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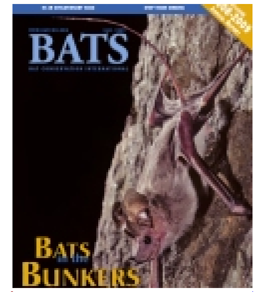

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Going to Great Lengths
Bats & flowers stage an evolutionary race
Nathan Muchhala

After hanging motionless for a spell, the bat suddenly stretches, cat-like, unfurling first one wing, then the other. It yawns widely and extends its tongue. And keeps extending it â€“ longer and longer in a remarkable display. This is a tube-lipped nectar bat, and its tongue, at full stretch, reaches more than 1 1?2 times its body length.

The bat in my screened-in tent in Ecuador laps sugar-water from the bottom of a plastic test tube â€“ and contributes to my efforts to determine why evolution produced such a spectacular tongue.

I discovered this unique bat during fieldwork for my Ph.D. dissertation for the University of Miami. In a paper coauthored with two Ecuadorian biologists, we named the species the tube-lipped nectar bat (Anoura fistulata) because of its distinctive elongated lower lip.

Subsequent research demonstrated that this bat can extend its tongue some 3.3 inches (8.5 centimeters), twice as long as other nectar bats and longer, relative to body length, than any other mammal. Novel modifications of its mouth and throat allow it to store large portions of its retracted tongue in a sleeve of tissue inside the rib cage.

What evolutionary pressures could have brought about such a spectacular tongue? In 2008, I returned to Ecuador with financial support from Bat Conservation International to explore this question.

One possible answer was suggested by Charles Darwin. He hypothesized that the remarkably long tongue of a giant hawk moth in Madagascar evolved in a "race of increasing lengths" with the exceptionally long nectar spur of the Malagasy star orchid. Although the term "coevolution" wasn't coined until the 1960s, this was one of the first descriptions of a coevolutionary process.

Darwin reasoned that, for moths, tongues equal to or longer than flower tubes would be required to reach all of the nectar. From the flowers' perspective, the tubes needed to be longer than moth tongues to ensure that the moth has to push its head into the flower, and thus pick up (or deposit) the pollen found there. A moth's tongue (or proboscis) functions like a straw: nectar is sipped through a groove in the center. So if a moth's tongue is longer than the floral tube, it could consume all of the nectar while hovering outside of the flower and never actually touching the flower's reproductive parts; the flower goes unpollinated. The result of those opposing needs is a repetitive loop: the flower grows longer to ensure pollination, while the moth's tongue lengthens to reach more nectar, which causes the flower to grow longer, and so on.

The diet of tube-lipped nectar bats includes nectar from the flower Centropogon nigricans, which stores its nectar at the base of 3- to 31?2-inch (8- to 9-centimeter) tubes. Could this plant and bat have coevolved in a race similar to that envisioned by Darwin? As with moths, the benefit of increased tongue lengths in nectar bats is clear: it allows the animal to

reach more nectar. The value of long tubes for the plant, however, is not as obvious. Unlike moths, Anoura fistulata and other nectar-eating bats drink nectar by extending and retracting the tongue, much as a dog laps up water. This means that the bats will fully insert their heads into even short-tubed flowers and extend their tongues only as far as needed to reach the nectar. So why would evolving a longer tube help the flower?

I suspected that although bats will fully insert their heads into any flower, they push especially hard against flowers with long tubes in an effort to reach that last drop of nectar. This extra force should mean that they pick up and deposit more pollen grains, which allows the plant to produce more seeds.

To test this idea, I traveled into the cloud forests of Ecuador's Bellavista Reserve. With the help of three field assistants, I set up nets around C. nigricans flowers and captured four tube-lipped nectar bats. I held these bats for four days in separate screened tents and performed two sets of experiments with them.

The first experiment involved flower proxies: plastic test tubes cut to six different lengths. I attached wire "stems" to the tubes and placed them in front of protractor-like plates designed to measure the force with which the bats pushed into the tubes. I poured small amounts of sugared water into the tubes, set them up in the tents and recorded the bats with night-vision video cameras. I scored each bat visit in terms of duration and force. The experiment showed that longer tubes resulted in longer visits, but had no effect on visit force.

Next, I used semiartificial flowers. I cut actual C. nigricans flowers near the base of their tubes and placed them in either of two different lengths of plastic tubes. This allowed me to manipulate the length of flowers without affecting the reproductive parts.

Like most flowers, those of C. nigricans have both male and female reproductive parts. Each flower goes through a male phase, producing pollen and placing it on visiting pollinators, for several days, followed by several days of a female phase, during which it collects pollen from pollinators to fertilize its seeds. Flower length could affect the success of either the male phase (how much pollen is "exported") or female phase (the "import" of pollen).

For each of the two tube lengths, I allowed the captive bats to visit a single male-phase flower followed by a single female-phase flower. I then collected pollen from the female-phase flowers and used a microscope to count how many grains had been transferred. Results showed a strong benefit to increased flower length: longer male-phase flowers exported 123 percent more pollen than the shorter flowers, and longer female-phase flowers received 144 percent more pollen.

I filmed these visits to the semiartificial flowers and recorded visit duration and force. Unexpectedly, the flowers that were most successful in transferring pollen did not receive longer or more forceful bat visits. Although longer flowers clearly enjoy better pollination, the reason remains unclear. I suspect that my method of measuring force was inadequate for the task, recording forces that push the flower up or down rather than those pushing directly into the flower.

But regardless which aspect of bat behavior is responsible for the difference, this research clearly demonstrates that bats are more efficient pollinators of longer flowers. In combination with a length benefit to bats â€“ longer tongues give access to more nectar â€“

this sets up the conditions for a coevolutionary race between plant and bat. The remarkable tongue of this recently discovered bat likely evolved in a "race of increasing lengths" similar to that envisioned by Darwin more than 150 years ago.

Not surprisingly, C. nigricans is completely dependent on tube-lipped nectar bats for pollination and only occurs where the bat species occurs. That's not so for the bats, howÂ-ever. I found pollen from other flowers on the fur of tube-lipped nectar bats. And although the range of the plant is restricted to a small part of the northwestern slopes of the Ecuadorian Andes, these bats have been confirmed throughout the eastern and western slopes and as far north as central Colombia.

This raises a whole new set of questions. For instance, what other flowers do tube-lipped nectar bats visit? Have other long-tubed flowers coevolved with it? Are the tongues of tube-lipped nectar bat populations shorter in forests with shorter flowers, as the coevolutionary scenario would predict? I hope to study the diet of these amazing bats throughout the rest of their range in order to address these sorts of questions.

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