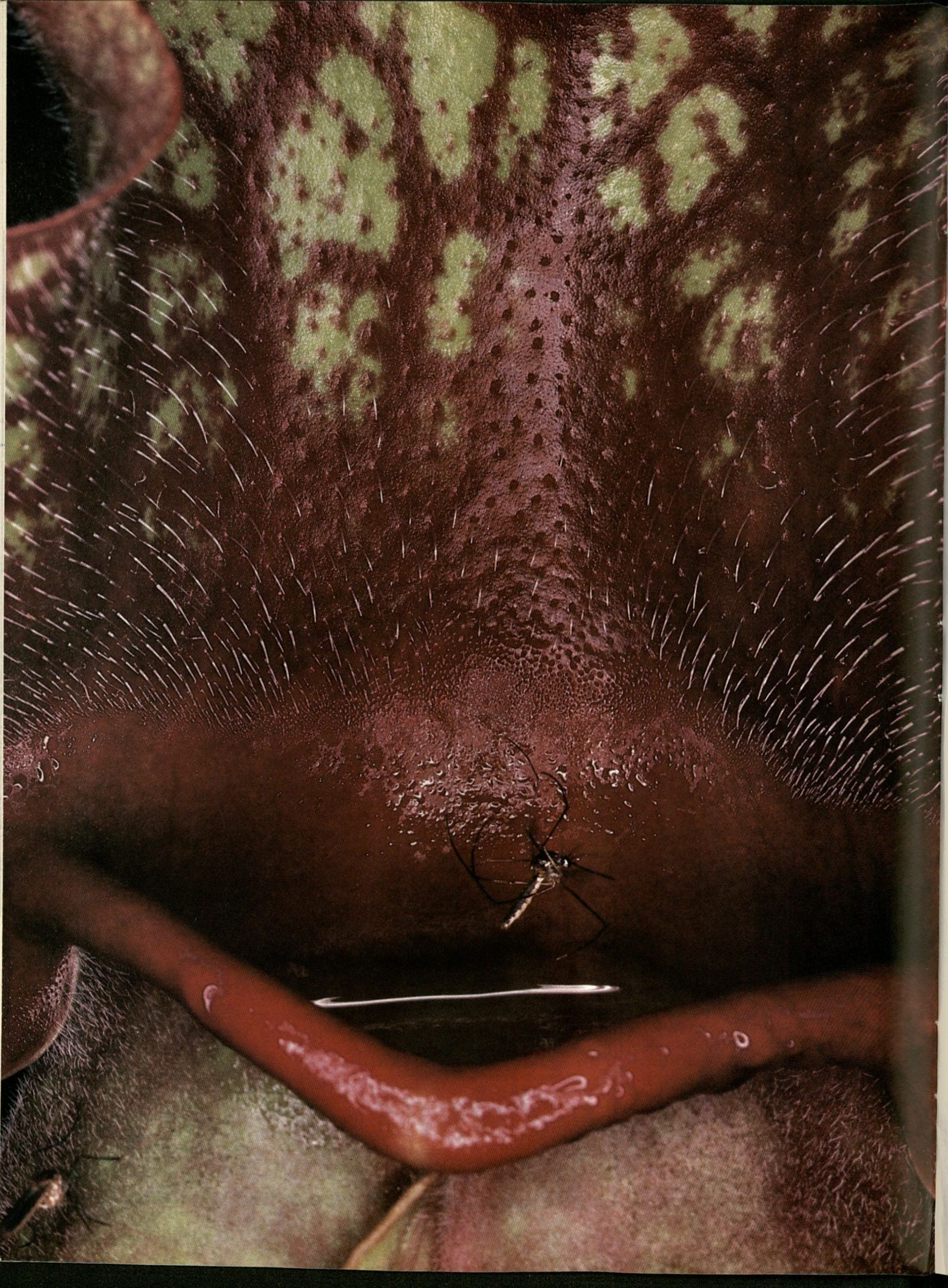

Life in a Deathtrap

These mosquitoes thrive in the stomach of a carnivorous plant

by William Bradshaw and Christina Holzapfel

The purple pitcher plant is a deathtrap for insects, millipedes, spiders, and even small frogs. This carnivorous plant has hollow, pitcher-shaped leaves that each contain a small pool of rainwater, in which their victims drown. However, to larvae of the pitcher plant mosquito, *Wyeomyia smithii*, this pitfall trap is a sheltered nursery—an energy-rich, enemy-free habitat.

Each pitcher has a hood studded with hundreds of stiff hairs. Nectaries at the base of each hood secrete chemicals attractive to insects and other arthropods, while the lip on the rim opposite the hood serves as a convenient landing pad. When lured from this perch to the fragrant nectaries, a potential victim finds no footing on the hood's downward-pointing hairs and falls into the water. Since it cannot climb up the pitcher's slick, waxy walls, it eventually drowns. As it decomposes, the carcass nourishes not only the host plant but also a small community of aquatic organisms, including mosquito larvae.

Although a fall into the pitcher plant's pool means certain death for most insects, several creatures besides mosquito larvae make it their home. Flesh fly maggots hang from the water's surface and, like vultures, seek out and feed on dead insects. When the half-eaten remains sink to the bottom, midge larvae chew them further. Both of these scavengers hasten the disintegration of the corpse, creating greater opportunities for bacteria to feed. The bacteria, in turn, are eaten by a variety of protozoans. Finally, the mosquito larvae, with their brushlike mouthparts, filter out the bacteria, protozoans, and leftover bits of the victim for their dinner.

Avoiding entrapment, a female pitcher plant mosquito hovers just above the pool at the mouth of a carnivorous pitcher plant. Her swollen abdomen indicates that she is about to deposit an egg on the surface of the water.
Francis Gilbert

A mutually beneficial relationship has evolved between the pitcher plant and its inhabitants, involving gas and nutrient exchange. The leaves release oxygen into the water as a byproduct of photosynthesis. The aquatic organisms, on the other hand, give off carbon dioxide as a byproduct of their respiration and nitrogen-rich ammonia as a byproduct of their metabolism. During the afternoon, increased heat and light accelerate the leaves' oxygen production and boost their need for carbon and nitrogen. This cycle in the leaves meshes with the increased respiration and metabolism of the aquatic community. In fact, the microhabitat is very rich in oxygen; its resident midge species is probably descended from swift-stream dwelling ancestors, and the pitcher plant mosquito may be the only mosquito whose larvae can develop and mature without atmospheric oxygen. While these organisms enrich the pitcher with their wastes, the host plant not only provides oxygen for them to breathe but also attracts dinner for its "guests" and cleans up the scraps.

As we often observed during our studies of mosquitoes in Florida's Appalachicola National Forest, the female is very choosy about where she lays her eggs. We observed a female mosquito fly to a cluster of pitcher plants, hover over one plant, then head directly into its youngest open leaf. Next, she flew up and down inside the pitcher. She dipped her abdomen three times toward the surface of the plant's enclosed pool and, each time, without touching the water, deposited a single white egg. Then she visited two other plants in the cluster, repeated the same behavior, and departed, having laid eggs only in the youngest pitcher of each plant.

A mosquito's timing of her egg laying must be precise, because the predatory effectiveness of pitcher plant leaves varies with their age. For a few days after opening, the leaves remain soft as they expand and fill out. If trapped, a vigorous insect could tear its way out. Thus damaged, a leaf could not repair itself or hold water. Seven to ten days after opening, the leaves darken, harden, and begin to attract insects. They are most efficient predators from two to four weeks of age, but their ability to capture prey declines sharply thereafter; they remain green and photosynthesize for about fifteen months.

Thus, the female mosquito's egg-laying behavior anticipates the future needs of her offspring. When her larvae hatch and require increasing quantities of food, the young leaf she has selected will be capturing the most insects. Natural selection favors females that deposit their eggs in these young leaves and rewards the first group hatching in them. Larvae hatching later find that resources have been consumed by earlier broods and that the plant no longer attracts many new prey. Latecomers become stunted adults; if female, they live shorter adult lives and produce fewer offspring. Also, because they can filter more and larger food particles, the first to hatch gain a competitive advantage over smaller, younger larvae.

One curious fact about pitcher plant mosquitoes is that females from only the southern populations are blood feeders. In the insect's northern and southern ranges, females produce and lay their first batch of eggs without the nutritional boost of a blood meal from a vertebrate host. But southern females must bite before they can produce their second and all subsequent broods. We have seen southern females taking blood not only from ourselves but also from box turtles. Females from populations in New Jersey and northward have never been observed to bite and may produce repeated batches of eggs without blood feeding.

Of its tropically distributed genus, only the pitcher plant mosquito has invaded and survived northern habitats. Following the distribution of its host plant, it ranges from the Gulf of Mexico to Canada, from Saskatchewan to Labrador. Indeed, the purple pitcher plant is common in the bogs of Newfoundland and has been designated the province's official flower.

Freezing temperatures kill mosquito larvae, but entomologist G. C. Paterson in New Brunswick, Canada, has found that snow can insulate the bogs. During winter, larvae hibernate and survive within pitchers beneath the blanket of snow, even when air temperatures above the snow plummet to −40°. The beginning and end of hibernation are triggered by the mosquito's internal biological clock and the length of daylight. Progressively shorter days induce and maintain a state of reduced metabolism, while longer days avert or end it. Larvae rely upon the length of day to cue hibernation even when conditions are otherwise favorable for development. In eastern Massachusetts, for instance, temperatures are warm and food is abundant in mid-August, but the shortening days halt development and the larvae enter hibernation, anticipating the future winter. They do not reinitiate development until April, when lengthening days herald the coming of spring.

The life cycle of the pitcher plant mosquito has evolved in synchrony with its host. By selecting only young leaves in which to deposit their eggs, female mosquitoes coordinate their offspring's development with the leaves' life cycle. Pitcher plant leaves capture resources, remove waste gases and metabolites, and constitute a predator-free nursery for developing larvae. In addition, the leaves provide a haven from extreme winters. Through the use of a highly accurate biological clock, the mosquitoes program their seasonal development in concert with the progressively harsher northern winters. This mosquito—alone among the 300 most closely related tropical species—has been able to invade, and thrive in, a northern, temperate climate because of the protected habitat in which it lives: the stomach of a carnivorous plant. □

The Swarms of Summer

Once upon a time in Florida, clouds of marsh mosquitoes set long-distance records

by D. Scott Taylor

Perched in the top of a twenty-five-foot-high mangrove tree overlooking a sixty-acre salt marsh, Jim Haeger nervously awaited sunset on an August evening in 1955. This scientist from Florida's Entomological Research Center had waited much of the summer for the marsh below him to produce a huge "brood" of the black salt-marsh mosquito (*Aedes taeniorhynchus*), and now the moment had come. The estimated 2 billion larvae had developed throughout the week, and earlier in the day the adults had emerged and climbed into the reeds and swamp grass preparatory to their migratory flight. At precisely fourteen minutes past sunset, as if cued by an unheard gong, the brood took flight. Later, Haeger described the event as follows:

> There was a massive movement of ascending mosquitoes, almost darkening the sky. The flight just above my head consisted of a great band of millions of mosquitoes, all moving in unison, probably 2–4 feet thick and several hundred feet wide. I would compare the movement to a huge belt or tread of a caterpillar tractor moving on rollers over the tops of the trees, only missing them by a few inches and dipping down between. There was a tremendous singing hum of millions of frenzied wing beats.

Twelve minutes later it was over, and the air was calm and free of mosquitoes. Haeger was impressed, and a few days later so were people living miles away in the flight path of the brood, when the females sought their first blood meals. This spectacle is not often witnessed in modern Florida, thanks to the efforts of mosquito-control districts, which were organized in 1927 to combat the salt-marsh mosquito problem. However, the aboriginal inhabitants and early homesteaders must have been hardy souls to tolerate the biting swarms. Early Indian tribes may have moved their villages seasonally when their smudge fires were unable to keep the insects at bay. A century ago, Florida residents commonly kept whisk brooms hanging near their front doors so that people entering their homes could first brush off the clinging mosquitoes.

Over the years, the salt marshes that originally bordered both coasts of Florida have been ditched, dredged, and filled, or diked off and kept flooded (female salt-marsh mosquitoes must lay their eggs on damp, unflooded soil). Nevertheless, the black salt-marsh mosquito remains Florida's main pest species.

This wily creature is hard to keep in check for two reasons: it is incredibly fecund (10,000 eggs have been counted in one square foot of marsh sod), and more importantly, it is a strong flier (while some species of mosquitoes never venture more than a few hundred feet). Entomologists have trapped salt-marsh mosquitoes 110 miles from shore, and shrimp boat crews have been attacked at an equal distance. In the 1950s, some entomologists began to suspect that the species might be truly migratory, with large populations moving from one breeding site to another.

Research showed that massing of great numbers of individuals begins in the larval stages, when synchrony of egg hatching and development leads to enormous densities in the marshes. In their later stages, larvae cluster together to form huge "rafts" twenty feet or more in diameter. The larvae disperse widely over the marsh surface at night, but at sunrise they aggregate and "migrate" toward the shoreline, where the rafts are formed. These early life-history observations and the mass exodus of the adults from the breeding site stimulated scientists to look further at the insects' flight behavior.

How far and how fast do the swarms of adults travel? In 1951, entomologist M. V. Provost and a team of twenty-six workers tried to answer this question in the most grueling and exhaustive series of mark-release studies of mosquitoes ever undertaken. Provost marked a total of 6 million larvae with a radioactive tracer, raised them to adults, and released them on the east and west coasts of Florida. An as-