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 howler monkey parasites. The island was separated from the mainland in 1912, during the construction of the Panama Canal, a site of four miles of forest since the 19th century, managed by the Smithsonian Tropical Research Institute. In my first exhausting but exciting week settling into new quarters and venturing on my own into the forest, I noticed that many howler monkeys had peculiar lumps under their tails. Sometimes, the sores would sometimes be 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 up a massive geyser; many adults resembled something out of a 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: "Howler flies". The flies from the butterflies? I'd never heard of them, but they sounded pretty alarming. I learned that Dermanota hominum, the "human" howler fly, is well known to science because of the dubiously clever way it finds hosts for its offspring. A female ready to deposit eggs seek out a blood-sucking insect, generally a fly or mosquito. She grasps the insect—known in the trade as an egg porter—and holds it firmly in flight while she attaches rows of eggs to it with a water-soluble glue. She then releases the insect unharmed. Now, though, it is nearly decorated with twenty-orange howler fly eggs. Each fly egg hatches quietly until they're ready to hatch. The trigger for hatching comes from a third animal species. When the egg porter makes a meal from the blood of a mammal—a nasal required for the insect's own reproduction—the howler fly embryonates, hatches, and burrows from the mammal's body and erupts from its 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 howler fly larva (L diiristrus) pictured at the third-moon stage, the last stage before pupation. Staining out cream colored, the third phase has additional weight and darkness. A fully developed larva is nearly an inch long and can weigh more than a tenth of an ounce. Male howler fly larva (L diiristrus) has a distinctive stripe on each eye. The insect is about seven-eighths of an inch long.

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 in for treatment, and when a howler monkey arrived one day, he removed it from its box and put it in a preservation, and mailed it to an entomologist friend at Washington State University in Pullman, the later Paul C. Catt. Catt recognized that they were larvae of an entirely different species, Acanthorhynchus barbouri, the howler-moon howler fly. That was big surprise, but also a big relief: the reason the howler monkey was infected with the larvae was that the fly is host-specific. Catt had written an extensive review describing the members of Cletrecbidae, the New World family to which both Dermanota and Acanthorhynchus belong. From Catt's review it was clear that Dermanota is a murderer. Other species in the family tend to associate closely with just one mammal species, typically a rodent or a 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 reduced set porters, for instance, might leave its eggs on grass or trees near the trail of its species. Dermanota, which passes by, the heat from its body alarm the larvae, which emerge instantly from their eggs 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 nostrils, 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-moon howler fly larva, but wherever it settles, it opens a breathing hole and encases itself in its wrinkle to mature, a process that takes six or seven weeks.

So little was known about Acanthorhynchus barbouri, 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. When fully developed, the larvae were black and hung an inconspicuous-looking miniature hand grenade [see upper photograph on this page].

But getting the larvae to mature was less straightforward. I set up two screened enclosures where they could pupate, one in the forest and one in an indoor room. All I had to do, I assumed, was check them each day and collect my adult
A bout a year later I began a re-
search collaboration with Dou-
glas D. Colwell, a bee fly expert at the 
Lethbridge Research Centre in Al-
berta, 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. Col-
well proved to be a deft hand at rais-
ing 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 pho-
tograph on preceding page). (Lucille lacked 
this distinction, by the way, confirm-
ing 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, ridge eggs, 
in rows of about 250 each. The fe-
males preferred to lay their eggs in the 
creases of moist paper towels. (For the 
laboratory bot flies that was the end;
no monkeys were used in these ex-
periments.) We have still not found 
the bot flies’ site of choice for egg lay-
ing in the natural environment, 
though our prime suspects are tree 
leaves and branches.

No one has seen *Babontomyza* mate 
in the wild, but males in the Cutter-
bridge family typically develop more 
quickly than females do, and then 
spend much time in trees or other high places.

Again, no one knows why, but per-
haps males in a group can attract 
more females per male, on average, 
than a single male could act alone.

That would improve each male’s chances of mating, despite the com-
petition. In any case, unmated females 
that fly near the group appear to have 
some way of advertising their virgin status, 
and the waiting males pursue 
them. When a male succeeds in clas-
ing a virgin female, the pair slights to 
complete copulation.

Although the details of bot fly life 
history fascinated me, I particularly 
wanted to understand the interactions

![Bot fly in a Cecropia tree, whose young leaves as well as flowers and fruits are an important source of food.](image)
of howler-monkey bot 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 Alouattatamia. 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-instar larva can weigh more than a tenth of an ounce, ten larvae would be a heavy metabolic load, particularly for an immature monkey. My census of howler monkeys, about 1,200 individuals, also showed the proportion of juveniles was suspiciously low. Although about 300 infants were born each year, I estimated that there were only about 150 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 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, though 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 larva 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 in jeopardy. Repeated attacks by bot fly larvae may exhaust the howler monkeys' fat reserves, which would normally carry them through the annual food shortages. Immature or 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 their prey. When the howler monkeys increase 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 numbers out of proportion to their hosts. That 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 rate drops, and the howler monkey population gradually recovers.

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