NATURAL HISTORY

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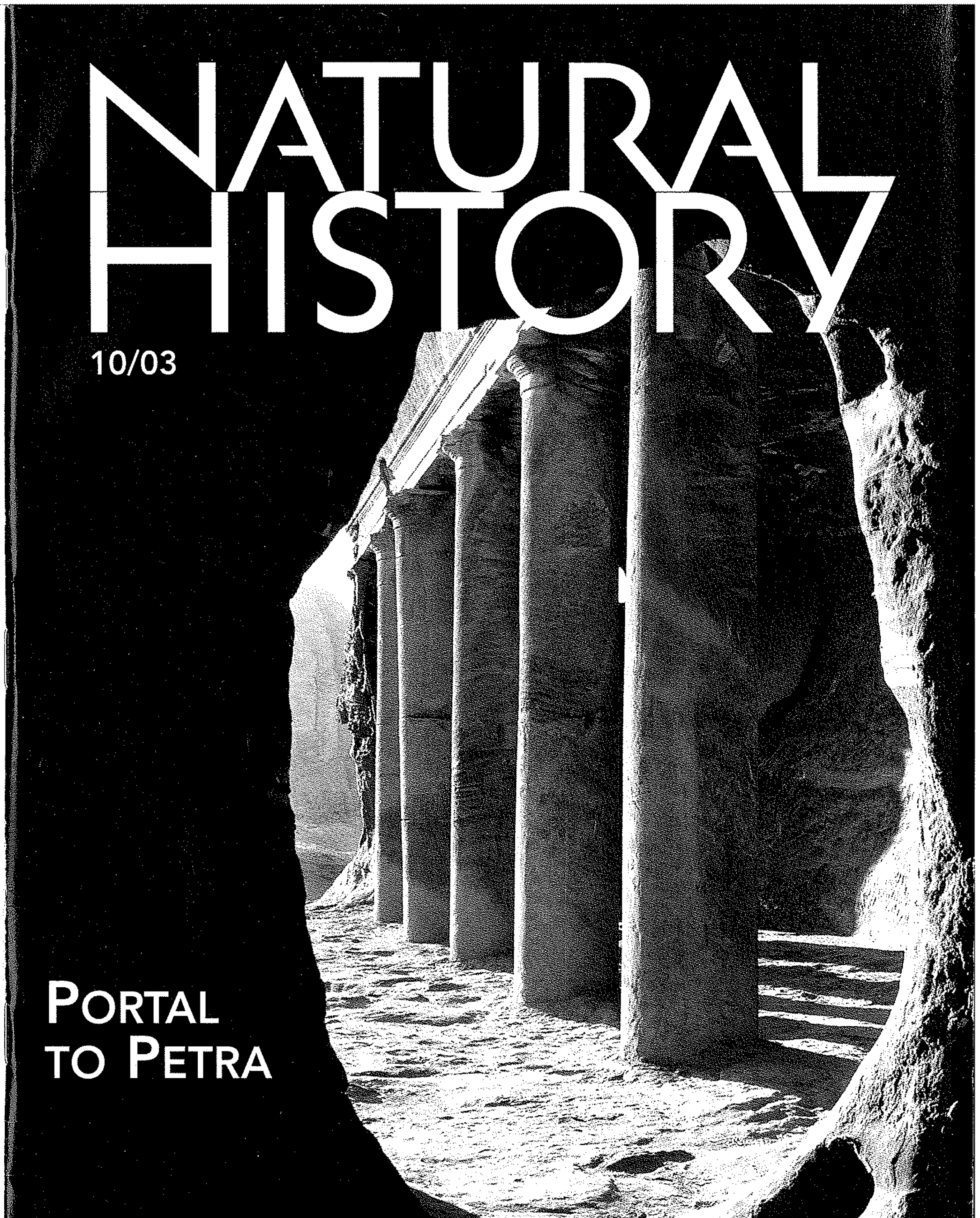


PORTAL TO PETRA

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 settling into new quarters and venturing 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 goiter; many adults resembled something out of B-movie sci-fi.

Juvenile howler monkey is heavily burdened with bot fly larvae on its neck. Each larva develops in a pocket of the monkey's skin, conspicuous for its open breathing hole. The parasites take a toll on their hosts and can lead to death, particularly in immature or weakened individuals. This juvenile is only half the size of an adult; it probably weighs between six and eight pounds.

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 *Dermatobia 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 porter—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 unharmed. Now, though, it is neatly decorated with twenty-odd bot fly eggs. There the bot fly embryos grow 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 meal required for the insect's own reproduction—the bot fly embryos, by now developed into tiny threadlike larvae, sense the heat from the mammal's body and burst from their eggs. The larvae burrow directly into the mammal's skin, where they make themselves at home.

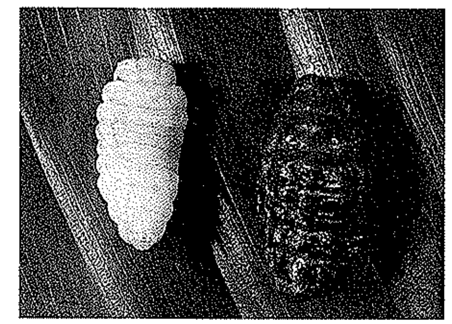
Each larva lives in what is known as a warble, a pocket or chamber that forms in the host's skin. In its warble, which has a small breathing hole open to the air, the larva feeds on a rich soup of tissue fluids produced by the host. There the larva passes through three more "instars," or developmental stages, growing larger all the while. At the end of the third instar, the larva wriggles out of its warble, falls to the ground, and burrows into the soil to pupate. Some weeks later an adult fly emerges from the soil to seek a mate, and the cycle is repeated. Because most egg porters are not picky about whose blood they sip, the larvae of *Dermatobia hominis* can end up on almost any warm-blooded animal—from a squirrel to a monkey to (as the name implies) a human being. Double Eek!

My fellow scientists on the island regaled me with dramatic tales of intensely painful bot fly larvae growing in inaccessible places, in disgusting places, in very private places. According to these battle-scarred veterans, the best way to get rid of a larva is to plaster a thick piece of bacon on your skin above the breathing hole of a larva's warble. In desperation (since bot fly larvae have to breathe), the larva crawls out of its warble and up into the bacon. Then you whip off the bacon with the larva trapped inside. Poor howler monkeys, up in the trees with no bacon, nor even with the manual dexterity to force larvae out of the warbles by hand—my heart went out to them!

I went on with my field study, and months went by. Thankfully, I acquired no bot fly larvae, and neither did anyone else on the island. In fact, none of the other monkey species on the island—capuchins, spider monkeys, tamarins—were infested with bot fly larvae either, even though during some months virtually every howler monkey I saw bore multiple warbles. The other biologists noticed the same thing. As it turned out, none of these scientist-raconteurs had ever gotten a *Dermatobia* larva on Barro Colorado Island; all their exciting stories were based on experiences elsewhere in the neotropics. Perhaps these larvae were not that same notorious pest after all.

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 bot fly larvae, put them in a preservative, and mailed them to an entomologist friend at Washington State University in Pullman, the late E. Paul Catts. Catts recognized that they were larvae of an entirely different species, *Alouattamyia baeri,* the howler-monkey bot fly. That was a big surprise, but also a big relief: the reason only howler monkeys were afflicted with the larvae was that the bot fly is host-specific.

Catts had written an extensive review describing the members of Cuterebridae, the New World family to which both *Dermatobia* and *Alouattamyia* belong. From Catts's review it was clear that *Dermatobia* is a maverick. 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 rodent bot fly, for instance, might leave its eggs on grass or twigs near the trail of its specific rodent host. When the rodent passes by, the heat from its body alerts the larvae, which emerge instantly from their eggs and attach themselves to the animal's whiskers or fur.



Howler-monkey bot fly larvae (upper photograph) are pictured at the third-instar stage, the last stage before pupation. Starting out cream colored (left), the third instar puts on additional weight and darkens (right). A fully developed larva is nearly an inch long and can weigh more than a tenth of an ounce. Male howler-monkey bot fly (lower photograph) has a distinguishing stripe on each eye. The insect is about seven-eighths of an inch long.

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-monkey bot fly larva, but wherever it settles, it opens a breathing hole and ensconces itself in its warble to mature, a process that takes six or seven weeks.

So little was known about *Alouattamyia baeri,* 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 heavily corrugated, resembling miniature hand grenades [*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 another in a well-aired room. All I had to do, I assumed, was check them each day and collect my adult

Howler monkey rests in a Cecropia tree, whose young leaves as well as flowers and fruits are an important source of food.

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 fungi 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 captive was more than half an inch 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 Cuterebridae 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 throes. The cause was old age. It was a sad moment. Her pinned remains still occupy a place of honor in my office in Berkeley.

About 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 monkeys were used in these experiments.) We have still not found the bot flies' site of choice for egg laying in the natural environment, though our prime suspects are tree leaves and branches.

No one has seen *Alouattamyia* mate in the wild, but males in the Cuterebridae family typically develop more quickly than females do, and then gather in trees or other high places. Again, no one knows why, but perhaps males 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 near the group appear to have some way of advertising their virgin status, and the waiting males pursue them. When a male succeeds in clasping a virgin female, the pair alights to complete copulation.

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