Some hummingbirds resort to sneaky methods to obtain nectar

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Fiery-throated Hummingbird, Paraiso Quetzal Lodge, Costa Rica, January–February 2018. Credit: Hans Norelius from Älvsjö, Sweden/Wikimedia Commons, CC BY

A 50-year project recently came to fruition for UConn researchers. In their paper recently published in *The American Naturalist*, Ecology and Evolutionary Biology Emeritus Professor Robert Colwell and his colleagues—all UConn Ph.D. graduates—Thiago Rangel, Karolina

Fučiková, Diego Sustaita, Gregor Yanega, and Alejandro Rico-Guevara worked to solve a mystery that had perplexed Colwell for years.

It started when Colwell, who was leading a graduate course in Costa Rica for the Organization for Tropical Studies in 1971, observed certain hummingbirds using a sneaky shortcut to gather nectar.

"We were at a site about 10,000 feet above sea level studying hummingbirds, and I noticed that the largest of the four species of hummingbirds at that elevation, the long-billed Magnificent Hummingbird, weighing nine grams, actually had smaller feet than the much lighter, six-gram Fiery-throated Hummingbird, with a much shorter bill," Colwell says.

Though all hummingbirds have tiny feet, Colwell adds, the feet of the Fiery-throated are proportionally much bigger than expected, for its smaller body size, enabling an unorthodox feeding behavior for a hummingbird. Rather than hovering to feed from the mouth of a flower, delivering or receiving pollen in the process, these nectar thieves perch on the plant with the help of their bigger feet and use their shorter bills to punch small holes in the base of the flower to pump out the nectar, without pollinating the flower in the process.

Colwell was curious. Did the trait of bigger feet evolve because of this feeding strategy? Unfortunately, the subject of hummingbird feet was an overlooked topic at that time, so Colwell had to start from scratch. He began tracking down as many specimens as he could to take measurements of their feet and beaks and record their body weight.

With some 340 species, hummingbirds represent an enormous single, ancient branch within the avian evolutionary tree. They're only found from Alaska to Tierra del Fuego, but are most diverse in the tropics, says Colwell.

Since he was teaching there at the time, Colwell started with the University of California Berkeley Museum of Vertebrate Zoology where he examined more than a hundred species of hummingbird specimens, taking careful bill and foot measurements.

By 1986, Colwell says had enough data and he wrote a paper but decided to withdraw it from publication. Instead, he opted to gather more data and do more analysis, including looking more specifically at potential differences between male and female hummingbirds.

The other missing detail, he says, was that researchers did not yet have a phylogenetic tree for hummingbirds, which is crucial to show the evolutionary history of different groups and their relationships to one another through time. With the phylogenetic tree, scientists can answer questions such as whether a characteristic is shared across different groups because they share a common ancestor.

Colwell explains that if an interesting trait like bigger feet in nectar thieves is simply due to a common ancestor, that is not significant as a case where the same trait is shared with another, unrelated group of hummingbirds. This is called evolutionary convergence, where similar traits evolve independently in distantly related organisms—for example, flight in both vertebrates (birds and bats) and invertebrates (insects).

"Luckily, I wasn't in a hurry, I just decided to not publish the paper in that form," Colwell says. "Eventually, in 2014, a phylogeny was published for 284 species of hummingbirds by a group led by Jimmy McGuire, at Berkeley."

Colwell kept measuring and, after joining the faculty at UConn, he began collaborating with Margaret Rubega and her doctoral students Rico-Guevara and Yanega, who started measuring hummingbird feet at Colwell's encouragement while performing their fieldwork and when visiting museum collections. Meanwhile, Sustaita, a third Rubega doctoral student, a specialist on bird feet and the biomechanics of perching, began to model the mechanics of perching for feeding observed in hummingbirds.

Rangel, a former student in Colwell's group, worked on phylogenetic statistics, and Fučiková, from UConn Ecology and Evolutionary Biology Professor Louise Lewis' lab, developed alternative phylogenies to account for uncertainty, and mapped the evolutionary origins of foraging behaviors.

Eventually, the team gathered measurements from 1,172 museum specimens and 386 field captures, representing 220 species of hummingbirds. Additionally, the researchers pooled all the behavioral data on hummingbirds clinging to feed they could find from the literature and from their own field research, and Colwell went through every photograph and video on the Birds of the World website to look for additional examples. They found evidence of clinging to feed for 66 species.

"With this great team we ended up finding out that, yes, there is a negative correlation between foot size and bill size," says Colwell.

Colwell explains that excluding effective body size and the effect of phylogenetic relationships, and any physiological differences driven by species living at different elevations, the negative correlation between bill size and foot size is driven by short-billed species, many of which are nectar robbers.

"We show on the phylogenetic tree where this behavior arose, and this behavior of perching or clinging to feed arose in two dozen independent instances. This evolutionary convergence is a big deal and very rare to find more than a few examples within one evolutionary tree, one clade.

The fact that we have so many independent origins is a strong and unusually rich example of evolutionary convergence."

Colwell adds that this convergence makes sense, because hovering is the most energy-intensive mode of movement in the animal world and hummingbirds must consume around their own body weight in sugars each day for survival.

"Anywhere that a hummingbird can get nectar or arthropods without hovering is an advantage," Colwell says. "There's always a strong selective pressure to minimize the hovering necessity that is forced on long-billed birds by the way long-tubed flowers are presented by plants. Clinging to feed saves a lot of energy and the clinging birds with shorter beaks and longer feet can pollinate and feed legitimately on short flowers, although many rob nectar through the flower base."

The nectar thieves' feeding habit often doesn't seem to damage the flower, says Colwell, and sometimes the flower is able to seal the hole. Otherwise, the hummingbirds access nectar through preexisting openings. The only downside for the flower, besides not being pollinated, is that this mode of feeding makes those flowers less attractive to hummingbirds that feed legitimately and pollinate the flowers, says Colwell. Further research will yield new insights into this and many other questions using the data the team has amassed.

"After 50 years, this has finally come to fruition because of the wonderful colleagues I have had here at UConn. I'm very, very happy about the outcome and very proud of the team we put together."

More information: Robert K. Colwell et al, Repeated evolution of unorthodox feeding styles drives a negative correlation between foot size and bill length in hummingbirds, *The American Naturalist* (2023). [DOI: 10.1086/726036](https://dx.doi.org/10.1086/726036)

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