestlings are quite naked, with tightly closed eyes and lower mandibles that slightly exceed the upper in length. The heel joint is protected by a ring of spikelike projections.

The single surviving nestling developed with extreme slowness. Still practically naked at the age of 3 weeks, at 5 weeks it was feathered, much in the pattern of the adults. The bill grew slowly: 3 weeks after hatching it was about as long as the head, and when the nestling left the hole it approached that of the adults in size but was more plainly colored.

The adult toucans were so excessively wary that it was difficult to study parental care, even from a blind. They fed the nestling chiefly on fruits and arillate seeds, with occasionally an insect. Although they failed to carry away the seeds they had regurgitated while incubating, they removed all the nestling's droppings and kept the nest cavity clean. Diurnal brooding soon ceased, but a single parent slept with the nestling until it was at least 40 days old.

The nestling raised in 1968 left the hole when 47 days old, possibly having been induced to depart by its parents, who had become extremely nervous as a result of our periodic visits. In the preceding year, when the nest was more rarely visited, the nestling evidently left at an even more advanced age.

After the nestling's departure, neither the parent nor the juvenile slept in the nest hole. Although it is well established that middle-sized toucans of the genus *Pteroglossus* sleep several together in holes, observations on the roosting of *Ramphastos* seem to be lacking. Indirect evidence indicates that these large toucans sleep amid the foliage.

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