All the Right Curves

In an island hummingbird, the shape of the female's bill enables her to feast on local flora inaccessible to the male.

By Ethan J. Temeles

On what has become an annual expedition, each May and June I lead a group of my students to Saint Lucia, one of the eastern Caribbean islands that make up the Lesser Antilles. Our destination is the Quilesse Reserve, the largest of the four areas of rainforest on the island. Although Saint Lucia is small—twenty-seven miles long and fourteen miles wide—its topography is dramatic, and traveling inland to Quilesse takes no trivial effort. Only about 19 percent of the island's original rainforest still remains, all in reserves on the mountain slopes of the interior. The potholed six-mile feeder road leading from the east-coast highway to Quilesse takes an hour to drive. Once we reach the reserve, we get out and start hiking. As is typical on Saint Lucia, the climb is almost straight up. And though relatively few visitors to the island scale the remote slopes, even casual tourists can appreciate the steepness of the terrain: on the southwestern coast the national landmarks, two extinct volcanoes called the Pitons, rise 2,000 feet up from the sea.


ROBERT RATTNER

The Pitons, twin peaks on the coast of Saint Lucia, are dramatic reminders of the island's volcanic origin.

As we first work our way along the muddy slopes of the Quilesse trail, we hear the squawk of Saint Lucia parrots. Twenty years ago the population of these parrots had dropped to 150, and the species had become the world's thirteenth rarest bird. Now, protected from hunting and from habitat destruction, the species has rebounded to about 500 individuals and has been named Saint Lucia's national bird. But we have come to study another, much smaller, island resident: the purple-throated carib.

Native to the mountain rainforests of the Lesser Antilles—from Saint Kitts and Nevis in the north all the way south to Saint Lucia and Saint Vincent—the purple-throated carib is one of the most beautiful of hummingbirds. Both males and females are predominantly black with a glittering, rosy throat patch, or gorget, and emerald wings. Many hummingbirds have iridescent gorgets, but the purple-throated carib is one of only two out of some 320 species of hummingbirds to have iridescent wings. Flashing green and black through the rainforest, these hummingbirds resemble imperial fighters from *Star Wars*. The analogy is apt, not only because of the birds' speed and maneuverability but also because of their pugnacious behavior.

Although alike in color, male and female purple-throats display one of the most extreme differences in bill size and shape of any bird. Males are 25 percent larger than females, weighing in at ten grams (roughly three times the weight of a penny). But the bills of females are 30 percent longer than those of males and curve downward at a 30 degree angle, compared with the 15 degree slant of the males'. Males and females of some other hummingbird species also differ in bill size, but the discrepancy among purple-throated caribs is so

great that an observer can readily tell the sexes apart by bill characteristics alone.

Sexual differences in size and color are widespread in the animal kingdom. For example, male elephant seals, which battle each other for access to mates, are two to three times larger than females; the extravagant plumage of peacocks contrasts with the drabness of peahens. Among arthropods, such differences, or sexual dimorphisms, can be just as striking, though they tend to go the other way: the females, which carry eggs, tend to be the larger sex. Darwin was the first to suggest how such differences may have evolved. One possibility is sexual selection: a brightly colored male fish or a male deer sporting large antlers may have a better chance of attracting or fighting for mates than males that lack such traits. The second possibility is fecundity selection: if larger female arthropods produce more eggs than smaller ones, then genes for larger female size may predominate in succeeding generations.

But Darwin also proposed a third selective mechanism. Some sexual dimorphisms, he suggested, may have evolved through the ecology of feeding: the sexual differences simply enable males and females to consume different foods. The clearest examples are certain mosquito species in which the mouthparts of males are adapted for drinking nectar and those of females for imbibing blood. But

ROBERT A. TYRRELL

A female purple-throated carib settles on her nest. In hummingbirds, all care of eggs and chicks falls to the female.

other good examples have been hard to pin down, because in many species the size of an individual determines what the animal can eat, making it unclear whether sexual differences in diet are the cause, or the consequence, of sexual dimorphism.

Darwin was well aware of the difficulty of relating the evolution of sexual dimorphism to differences in diet. Hence he maintained that any scientific claim for such a relation should be grounded in dimorphisms associated primarily with the feeding apparatus. An example Darwin cited was the New Zealand huia. (Unfortunately, this bird was so highly prized by the indigenous Maori and, later, by Europeans for its large black-and-white tail feathers that it became extinct by 1930.) The sexes were similar in size and plumage, and both fed on insects. But their means of feeding and their bills were different. Males, which chiseled into wood for their prey, had short, thick, straight bills. Females, which probed crevices for insects, had long, slender, curved bills. Ornithologists and naturalists, including the renowned nineteenth-century illustrator John Gould, originally classified male and female huias as two different species.

JOHN GOULD, *THE BIRDS OF AUSTRALIA, AND THE ADJACENT ISLANDS*, 1837–38; AMNH

The bills of male and female huias, depicted by painter John Gould, top, are echoed in the profiles of purple-throated caribs. The bill of the female in the photograph at the far right is substantially longer and more sharply curved than that of the male on the left.

As an undergraduate, I had read about another group of birds whose bills were associated with differences in diet: Darwin's finches of the Galápagos Islands. If feeding ecology could give rise to differences in the shapes of bills from species to species, couldn't it do the same for the sexes? But since the huia was extinct, I had to search for years for another species that would enable me to investigate that hypothesis. Then I discovered Larry L. Wolf's work with the purple-throated carib. It was Wolf, a biologist at Syracuse University, who noted how easily male and female could be distinguished in the field by their bills. Here at last was an avian candidate for a study of feeding and sexual dimorphism. So in May 1999 I embarked with my students on our first field expedition to Saint Lucia.

Wolf and another investigator, Karl Schuchmann, an ornithologist at the Alexander Koenig research institute in Bonn, Germany, had focused mainly on the purple-throated carib's courtship and nesting behaviors. Little was known, however, about the bird's food plants. I decided that our first step would be to hike through Saint Lucia's four rainforest reserves and record all the plants that hummingbirds did, or could, feed on. The task was not without its hazards. In addition to being deceptively steep, slippery, and often exceedingly narrow, the trails through the rainforests are also home to the fer-de-lance, one of the Western Hemisphere's deadliest snakes.

On our first trip, after several snake-free days of hiking, my students and I determined that the only food plants available to purple-throated caribs near the ground during the months of our initial observations (May and June) were two species of *Heliconia*. We have since confirmed that those two *Heliconia* are the birds' primary food plants from January through July. (Purple-throats also feed from flowers of morning glory and tree hibiscus in the treetops.)

Commonly known as lobster claws, *Heliconia* are close relatives of ginger, banana, and the bird-of-paradise plants familiar from florists' shops. In the wild, *Heliconia* often reach heights of thirty feet and have broad leaves from nine to twelve feet long. But it is the colorful inflorescence, or flower stalk, that defines the plant. Each inflorescence includes between one and twenty-four bracts (the parts that resemble lobster claws). The bracts are actually modified leaves that may carry from one to as many as fifty flowers, depending on the species. What makes *Heliconia* a delight for flower fanciers is the tremendous variation in the colors of the bracts. A single species may have several color varieties, or morphs, ranging from brown to red, orange, yellow, and even chartreuse. We found purple-throated caribs feeding

JED HORWITT AND IRVIN PAN

SCHAFER & HILL; PETER ARNOLD, INC.

Heliconia "lobster claws," or bracts, are thick, stiff structures that each enclose between one and fifty flowers.

from the flowers of a red-bracted morph of *Heliconia caribaea* and from a green-bracted morph—unique to Saint Lucia—of *H. bihai*.

To determine how male and female purple-throats were using the two *Heliconia* species, my students and I spent three weeks watching patches of the plants from dawn until midafternoon, recording all avian visitors. We found that purple-throated caribs are the sole pollinators of both *H. caribaea* and *H. bihai,* and that, as we had hypothesized, the sexes differ markedly in their use of the two plant species. Of the birds we observed, all of the fifteen males but only seven out of the eighteen females fed at *H. caribaea*. The males were more sedentary than the females and tended to monopolize the largest, densest stands of *H. caribaea,* which bear two to three times as many flowers as *H. bihai*.

It turns out that, compared with the flowers of most hummingbird-pollinated plants in North America, *Heliconia* produce copious nectar. By covering flowers with bags to exclude hummingbird visitors, my students and I determined that a single *H. caribaea* or *H. bihai* flower can produce a hundred microliters of nectar in twenty-four hours. That is more than fifty times the amount produced by a single jewelweed or bee balm flower visited by ruby-throated hummingbirds during the summertime in eastern North America. Because a single inflorescence of *H. caribaea* can have as many as twenty-four bracts, each supporting twelve flowers that bloom sequentially over several weeks or months, a patch of forty or more inflorescences is the hummingbird equivalent of Fort Knox.

Such riches are not without robbers, and we observed male purple-throats defending their patches, repelling other purple-throats as well as Saint Lucia orioles and Lesser Antillean bullfinches. The latter two species intruded on the purple-throats' territories not to steal nectar but to consume flowers—petals, sepals, nectar, and all. Male purple-throats were so protective of their flowers that they even attacked *us;* one particularly aggressive male struck me in the chest as I tried to measure one of the flowers in his territory.

Female purple-throated caribs behaved very differently. They ventured into male territories to feed and to mate. They also fed at small patches of *H. caribaea* and at both large and small patches of *H. bihai*. Those differences between male and female behavior arise from differing reproductive and social roles. Female purple-throats, like the females of all other hummingbird species, incubate eggs and rear offspring without any male assistance. While on the nest, a female cannot guard a flower patch, and so she must feed from undefended patches or steal nectar from territories of males. All the nests I have identified have been situated near small patches of *Heliconia* or near richer, male territories. Of course, once their young have left the nest, females can defend *Heliconia* territories. But their smaller size precludes them from competing successfully against males for the richest territories, which usually contain flowers of *H. caribaea*. In four field seasons, we have never observed a female in possession of an *H. caribaea* territory.

A patch of forty or more nectar-rich inflorescences of Heliconia caribaea *is the hummingbird equivalent of Fort Knox.*

To find out whether the differences in flower use were directly related to the shapes of bills, we needed to measure the length and curvature of *Heliconia* flowers. Because so many animals (birds, ants, and beetles, to mention a few) eat *Heliconia* flowers,

species such as *H. caribaea* and *H. bihai* have responded by burying their flowers deep within the plants' bracts. There the flowers are surrounded by thick tissue and, in some cases, even a protective moat filled with rainwater or the plants' own secretions. The only way to determine the size and shape of *Heliconia* flowers is to cut them from the bracts.

When we did so, we found that *H. caribaea* flowers are significantly shorter and straighter than the flowers of *H. bihai*. The lengths of the flowers differed, on average, by six millimeters. Remarkably, the bills of the male purple-throats were also just six millimeters shorter than those of the females. Similarly, the curvature of *H. caribaea* flowers, which measures about 20 degrees of arc, fitted the bills of males quite well, whereas the curvature of *H. bihai* flowers, which measures 30 degrees of arc, matched the bills of the females.

The 30 degree curvature of the flowers of Heliconia bihai *matched that of the female purple-throats' bills.*

Sturdy perch: a female purple-throat (the gorget is actually a rose hue) on a *Heliconia* bract

If males and females evolved different bill shapes to match the flowers of one or the other species of *Heliconia,* one would also expect each sex to feed most quickly at the flower corresponding to its bill. My students and I found that it took males only three seconds to feed from the short flowers of *H. caribaea,* whereas it took the longer-billed females four. Because males fed so seldom from flowers of the green-bracted *H. bihai,* we were unable to measure their feeding times at this plant species. Nonetheless, females fed nearly a second faster at the long, curved flowers of *H. bihai* than at *H. caribaea* flowers.

Our case for the role of feeding ecology in shaping the bills of purple-throats was bolstered when we looked at *Heliconia* from other Saint Lucia rainforests. The green-bracted morph of *H. bihai* is present at all four of the island's reserves, but *H. caribaea* is not. We discovered that at the two reserves where *H. caribaea* is rare or absent, *H. bihai* has developed a second morph, with red rather than green bracts and shorter, straighter flowers intermediate between those of *H. caribaea* and the green-bracted *H. bihai*. At both those reserves, males defend and feed from flowers of the red morph of *H. bihai,* whereas females mainly feed from the green morph.

Given the close correspondence between the bills of purple-throats and the size and shape of the *Heliconia* flowers they feed on, how might the bills originally have begun to diverge? Did the male and female purple-throats that arrived on Saint Lucia at first share food plants and feed in the same way? One likely scenario is that when these hummingbirds first colonized the island thousands of years ago, the males, having greater body mass, dominated the females and claimed access to the more rewarding *H. caribaea*. That left the females with the less profuse *H. bihai*. With time, the bills adapted to match the flowers on which the birds—males by dominance and females by default—usually fed. Each sex got better at extracting nectar efficiently.

The purple-throated carib is one of the most unambiguous examples to date of how feeding ecology can generate sexual dimorphism. But this species is not the only hummingbird to exhibit sexual differences in bill size. Recently, Robert Bleiweiss of the University of Wisconsin-Madison determined that sexual differences in bill length are common among hummingbirds. After looking at a number of species, Bleiweiss suggested that breeding and social behavior, as well as feeding ecology, have a major role in shaping the general patterns of sexual dimorphism. Among species in which males have the shorter bills, the males also typically defend and monopolize areas where nectar-rich plants are clumped. Females of these species visit male territories for feeding and mating, or feed from undefended patches of flowers—the dregs, according to Bleiweiss. Having a longer bill would enable females to make the best of the leftovers: they could feed from a broader range of plants than the males do, and from flowers of different length. In fact, I have been able to confirm those advantages of a longer bill experimentally in my laboratory.

The differences between the bills of male and female purple-throats make it hard not to draw parallels to another group of birds with amazingly variable beaks, Darwin's finches. Just as bills of Darwin's finches vary from island to island within the Galápagos, so, too, do bills of male and female purple-throats vary from island to island in the Lesser Antilles. The question is, Do inter-island differences in the bills of males and females correspond to inter-island differences in plants and flowers? If so, the purple-throated carib may be the sexual equivalent of Darwin's finches. My next step is to travel, as Darwin did, from one island to the next, documenting such variation. I've already booked my next visit. □

ROBERT A. TYRRELL

ROBERT A. TYRRELL