

LIFE HISTORIES OF HERMIT HUMMINGBIRDS

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Most hummingbirds spend much time in sunshine, either in the upper levels of woodland or in open or semi-open country of various sorts, and they have developed the glittering plumage for which their family is famous. A few, however, inhabit the depths of tropical woodland where only stray sunbeams penetrate. A number of these shade-dwellers have been called "hermits," not because they are less sociable than other hummingbirds, but because of their modest attire, in which browns predominate. Usually they have long bills, and often also long tails. In an earlier paper (Skutch, 1951) I gave an account of one of these shade-dwelling hummingbirds, Longuemare's Hermit, now frequently called the Little Hermit (*Phaethornis longuemareus*). The present paper includes additional information on this species, but it is mainly devoted to the related Long-tailed Hermit (*P. superciliosus*). A shorter account of the habits of the Green Hermit (*P. guy*) is also given. Finally, there is a brief section on the Band-tailed Barbthroat, also known as Rucker's Hermit (*Threnetes ruckeri*), whose nest I have never seen, but which I include because of its wonderful song.

LONG-TAILED HERMIT

The Long-tailed Hermit (*Phaethornis superciliosus*) is a large, generally brownish hummingbird about six inches long. In both sexes, the top of the head is dusky brown. The back, shoulders, and lesser wing-coverts are dull metallic bronze-green; the rump and upper tail-coverts buff or clay color with dusky bars. The long, narrow, terminal portion of the two central tail feathers is mostly white, whereas the broader basal part of these feathers is largely blackish, as are the much shorter lateral rectrices. Above and behind each eye is a broad streak of dull white, bordered below by a dusky band that covers the lores, cheeks, and ears. The chin and throat are brownish buff with a broad median stripe of pale buff. The remaining underparts are dull grayish buff, becoming whitish on the abdomen. The upper mandible of the remarkably long, conspicuously curved bill is largely black and the lower mandible is yellowish.

This easily recognized hummingbird ranges through the more humid lowlands from southern México to Bolivia, Brazil, and the Guianas. On the Pacific slope of southern Costa Rica it extends upward to somewhat over 3,000 feet above sea level. It is primarily an inhabitant of the lower stories of heavy rain forest, whence flowers rich in nectar entice it forth into neighboring thickets, plantations, and gardens. Like other hummingbirds, it is essentially solitary, although several males gather in the same area to compete for the females. One most often notices it hovering be-

fore a blossom on wings beating too rapidly to be seen. Among its favorites are the long, tubular flowers of wild plantains (*Heliconia* spp.), which are indigenous throughout its range, and those of the related bananas (*Musa*), of Old World origin but now widely planted in the American tropics. In a banana plantation near humid woodland, one is almost certain to see some of these graceful hummingbirds poised beside the great, dangling, red flower buds, thrusting their bills upward into the serried white flowers beneath an upturned bract.

The Long-tailed Hermit (along with the Green Hermit where it occurs) has almost a monopoly of the nectar richly secreted by the great scarlet passion flower (*Passiflora vitifolia*), whose complex structure prevents access to the floral nectaries by species with shorter bills, including the Little Hermit. The latter often visits these flowers to sip nectar from the glands on the bracts, or to gather small insects attracted to them; but I have not seen it try to reach down through the narrow collar to the floral nectaries; and it does not get its dark head dusted with pale pollen, as does its larger relative, which carries this pollen to other passion flowers. Although the vine which produces these flamboyant blossoms climbs well up into the trees of light woodland and the forest's edge and thus into areas of brilliant light, the flowers themselves are borne in the shaded areas near the ground on special, nearly leafless, whip-like shoots, and this low blooming may be an adaptation to secure the services of this low-ranging hummingbird as a pollinator. From one group of passion flowers a Long-tailed Hermit was chased away by a big Violet Sabre-wing (*Campylopterus hemileucurus*) who took possession of them (Skutch, 1952). The Long-tailed Hermit does not, however, confine its attention to those larger and more spectacular blossoms for which it is specially adapted. Small flowers, if abundant, often attract it.

As do several other forest hummingbirds, the Long-tailed Hermit often bathes in a still reach of a sylvan stream, half immersing itself in the limpid water by dipping down in hovering flight. After one or more partial immersions, it may perch on a neighboring twig and shake the water from its plumage, including its long tail, which is twitched from side to side so rapidly that it becomes a blur of white and brown, almost as invisible as the hummingbird's wings while it hovers.

In the manner of other brown hummingbirds of the woodland shade, including the Little Hermit and the Band-tailed Barbthroat, the Long-tailed Hermit often closely inspects an intruding human. But the behavior of one of these hermits at the Lancetilla Experiment Station in Honduras, many years ago, was unique in my experience. While I sat at my microscope in a screened room, the hummingbird, who had been probing the pink flowers of coral vine (*Antigonon leptopus*) and the great red

hibiscus blossoms outside the building, flew up and hovered in front of the small opening in the screen through which the microscope received light. After a few moments of close scrutiny of me and my activities, it floated in through the opening for a closer investigation. It poised a few inches above my head, where I could watch its long central tail feathers open and close like scissors as it regulated its position. Its apparent curiosity satisfied, it tried to leave the room by a route higher than that by which it had entered, only to find its exit blocked by the fine wire screen. It flew from side to side of the room, trying to leave at various points, but each time coming gently to rest when it encountered the screen. After several such frustrations, it became excited, and darted wildly around the room, twice dashing against the screen so violently that I feared for its life. I hastened to let down some awnings that would prevent its seeing the outer world through the screen, and while I was so engaged it vanished, possibly having escaped by the opening through which it had entered.

VOICE AND COURTSHIP

When excited or alarmed, the Long-tailed Hermit utters rapid twitters which hardly serve to distinguish it from other hummingbirds. Through much of the year, some of these hermits, evidently the males, sing in the dimly lighted undergrowth of heavy woodland. Each perches within a yard of the ground, where his brown form would be extremely difficult to distinguish from the brown fallen leaves if he did not incessantly wag his white-tipped tail up and down, rhythmically, as though beating time to his notes. Although the courtship songs of some kinds of hummingbirds enchant the attentive listener with their unexpectedly varied movements and miniature melodies, that of the Long-tailed Hermit is of the utmost simplicity. A single squeaky note, incessantly reiterated, seems to be the limit of his vocal attainment. Usually a number of males perch within hearing of each other, cooperating to attract the females for which they will later compete. I have found these gatherings of monotonously squeaking hummingbirds from Honduras to Panamá. In my forest in El General, I have discovered none of them, although I have found several nests. Evidently the females breeding here must fly a considerable distance to the males who fertilize their eggs. In British Guiana, Davis (1958), who calls this species the Buff-browed Hermit, found 32 assemblies, mostly from July to November. A large assembly may cover an area 250 yards (230 meters) in length and contain more than 100 hermits. One assembly in British Guiana was active in the same place for at least 12 years.

NEST AND EGGS

The eight nests of the Long-tailed Hermit which I have seen were in almost identical situations. Each was fastened beneath the drooping tip of a terminal segment of a frond of a small palm that bristled with long, needle-like, black spines. In height these nests ranged from 5 to 8.5 feet above the ground (about 1.5 to 2.5 meters), and all were in the deep shade of heavy forest. Each nest was shaped to fit the tapering, concave end of the palm frond that bore it; it was broadest at the top, in which was the hollow to hold the eggs and young, and it tapered downward to a point; roughly, it had the form of an inverted cone. The apex of the cone was prolonged as a thin, dangling tail, which hung free below the tip of the palm frond. One nest that I teased apart after the eggs vanished was composed of fine rootlets, the delicate branched stems of mosses and liverworts, fibers of various kinds, and similar materials. Most of the components of the nest were stiff and wiry, making it fairly rigid and harsh to the touch. Unlike the nests of many hummingbirds, it contained no soft, downy stuff. But in common with most, if not all, hummingbirds' nests, it was bound together by much cobweb, many filaments of which had been carried around the upper surface of the leaf to fasten the structure firmly to it. The general color of the nest was brown. The over-all length of this nest was 8 inches (about 20 cm), half of which was accounted for by the loose tail. In another nest that was 7 inches long (about 17.5 cm), the tail measured nearly 5 inches. These nests were about 2 inches (5 cm) in total width at the top. The diameter of the opening in the top varied from $1\frac{3}{8}$ to $1\frac{1}{2}$ inches, and the depth of this depression was $\frac{3}{4}$ to 1 inch. In site, shape, and color the nests of the Long-tailed Hermit closely resemble those of the Little Hermit in the same locality, but they may be distinguished by their obviously larger size. The six nests of the Long-tailed Hermit found by Davis (1958) in British Guiana were also attached beneath the tips of drooping leaves, usually palm fronds, but the birds showed no apparent preference for thorny kinds. These nests were from 2 to 5 feet (about 0.6 to 1.5 meters) above the ground in both primary and secondary forest. Unlike the nest which I dissected, they contained silky seed down.

Each of my eight nests contained two eggs or nestlings. In two instances, an interval of two days separated the laying of the first and second eggs, and the latter were deposited early in the morning (in one case, before 0730 hours). The pure white eggs are long and narrow, and both of those in one set measured 15.9 by 9.5 millimeters. In these 8 nests, all in my forest at Quizarrá in the valley of El General, about 2,500 feet above sea level, eggs were laid as follows: January, 1 nest; May, 3; June, 2; July, 1; August, 1.

From May to August appears to be the principal breeding season in southern Central America. For the Canal Zone, Eisenmann (1952: 26) records three nests in these rainy months. In the Caribbean lowlands of Costa Rica, Carriker (1910: 520) found a nest containing two fresh eggs on 9 May 1905. All of these nests were, like those that I have seen, attached beneath the tips of palm fronds. Carriker's nest was unusually low, only about two feet above the ground.

INCUBATION

By skillfully fastening her nest beneath the tip of the arching frond of a forbiddingly armed palm, the Long-tailed Hermit gains several advantages. She and the nest in which she sits are invisible from above and even largely screened on the sides by the back and incurved margins of the leaf tip. The green tissue forms a roof above her and keeps her dry in the hardest rain. Her eggs and nestlings seem to be inaccessible to many kinds of nest robbers. To offset these advantages, the hummingbird must sit in what appears to us such an unnatural, strained posture that we marvel that she can maintain it for as long as five minutes without becoming permanently crippled. She invariably incubates and broods with her head inward, toward the leaf surface to which her nest is attached. Since her bill is so long, she can sit with this orientation only by holding it straight upward, to do which she must throw her head so far backward that her hindhead almost rests upon her rump. Her crown is not far from her long tail, which is held obliquely upward and projects far beyond the free rim of the nest. Her body is bent double, her chest is turned almost straight upward—one cannot watch her for long without feeling sorry for her (Figure 1). One wonders why she does not punch a tiny hole in the tissue of the leaf in front of her, so that she might stick her bill through and sit in a more natural posture.

Doubtless the hermit has no need of our sympathy, for she can maintain this seemingly impossible posture for well over an hour, then dart away as though not a muscle or tendon were strained. An incubating bird whom I watched through the morning of 9 June 1949 took five sessions ranging from 19 to 95 minutes in length and averaging 44 minutes. The longest session came at the end of the forenoon. An equal number of recesses ranged from 4 to 76 minutes and averaged 15.8 minutes. The longest recess came between two sessions of less than average length. The hermit kept her two eggs covered for 63 per cent of the six hours. To extract herself from her narrow quarters when emerging, she unfolded her wings while still sitting on the eggs. Then, beating her wings rapidly, she rose upward and backward until clear of the nest. Next she hovered a moment facing it, reversed, and darted away. Once, while hovering so, she stuck her bill into the nest, apparently to turn the eggs. It was im-

possible for her to turn them while she sat, unless she did so with her feet.

At the end of four of her five excursions, the hermit returned with a contribution for her nest in her bill. When she brought a fiber, she first settled in the nest and then stuck the fiber into the wall beside her. But when she came with cobweb, her procedure was quite different; after almost sitting in the nest, she rose on wing and flew slowly around the tip

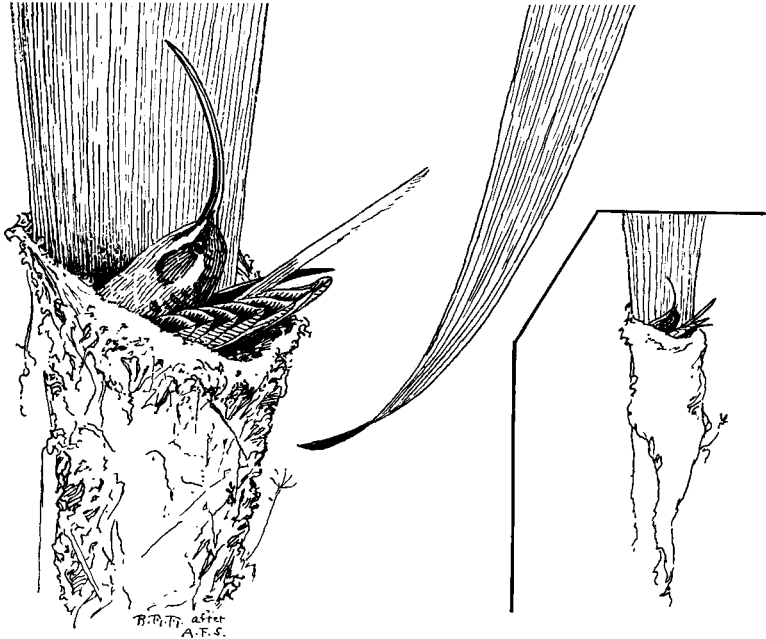


Figure 1. Long-tailed Hermit incubating in nest attached beneath tip of a frond of a spiny palm. Valley of El General, Costa Rica, 18 January 1944. Drawing by R. M. Mengel after a sketch by the author.

of the supporting leaf, facing it. Once she made two consecutive turns around the leaf tip, counterclockwise, then settled on her eggs. By this method she stretched cobweb from the sides of her nest around the outside of the leaf. The constant renewal of this attachment, throughout the period of incubation, prevents the nest from breaking away.

Hummingbirds have very rapid metabolism. They excrete frequently, and they could not take such long sessions on their eggs if it were not possible for them to do so while sitting. From time to time, the hermit rose up in her nest and shot her liquid excreta well beyond its rim, an act always preceded by a good deal of vigorous tail-wagging. Thus she could incubate for long periods yet keep her nest clean. Most birds leave their nests for this purpose.

In the course of the morning, I only once saw a second Long-tailed Hermit. Before sunrise, this hummingbird flew up and hovered all around the nest, almost touching it, while the sitting bird pointed her bill at the intruder. Finally she left the nest and chased the trespasser out of sight, to return in a minute and resume incubation. (This brief absence was not counted as a recess.) I do not know the relation of the second hermit to the nest's owner; perhaps it was just a curious intruder. This interpretation was strengthened as, in the course of the morning, three smaller hummingbirds flew up at different times and inspected the nest much as the second hermit had done, then darted away before I could identify them.

Shortly before I ended my watch at midday, a reddish-brown, black-faced weasel dug into a mound of loose earth close by the blind. Presently a frog jumped, or was thrown, out of the mound. The weasel caught it without much of a tussle, left it, then returned for it and carried it into a hole. The hummingbird continued to sit while all this went on a short distance from her, leaving only when the weasel passed beneath her nest on its way to retrieve the frog.

One nest contained a single egg when found at 0700 hours on 23 August 1950. At 0820 next morning there were two eggs. At 0800 on 10 September there was a single nestling, and by 1650 on the same day there were two nestlings. The incubation period was 17 or 18 days. At another nest it was at least 17 days.

THE NESTLINGS

The nestlings hatch with the dark skin, sparse down, tightly closed eyes, and rudimentary bill typical of newborn hummingbirds. Soon after hatching, each orients itself with its head toward the surface of the leaf to which the nest is attached and its posterior end outward, which is just the position taken by the incubating and brooding parent, and until the young bird leaves the nest it preserves this orientation rather constantly. I have only exceptionally found nestlings otherwise aligned. One day, when the brooding parent flew from week-old nestlings as I approached, I found both of them lying with their heads toward the edge of the leaf rather than toward its middle; their bodies were parallel to the supporting surface of the leaf. They maintained this exceptional orientation for the next 10 minutes. On a few visits, I found these nestlings facing the leaf obliquely. But until the last one flew, they were usually found with their heads directly inward.

On 12 June 1949, I spent the first seven and one-half hours of the day in view of a nest which held two nestlings in pinfeathers. They received their first meal at 0638 on this drizzly morning, and when I left at 1323 they had been fed 11 times, or at the rate of 0.8 visits with food per nest-

ling per hour. I saw nothing to suggest that more than one parent was in attendance. Flying up through the undergrowth of the forest, she would hover beside the nest beneath a palm frond and utter a single *cheep*, which nearly always caused the nestlings to stretch their scrawny necks far upward and open their yellow mouths. To feed them, the parent never alighted on the rim of the nest; on none of her visits did I see her so much as touch it with her feet or any part of her body. She hovered well out from the nest with her feet folded up and invisible, as when she visited a flower, and reached over the backs of the nestlings to insert her long, curved, black bill far down into the mouth and throat of one of them, as though she were about to suck nectar from a corolla tube. But now, instead of drawing in nourishment, she forced it upward and outward, feeding her offspring by regurgitation.

When the parent finished feeding a nestling, she drew slightly away from the nest and dropped a little lower. Since her bill was still in the young bird's throat, this movement bent its head far back toward its tail, in what appeared to be a most uncomfortable and even dangerous posture. After removing her bill from the mouth of one nestling, she might continue to hover before the nest, and by means of a sideward twitch of her long tail deftly effect the slight lateral movement of her body which would place it in precisely the position most favorable for feeding the other nestling. On most of her visits to the nest, both youngsters were given food twice or thrice, alternately. Sometimes one was given three portions and the other only two, but usually both received the same attention. In the middle of the morning, the parent flew up and hovered around the nest as though she had come to feed the nestlings, but they did not as usual raise their heads when they heard the hum of her wings, doubtless because they were not hungry. She did not coax them to eat, as many avian parents do, but perched nearby for a short while, then flew away.

The parent never cleaned the nest. To void, the nestlings raised their hindquarters above the nest's rim and shot their liquid excreta into the air, much as their mother had done while she incubated. Their habitual orientation with their heads toward the leaf and their tails outward is evidently an arrangement for keeping the nest clean. Were they to reverse this orientation, it would soon become foul. Once one of the young hummingbirds rose in its nest and rapidly beat its wings with their still rudimentary sprouting pinfeathers.

Unlike most birds that I have watched from a blind, this female hummingbird seemed to be curious about the contents of the large brown object that had so suddenly sprung up close by her nest. She repeatedly hovered facing a window, her dark, beady eyes only a few inches from mine. The light streak on her brownish throat was balanced by a liberal

deposit of pale yellow pollen on her dark forehead and crown. Her scrutiny of the blind and its occupant completed, she fed her offspring, or rested for a few minutes on a low, slender twig a few yards away.

When about two weeks old, the nestlings are well feathered, but they remain in their swinging home, still facing the supporting leaf, for another week or more. From one nest, the two young departed when respectively 22 and 23 days old. At a nest observed by Davis (1958), the nestling period was at least 23 and possibly as much as 27 days.

It is hard to imagine a safer site for a nest than that which the Long-tailed Hermits choose, yet most of their nests suffer depredations. Of seven nests of which I know the history, only one was successful. Two nests vanished completely, along with the eggs or nestlings they contained. From two other nests, the eggs mysteriously disappeared while the structures remained intact. From one nest, the nestlings were torn away. From another, one nestling vanished and the other remained clinging to the rim, with its body thrown backward into the bowl and blood on its neck. On the following day it too was gone.

What could take these eggs and nestlings? I think that a snake could not reach them, and it would hardly swallow or carry off the nest. A small mammal would almost certainly leave telltale traces in a torn leaf or nest, yet in some instances the eggs or nestlings vanished leaving the nest and its support uninjured. Swallow-tailed Kites (*Elanoides forficatus*) carry away the nests of a variety of small birds and remove their contents while soaring, but these wide-winged predators do not descend beneath the forest canopy. I cannot imagine a clumsy toucan reaching a hermit's nest; moreover, they usually remain higher in the forest. This about exhausts the list of known avian predators in this forest except hawks, especially the little Barred Forest-falcon (*Micrastur ruficollis*) that frequents the lower stories, and an occasional owl. Perhaps the forest-falcon is the culprit, but my suspicion falls on bats. Here is another of the innumerable mysteries which the tropical forest jealously guards.

GREEN HERMIT

The Green Hermit (*Phaethornis guy*) resembles the Long-tailed Hermit in its large size, its long and strongly down-curved bill, and its elongated, white-tipped central tail feathers, but its prevailing color is green instead of brownish. In the male, both the dorsal and ventral plumage are largely metallic bluish green. The female has the whitish, narrowed portion of the two central tail feathers much longer and broader than in the male, and her ventral plumage is grayer. In both sexes, there is a fairly conspicuously tawny or rust-colored streak along the center of the throat.

This hummingbird ranges from Costa Rica to Perú, Venezuela, and

Trinidad. It occurs mostly at higher altitudes than the Long-tailed Hermit, although there is some overlap in their vertical ranges. On the Caribbean slope of Costa Rica it has been found from 1,500 feet (Carriker, 1910: 519) to about 5,500 feet, where I saw it at Vara Blanca in the Cordillera Central. On the less constantly rainy Pacific slope, this hermit seems to stay somewhat higher. Sometimes, especially in rainy spells, it enters our garden at about 2,500 feet, and here it may meet Long-tailed Hermits from the adjoining forest. But the green visitors seem to be wanderers from the higher hills to our north, and I have no record of courtship or nesting by Green Hermits below 3,000 feet on the Pacific slope.

Although their preferred habitat is the dark undergrowth of humid mountain forests, Green Hermits may wander far beyond them in search of the flowers which provide them with nectar and probably also small insects. On our farm they are attracted by the scarlet passion flowers but visit them less frequently than the resident Long-tailed Hermits. Green Hermits also glean spiders and tiny insects from the foliage. One morning, while I stood amid the dense low growth at the forest's edge, one of these birds foraged all around me. Hovering on wings vibrated into a haze, it examined the lower sides of the leaves and plucked things from them. Once it poised so close that it nearly brushed my face with the tip of a wing, remaining in this position until it had finished its examination of the foliage beside me.

One day I watched a Green Hermit resting on a low twig in bright sunshine. It puffed out its feathers and scratched its neck with a foot raised between a wing and its body, hence passing its foot above the base of its wing. Then it bent its head far backward, until its long bill pointed almost straight upward and its breast protruded in front. One who did not know that this was approximately the posture of an incubating hermit might have supposed that this grotesquely contorted bird was stricken with some paralyzing disease, but doubtless it was merely basking in a comfortable posture in the sunshine.

VOICE AND COURTSHIP

As in other species of *Phaethornis*, a number of male Green Hermits gather in the dark undergrowth of the woods to sing persistently day after day. Each perches within a yard or two of the ground and vigorously swings his long, white-tipped tail up and down while he repeats with clocklike regularity his single monotonous note. This monosyllable is full and rather hoarse; long ago I described it as a "loud barking note." The monotonous performance continues through much of the day. Often a number of males sing within hearing of each other, and sometimes one will settle a few inches from another. Such a visit usually gives rise to a spir-

ited pursuit, in which the birds dash through the tangled undergrowth with such speed that one wonders how they avoid a disastrous collision with the vegetation. When taking wing, or as they settle on a singing perch, these hummingbirds sometimes make a loud, rather explosive, "smacking" note.

On the Caribbean slope of Costa Rica, I found one of these singing assemblies in very dense undergrowth of forest that had been thinned by lumbering, above Pejivalle at an altitude of about 2,500 feet. Another assembly was located in the epiphyte-laden mountain forest at about 5,300 feet, near Vara Blanca. These assemblies were active in January and March, in the drier part of the year. In El General on the Pacific slope, I have found Green Hermits performing in the forest at about 3,000 feet. Here, where the dry season in the first quarter of the year is more pronounced, singing is interrupted at this time, but it continues through the remaining wet months.

NESTING

On 30 December 1935, while we collected plants along a rivulet that flowed through a narrow ravine whose rocky walls were overgrown with a rich profusion of ferns and other vegetation, on the mountain slopes above the valley of El General at about 4,000 feet, my assistant found a nest of the Green Hermit. It was supported, at a height of six feet above the stream, by a wild plantain or *Heliconia*, a giant herb whose great leaves, at first entire, are readily torn by wind or other disturbances into transverse strips which extend from the margin to the massive midrib, just as happens in the related banana. The hummingbird's nest had been skillfully fastened to the lower surface of a broad strip of leaf, which formed a sloping green roof above it. In form it was roughly an inverted cone with a deep, upward-facing hollow in its broad top, from which it gradually contracted to a thick, blunt tail, about 4 inches (10 cm) long, which hung well below the edge of the leaf and made the structure more conspicuous than it needed to be. In the bottom of the pensile cup reposed two homely, nearly naked nestlings, whose mother refused to feed them while I watched for nearly an hour, seated amid the lush vegetation on a neighboring log. But she hovered nearby and complained.

I did not revisit this nest in the remote mountains until three weeks later, when the young had flown. I now tore the structure apart to learn of what materials its thick, soft walls were made. I found the chief one to be the long, slender, brown scales or ramenta of tree ferns, intermixed with which were many fine fibrous roots and much cobweb. The nest was everywhere densely covered with cobweb, many strands of which extended from it around the outer face of the supporting strip and so bound the structure firmly to the slippery leaf.

In the cloud forest near the summit of the coastal range that separates the valley of El General from the Pacific Ocean, at an altitude of about 3,400 feet, we found another nest, on 6 February 1939. Like the first nest, this was attached beneath a flap of a broad, torn leaf of *Heliconia*, and it appeared to be quite similar in construction. Its owner was more confiding than that of the first, and she settled down to incubate or brood nestlings while three of us watched. She faced the leaf surface to which her structure was affixed, sitting with her head thrown so far back that her long, curved bill was almost vertical. Her long tail projected far beyond the rim on the free side. Unfortunately, I had forgotten the mirror which I use for looking into nests above my reach, and I could not tell whether this one held eggs or young.

LITTLE HERMIT

COURTSHIP

In my earlier paper (1951) on the Little or Longuemare's Hermit (*Phaethornis longuemareus*) I described the courtship assemblies, in which a number of males sing within hearing of each other while perching within a foot or two of the ground, wagging their tails rhythmically up and down. Such assemblies are usually situated amid the tangled undergrowth of light second-growth woods and they are active through most of the year, except at the height of the dry season when flowers become scarce. These assemblies occupy the same area year after year, and one near our house has been established for at least 18 years. I also described the aerial display, in which the courting bird, whose head and tail are turned upward giving him the form of a tiny boat with upcurved bow and stern, floats in the air and performs intricate movements above a spectator who perches near the ground. Since then, I have witnessed a few variations in courtship procedure which seem worthy of recording.

The first of these unusual courtship episodes occurred in the undergrowth of tall secondary woods where the Little Hermits have maintained a singing assembly for many years. Here, on 22 April 1957, I watched a hermit perch on a long, slender, arching, dead leaf stalk of *Cyclanthus bipartitus*, about eight inches up, wagging its tail rapidly up and down and pointing its bill toward another hermit who performed above it. The active bird hung between rapidly vibrating wings a few inches above the spectator's upturned head. It floated slowly from side to side, over a space of a few inches, at the same time slowly rotating to face now to one side, now to the other. At intervals it darted much more swiftly back and forth, for a distance of perhaps a yard, while it made a sharp noise, apparently with its wings.

After a while, the spectator rose into the air and the performer settled on the perch that the other had just left. The roles of the two hummingbirds were now reversed; the displaying one became the passive watcher, the original spectator became the performer. I saw clearly that this reversal of roles occurred several times, but I was not certain just how many, as the swiftness of the birds' movements made them difficult to follow. I saw no difference between the performances of the two individuals when in the air. Sometimes the hovering bird held both head and tail upward, giving it the crescent shape characteristic of this display, whereas at other times it floated in the air with its tail bent strongly downward. This mutual display continued for perhaps a minute, although it seemed much longer than this. Then one bird chased the other, or possibly they chased alternately, back and forth above their perch, and finally they darted off together through the woods. Unfortunately, I could not tell their sexes; possibly both were males.

On the afternoon of 26 April 1959, I watched a Blue-throated Golden-tail Hummingbird (*Hylocharis eliciae*) incubating in a mossy nest in the big bamboo that grows in a corner of our garden. Presently a Little Hermit alighted on a spray of bamboo, 30 or 40 feet (about 10–13 meters) above the ground. While it perched here with its head tilted upward and its tail swinging rhythmically through a wide vertical arc, a second hermit arrived and began to display by floating back and forth above the first, with body bent into the usual crescent shape. Soon both rose into the air, then one settled on a neighboring twig and the performance was repeated. I could not ascertain whether the aerial display was always given by the same bird, or whether the two alternated. The point of interest was the height at which this display was made, for usually it is given in the undergrowth near the ground. The bamboo was several hundred feet from the nearest singing assembly.

INCUBATION

Except at their singing assemblies, hummingbirds show little sociability. It is unusual to find two nests, of the same or different species, within sight of each other. In a Panamanian garden, where there was an unusual concentration of nesting Rufous-tailed or Rieffer's Hummingbirds (*Amazilia tzacatl*), building birds frequently stole materials from their neighbors' nests, sometimes destroying them and preventing reproduction (Skutch, 1931). Along a Costa Rican stream, however, I found nests of the Violet-headed Hummingbird (*Klais guimeti*) close together, and one in which two eggs were being incubated was only four feet from another with feathered young that were attended by a different female (Skutch, 1958). But such proximity of nesting hummingbirds is so rare that when, in 1955, I found two nests of the Little Hermit only 12 feet (3½ meters)

apart in the forest on our farm, I suspected that both had been built by the same individual.

These two nests of the Little Hermit were situated in the forest near its edge, at the top of a steep, eastward-facing slope where more than the usual amount of sunshine reached the ground. Each nest was fastened beneath the tapering tip of a living frond of a small palm that bristled with wicked black spines—the most common situation of such nests. The lower of these nests was three feet (one meter) above the ground and already held a tiny white egg. The higher nest, seven feet up, was nearing completion. After finding these nests at about 0800 hours on 13 April, I watched for an hour, in which time material was brought six times to the higher nest and twice to the lower nest with the egg. When the builder came with cobweb, she first flew up to the nest beneath the tip of the supporting leaf, then, hovering on wing and continuing to face the leaf, she circled twice around its tip and the nest on a spirally descending course, thus wrapping the filament around the end of the leaf and fastening the structure more securely to it. To place downy material, the builder alighted in the cup, then pushed the tuft into the fabric beside her. Twice, after adding a contribution to the lower nest, the hummingbird remained sitting on the egg for several minutes. At no time were two hermits in sight simultaneously.

The second egg was laid in the low nest on 15 April, and by 20 April the high nest also held two eggs. Evidently two hermits were nesting close together. On this date, I at last saw both of them sitting in their nests simultaneously. Seated in the forest with no concealment, since both hummingbirds seemed indifferent to my presence, I watched them incubate from 0543 to 1200 on 23 April and from 1210 to 1800 on the following day. In slightly more than 12 hours, the hummingbird at the low nest took 9 sessions on her eggs, ranging from 16 to 92 minutes and averaging 60.7 minutes. An equal number of recesses ranged from 10 to 25 minutes and averaged 18.3 minutes. This hermit covered her eggs for 77 per cent of the 12 hours.

In the same period, the hummingbird at the high nest took 14 sessions, ranging from 9 to 59 minutes and averaging 27.9 minutes. Her 15 recesses varied from 9 to 29 minutes and averaged 15.1 minutes. She incubated with a constancy of 65 per cent. She added material to her nest five times, whereas her neighbor, who was more assiduous in covering her eggs, did so only twice. As in other incubating hummingbirds, nest building was largely confined to the forenoon, and the latest time at which a contribution was brought was 1212. On this occasion, the hermit flew three times clockwise around the tip of her leaf, always facing it, while she applied cobweb to strengthen the attachment of her nest. Neither

hummingbird gave any indication that she saw her neighbor or her neighbor's nest only 12 feet ($3\frac{1}{2}$ meters) away, and both were equally indifferent to me. While I made this record, both the morning and afternoon were largely cloudy, with some bright sunshine between 0800 and 0900 and two slight showers between 1300 and 1400.

When I began to watch, the hummingbird at the low nest had been incubating her completed set of eggs for eight days, but the less constant sitter at the high nest had laid her second egg only three days earlier. Perhaps her lower constancy was due to the less advanced stage of incubation. To test this supposition, I watched again through the morning of 3 May, when the eggs in the high nest were almost ready to hatch, while the low nest already held nestlings. In six hours, the high hummingbird took 9 sessions ranging from 17 to 36 minutes and averaging 27.1 minutes and 9 recesses ranging from 9 to 15 and averaging 12.6 minutes. She incubated for 68 per cent of the time and was only slightly more attentive than she had been on the morning of 23 April, when her sessions averaged 31 minutes and her recesses 17.3 minutes. Evidently the difference in the constancy of the two neighbors which I had observed on 23 April was not due to the stage of incubation but to innate differences in the birds themselves. At an earlier nest, which I watched for six hours, the hermit incubated for 72 per cent of the time; and at a nest watched for four hours, the eggs were covered for 62 per cent of the observation period (Skutch, 1951: 192).

At each of the neighboring nests, the hummingbird's shortest session was terminated when some small bird, which I did not see well enough to identify, suddenly flew close by the nest. Aside from this interrupted session of 16 minutes, the shortest session of the low hummingbird was 27 minutes. In the case of the high nest, the interrupted session lasted 9 minutes, and the shortest session that ended spontaneously lasted 14 minutes. Both hermits took their longest sessions in the forenoon.

At both of these nests the incubation period was 16 days, which agrees with earlier determinations (*op. cit.*: 192).

THE NESTLINGS

As previously recorded, soon after they hatch the tiny, blind, nearly naked nestlings orient themselves in the nest with their heads toward the point of the leaf to which the structure is attached. Thus their orientation is the same as that constantly maintained by the incubating or brooding parent. In the present study, I only rarely found a nestling resting in some other position, with its head toward the side of the nest or outward. The usual orientation permits the nestling to eject its droppings free of the nest and leaf, as their mother sometimes does while she sits. One day,

when the nestlings in the low nest were respectively two and four days old, I found both facing sidward rather than toward the surface of the leaf. Presently one of them turned to face the leaf, then elevated its posterior end and shot its excreta over the rim.

On 3 May, while I watched the hermit incubate in the high nest, her neighbor attended two nestlings that had hatched two and four days earlier. In the first six hours of the morning, she brooded them 11 times, for intervals ranging from 9 to 27 minutes and averaging 14.7 minutes. Her 10 absences ranged from 9 to 23 minutes and averaged 18 minutes. She was in the nest only 45 per cent of the morning, which was a considerable reduction from the time she sat while she incubated. She fed the nestlings only 8 times, which was at the rate of 0.66 feeding visits per nestling per hour. She seemed to regurgitate food to both nestlings on a single visit, but they remained so low in the nest that on only one occasion did I definitely see this.

These neighboring nests did not prosper. At the low one, both nestlings died before they could fly, possibly from an infestation by *tórsalos*, larvae of a dipterous fly which live beneath the skin and cause great swellings. At the high nest, one nestling died, but the other lived to fly away. When this survivor was 13 or 14 days old and already feathered, I again spent the morning watching. Brooding had ceased, at least on a rainless forenoon. The nestling was fed 15 times in six hours, or at the rate of 2.5 feeding visits per hour. The meals were spaced fairly evenly through the morning, the interval between successive feedings varying from 17 to 35 minutes. The rate of feeding was somewhat slower in the second half of the forenoon than in the first half. The parent nearly always regurgitated to the nestling in two installments at each visit, removing her bill from its mouth for an instant between the two acts of regurgitation. Possibly she was following a habit formed by feeding the two nestlings which had earlier been present. Once, when the nestling seemed satiated, she fed it in three installments. Each continuous act of regurgitation usually lasted 6 seconds, with extremes of 3 and 12 seconds; and on each visit from 11 to 16 seconds were devoted to regurgitation. Sometimes the parent fed the nestling while hovering without touching the nest, as when sipping nectar from a flower, but at other times she clutched the rim with her feet but continued to beat her wings while she regurgitated, almost as though she were hovering. On a single visit to the nest she might follow only the first method, only the second, or she might hover while delivering the first course, and hold to the rim while giving the second. The meal over, she darted swiftly away, never cleaning the nest, a chore which the sanitary habits of the nestling made unnecessary.

This nestling flew away when between 21 and 23 days of age. In my earlier paper, the nestling period was given as 20–21 days.

BAND-TAILED BARBTHROAT

The Band-tailed Barbthroat or Rucker's Hermit (*Threnetes ruckeri*) resembles the foregoing hermits in its long, strongly curved bill and its lack of the glittering plumage typical of hummingbirds, but differs from them in its shorter, rounded tail. It is about four and one half inches long and the sexes are alike. Their dorsal plumage, including the middle pair of tail feathers, is metallic bronzy green. The other tail feathers are white on the basal half, then dull black; and all the rectrices have white or buffy tips. When spread, the tail presents a striking pattern. Each side of the head is marked with a dusky patch on the cheeks and ear coverts, outlined above and below by a buffy stripe. The chin and upper throat are dusky. The chest is crossed by a band of cinnamon-rufous, which fades to buffy gray on the more posterior underparts. The barbthroat ranges from Nicaragua to Colombia and Venezuela. An inhabitant of humid lowland forest, it extends upward to about 2,500 feet on the Pacific slope of southern Costa Rica.

Like other hermits, the barbthroat is almost fearless of man, and more than once one of them has hovered within arm's length of my face, fanning my cheeks with its wings, while it scrutinized the strange intruder into its sylvan domain. Sometimes a perching barbthroat has permitted me to examine it with my eyes less than a foot from its own.

This hummingbird spends much time hovering beneath the leaves of shrubs and low trees in the undergrowth, gleaning tiny creatures from them. Its fondness for stands of the great-leaved herbs known as "wild plantains" (species of *Heliconia*, *Calathea*, and related genera) has frequently been recorded. At the end of December 1930, I spent several mornings observing the floral behavior of a shellflower, *Calathea lutea*, on Barro Colorado Island, in Gatún Lake in the Panamá Canal Zone. A cluster of these herbs with broad, upright leaves grew in the sunshine on the lake shore, at the edge of a small banana plantation and close to the forest which covers most of the island. Day after day, a barbthroat spent much time on a slender dead vine among the giant shellflower leaves, and to this favorite perch it returned after each sally for food or exercise. As it rested there, usually facing me, its white-tipped tail was always wagging up and down, like the tails of singing Little and Long-tailed hermits, although this bird was silent. It continually protruded its long, forked, white tongue. Although it often visited the inflorescences of the *Calathea*, it did not sip nectar from the small yellow flowers, whose tubes were too narrow to admit its bill. It probed the water which had collected inside

the large, fleshy, two-ranked, folded bracts that surrounded the flowers, but whether to sip the liquid, or to extract the insect larvae which flourished there, I did not learn.

VOICE AND COURTSHIP

On 12 July 1941, while wandering through the forest on the land which I had recently bought in El General, I heard amid the dense undergrowth of a moist dell a song that was new to me. Thin, plaintive, long-continued, delivered so rapidly that it was almost a trill, the song was more tuneful and varied than those of most hummingbirds, which are often squeaky and extremely monotonous. The voice seemed charged with feeling, and to me it suggested the melancholy of insatiable yearning. My first surmise was that I heard a wood warbler (*Parulidae*) of an unfamiliar kind, and I searched long for a small bird flitting through the tangled underwood before I noticed a barbthroat perching calmly on a dead twig a yard above the ground, tirelessly waving his tail up and down, sometimes through a wide arc and sometimes through a slight one. From time to time he sang. Each song lasted about four or five seconds, and successive performances were separated by far longer intervals of silence. This musically gifted hummingbird did not squander his voice like many other species, which pour forth their unmelodious notes with such abandon that they seem to be trying to compensate by quantity for their lack of quality.

For the next month, the barbthroat was to be found day after day in the same spot. He performed in both morning and afternoon, but so infrequently that it was often necessary to wait long for his pretty song, which carried afar through the woodland. He seemed to be always alone rather than a member of a courtship assembly. Here, near the upper limit of their altitudinal range at about 2,500 feet, barbthroats were rare, and in several years I heard only one other singing, in another part of the forest. In 1942 and again in 1943, however, a barbthroat performed in the spot where in 1941 I heard the bird above described, and, in view of the rarity of the species here, I naturally suspected that it was always the same individual.

Finally, in April of 1944, I found a second barbthroat singing not far from the presumptive first, who for the fourth consecutive season was occupying the same station. In 1947, at least three barbthroats were singing in this part of the forest. The two farthest apart were stationed about 250 feet from each other. The central one was in almost the same spot where I first heard a barbthroat sing in 1941; but now that the tradition of singing in this area was perpetuated by several birds, I no longer felt so confident that my original barbthroat was still present. All of the birds

sang while perching low, rarely more than head-high. When I stood very close to a performer, his notes were unpleasantly shrill, but they became mellow at a distance. Barbthroats continued to perform in this small area of the forest until 1956, or for at least 16 years. In July of 1958, I heard one singing amid dense undergrowth on the slope above the dell, but he did not remain.

In this vicinity, the barbthroats' singing seems to be confined to the first half, or a little more, of the rainy season. In 1947, when occasional showers kept the forest damp through the early months of the year, I first heard a barbthroat sing on 25 March; and in 1943 I heard singing on 29 March. In 1948, when the dry season was more prolonged, I first recorded the barbthroat's song on 25 April. In 1945, when the drought was severe, I heard no song until 7 May. In this region, the barbthroats have continued to sing at their usual stations until about the middle of August, or sometimes late August, after which I have heard them no more until the following year. But in the Pacific lowlands near the Golfo Dulce, I heard two, or possibly three, singing persistently within hearing of each other in the dark undergrowth of the forest on 24 December 1947.

Barbthroats have continued to sing while I watched almost at arm's length. One day I was amazed to notice that the songster opened his mouth while his long bill remained almost closed. The movements of his lower mandible did not follow or correspond to those of the lower jaw, as would have been inevitable if jaw and mandible formed a single rigid piece. Evidently there was a point of flexure between the jaw and the lower mandible, which permitted the former to move independently of the latter. Brauner (1953: 72) described a "hinge" in the lower mandible of the Poor-will (*Phalaenoptilus nuttallii*); in this short-billed bird with a huge gape, the point of flexure is in the middle of the lower mandible rather than near its base, as in the long-billed, small-mouthed hummingbird. The hinge permits the goatsucker to call without appearing to open its mouth, and this imparts a ventriloquial quality to its notes.

I have never seen a barbthroat's nest, but Carriker (1910: 518) found one beside the Sixaola River in the Caribbean lowlands of Costa Rica on 25 March 1904. It was about five feet up in a thorny shrub on a low gravelly beach. Constructed almost entirely of vegetable down and adorned on the outside with lichens, moss, and a few fragments of wild cane blades, it was held together by cobweb. On this date it contained two fresh eggs. If the attribution of this structure to the barbthroat is correct, it is evident that this species builds its nest in a site quite different from that chosen by other hermits.

SUMMARY

Hermit hummingbirds inhabit undergrowth of humid woodland and lack brilliant metallic colors. The Long-tailed Hermit and Band-tailed Barbthroat live in primary forest, mainly below 3,000 feet; the Green Hermit inhabits primary forest, in Costa Rica chiefly at 1,500–5,500 feet. The Little Hermit is usually found in lighter secondary woodland of the Humid Tropical Zone.

These hermits pluck small invertebrates from foliage in the undergrowth and suck nectar from various flowers, often entering clearings to seek them. Their long bills enable them to utilize flowers with long tubes, such as *Heliconia* and *Musa* and the scarlet passion flower, whose floral nectaries are, however, beyond reach of the Little Hermit. They are often curious and almost fearless of man.

These hermits sing persistently in courtship assemblies situated in the undergrowth of heavy or, in the Little Hermit, light woods. Each male perches near the ground and wags his white-tipped tail tirelessly up and down while he delivers his song through much of the day. The Long-tailed and Green hermits monotonously repeat a single squeaky or hoarse note. The Little Hermit's performance is more lively and varied, although hardly musical. The barbthroat has a long-continued, musical song that is sparingly given. The Little Hermit has also a display in which one bird hovers in the air and performs intricate movements above another that perches. Mutual display, in which two birds alternately take the active and passive roles, sometimes occurs in the Little Hermit.

The nests of the three species of *Phaethornis* are fastened by cobweb to the undersides of leaves. The Long-tailed and Little hermits prefer the tapering apex of a frond of a low, spiny palm. The Green Hermit selects one of the transverse strips into which the large leaves of *Heliconia* are often torn. The hummingbird keeps its nest firmly attached to the slippery leaf by continuing, until the eggs hatch, to renew the binding of cobweb, which it applies to nest and leaf by circling one or more times around both while hovering.

Two white eggs are laid. While sitting in the nest to incubate or brood, species of *Phaethornis* always face the supporting leaf, holding the bill almost straight upward, with the head thrown so far back that it nearly touches the rump. Nevertheless, both Long-tailed and Little hermits often sit continuously for well over an hour. Those observed incubated with a constancy of 62 to 77 per cent. The incubation period of the Long-tailed Hermit is 17–18 days; of the Little Hermit, usually 16 days or a little less.

Soon after hatching, the nestlings lie with their heads toward the supporting leaf, just as the parent sits. This orientation, which is maintained

until they fly, permits them to eject their liquid excreta over the rim without soiling nest or leaf. To feed them, always by regurgitation, the parent usually hovers in the air beside the nest and reaches over their backs. Usually both nestlings are fed from one to three times, alternately, on each parental visit. Feeding visits varied from 0.66 per nestling per hour for two nestlings a few days old to 2.5 per hour for a single feathered nestling. The nestling period of the Long-tailed Hermit is 22–23 days; of the Little Hermit, about 21 days.

When two Little Hermits nested only 12 feet apart, each ignored her neighbor and her neighbor's nest.

Despite the apparent inaccessibility of nests attached beneath the leaf tips of thorny palms, most are pillaged by unknown predators.

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