Something to Howl About

To earn her spurs as a tropical biologist, the author decided to study a parasite that even her colleagues wanted to avoid.

By Katharine Milton

In 1974, as a greenhorn to the tropics, I traveled to Panama to begin a study of the dietary behavior of wild howler monkeys on Barro Colorado Island. The island was separated from the mainland in 1912, during the construction of the Panama Canal; its six square miles of forest now serve as a field station managed by the Smithsonian Tropical Research Institute. In my first exhausting but exciting weeks sifting into new quarters and rearing on my own into the forest, I noticed that many howler monkeys had peculiar lumps under their fur, usually around the neck and throat but sometimes on the chest or stomach, on the back, even on a cheek or above an eye. The lumps were large, and they often made the monkeys appear grotesque; infants looked as if they had two heads or a massive gutter; many adults resembled something out of B-movie sci-fi.

Curious, I asked other biologists on the island about the lumps. They, too, were fairly new to the site, but their answer was immediate: “Bot fly larvae.” Bot fly larvae? Eek! I’d never heard of them, but they sounded pretty alarming. I learned that Dorsatobia hominis, the “human” bot fly, is well known to science because of the diabolically clever way it finds hosts for its offspring. A female ready to deposit her eggs seeks out a blood-sucking insect, generally a fly or mosquito. She grasps the insect—known in the trade as an egg potter—and holds it firmly in flight while she attaches rows of her eggs to its abdomen with a water-insoluble glue. She then releases the insect unharmful. Now, though, it is neatly decorated with twenty-or so bot fly eggs. There the bot fly embryo grows quietly until it’s ready to hatch.

The trigger for hatching comes from a host animal species. When the egg potter makes a meal from the blood of a mammal—a meal required for the insect’s own reproduction—the bot fly embryo, by now developed into tiny threadlike larvae, sends the heat from the mammal’s body and bursts from the eggs. The larva burrows directly into the mammal’s skin, where they make themselves at home.

Each larva lives in what is known as a wattle, a pocket or chamber that forms in the host’s skin. In its wattle, which has a small breathing hole open to the air, the larva feeds on 2
A veterinarian friend in Panama named Nathan B. Gale, the director of the Veterinary Public Health Laboratory, took an interest in the problem. Sick or wounded wild animals were occasionally brought to his clinic for treatment, and when a howler monkey arrived one day, he removed its body from the soil, put it in a preserving, and mailed it to an entomologist friend at Washington State University, Dr. E. Paul Cota. Cota recognized that they were larvae of an entirely different species, A. bari, the howler-monkey but fly, that was a big surprise, but also a big relief: the reason only howler monkeys were affected with the larvae was that the but fly is host-specific.

Cota had written an extensive review describing the members of Cucurbitale, the New World family to which both Dermatobia and A. bari belong. From Cota’s review it was clear that Dermatobia is a marvel. Other species in the family tend to associate closely with just one mammalian host, typically a rodent or rabbit. In general, they also place their eggs not on egg porters but rather in areas of habitat likely to be visited by the host. A nectar-visiting fly, for instance, might leave its eggs on grass or twig near the trail of its specific rodent host. When the rodent passes by, the host’s body allows the larvae, which emerge instantly from their egg and attach themselves to the animal’s whiskers or fur.

In most cases the larvae enter the host’s body not by burrowing directly into the skin but by passing through the nostril, eyes, or mouth. Larvae then spend several days migrating through internal organs and tissues, finally coming to rest at a preferred site on the host’s body. The neck region is the most frequent target for the howler-monkey but fly larvae, but wherever it settles, it opens a breathing hole and encloses itself in its wrinkle to mature, a process that takes six or seven weeks.

So little was known about A. bari, however, that I decided I was in an ideal place to study its life cycle. My first task was to find out what the adult fly looked like. No one in Panama, including me, actually knew. The thing to do was to collect some larvae and wait for them to mature.

Collection was easy enough. The larvae were plentiful on recently dead howler monkeys in the forest or howler monkeys temporarily captured for marking or weighing. I could easily find a few in the forest or in a well-stocked room. All I had to do, I assumed, was check them each day and collect my adult
flies as they emerged from pupation. But day after day the enclosures remained empty. After nearly five weeks of waiting, I was almost positive that humidity and fungus had killed all the pupae. Then on the forty-eighth day, when I went to check the screened enclosure in the room, I found a large fly buzzing around inside. My cup was more than half as much long, covered with short, dense, velvety black hair, and had transparent, amber-brown wings. My joyful cries alerted everyone within shouting distance to come and see this amazing fly. I named her Lucille.

The life of "Lucille, the Famous Fly"—as she became known to everyone on Barro Colorado Island, may have been a happy one, but it was not long. Flies of the Cataractidae family emerge from their pupal cases, mate, and die in just a few days. Just three and a half days after Lucille first appeared, I witnessed her death chases. The cause was old age. It was a sad incident. Her pinned specimens will occupy a place of honor in my office in Berkeley.

Above a year later I began a research collaboration with Douglas D. Colwell, a bot fly expert at the Lethbridge Research Centre in Alberta, Canada. In Panama Colwell and I collected more than fifty third-instar larvae, and he took them back with him to his lab in Canada. Colwell proved to be a deft hand at raising flies. Ultimately he was blessed with fifteen males and nine females. The female flies were noticeably larger, and their eyes spaced more widely apart. The live male bot flies had a red vertical stripe on each eye—a striking characteristic that fades and disappears after death (see lower photograph on preceding page). Lucille lacked this distinction, by the way confirming that she was a female, and thus correctly named.

Bot flies at Lethbridge were willing to mate, and each female deposited, on average, 1,400 black, ridged eggs, in rows of about 250 each. The females preferred to lay their eggs in the creases of moist paper towels. (For the laboratory bot flies that was the end; no moths were used in these experiments.) We have not found the bot flies’ site of choice for egg laying in the natural environment, though some prime suspects are tree leaves and branches.

No one has seen Achatinafasciata mate in the wild, but males in the Cataractidae family typically develop more quickly than females do, and then gather in trees or other high places. Again, no one knows why, but perhaps male in a group can attract more females per male, on average, than a single male could acting alone. That would improve each male's chances of mating, despite the competition. In any case, unmated females that fly to the group appear to have some way of advertising their virgin status, and the waiting males pursue them. When a male succeeds in clamping a virgin female, the pair alights to copulate copulation.

Although the details of bot fly life history fascinated me, I particularly wanted to understand the interactions
of howler-monkeys for flies and their hosts. Received entomological wisdom holds that a "prudent" parasite does not kill its host. Such restraint might seem particularly important for a host-specific parasite such as *M. amoena*. After all, if the parasite eliminates its natural host, it has nowhere to raise its larvae. Yet many of the dead howler monkeys I found in the forest still bore a large number of bot fly larvae—ten or more. Because one third to one half of a larva can weigh more than a tenth of an ounce, the larva would be a heavy metabolically load, particularly for an immature monkey. My census of howler monkeys, about 1,200 individuals, also showed the proportion of juveniles was unusually low. Although about 300 infants were born each year, I estimated that there were only about 400 juveniles in the population. Perhaps, at times, "prudent" parasites weren't being quite prudent enough.

For the next five years I kept a monthly record of the number of bot fly larvae present in a representative sample of howler monkeys. I found a few afflicted monkeys in every month of the year, but the infestations seemed to peak in two or three times a year, both in the number of monkeys afflicted and in the average number of bot fly larvae present on each monkey. The peaks came during the rainy season, which lasts from May through November, although the largest of them usually did not take place until July or later. Throughout that same five-year period I also kept track of howler-monkey deaths. Scientists and visitors on the island alerted me or my assistants whenever a monkey was found dead, and we collected the remains. Although the procedure couldn't give us a complete tally of deaths, it did enable me to chart the pattern of annual mortality. The death rate was highest in July through November, the mid- to late rainy season. At that time of year the energy-rich fruits and protein-rich young leaves the monkeys prefer to eat are in short supply. Were the high death rates caused by a food shortage, or by the cool, wet, cloudy weather? Perhaps those factors played a role, but, by themselves, they probably weren't sufficient. I found no overt signs of starvation or illness in the population. But I did note that bot fly larvae infestations peaked at the same time. A more complete account of the higher death rates probably goes something like this. The immune system of a howler monkey in good physical condition appears able to limit the number of larvae that can establish themselves at any one time. But howler monkeys in poor condition seem to jeopardize. Repeated attacks by bot fly larvae may exhaust the howler monkey's fat reserves, which would normally carry them through the annual food shortages. Immune system of fat-depleted hosts would be particularly at risk, combined with the stresses of cool, wet weather and low-quality food, many such monkeys would die.

Our data on infestation and mortality, as well as similar accounts of other bot fly-host interactions, suggest that populations of howler monkeys and their bot flies swing up and down like many other populations of predators and prey. When the howler-monkey population increases in number, all else being equal, the density of the howler-monkey bot flies increases as well. At times, though, the bot flies escalate their number outweigh prey. This leads to the deaths of so many howler monkeys that their population drops. But here the bot flies pay for their violation of the "prudent parasite" rule. They die off for lack of hosts. Hence the infestation time drops, and the howler monkey population gradually recovers.