Samurai Aphids

SURVIVAL UNDER SIEGE

ARTICLE AND PHOTOGRAPHS BY
MARK W. MOFFETT

Clambering about on a dangling white mass of Asian flowerfly eggs, two aphids crush one egg after another between their powerful forelegs. One begins the return climb to the bamboo above (facing page), where the rest of the aphid colony lies just out of view. Suddenly the wind whips the thread, setting the eggs into a spin so swift that the aphids become a blur. For a few seconds the climbing aphid clings precariously to the thread before being flung five feet—about a thousand times the insect's length—to the ground below. Lost from her colony, the fallen aphid is doomed.

This drama unfolds within a clattering clump of bamboo on a forested hill near Kagoshima, Japan. I had been watching the tiny silk strand (half a centimeter long) for several days and had seen this incident repeated half a dozen times.

Why do these *Pseudoregma bambucicola* aphids hang their fate on such a slender thread? Because they are the exclusive food of this flowerfly's larvae, and killing the eggs may reduce the depredation of the aphid colony.

Indeed, the egg-crushing aphids are soldiers—sterile females that go out of their way to defend the reproductive members of the society. Using enlarged forelegs and armored heads reminiscent of the helmets of ancient Japanese samurai warriors, *Pseudoregma* soldiers fight off a battery of predators that assault the colony.

Of some 4,000 aphid species only about 20—most from the Orient—are known to breed soldiers. Those of *Ceratoglyphina bambusae* even attack people; their bite causes an intense itch. Researcher Utako Kurosu (left) extends a pole tipped with clippers into a tree to collect the large white galls that house this species of samurai aphid.

Aphid soldiers were a revelation when first described by Japanese scientist Shigeyuki Aoki in 1977. He and his wife, Kurosu, are among the few scientists forging the way in aphid-soldier research.

Pseudoregma aphids were one of the first samurai species Aoki discovered. Here members of a colony cluster on a freshly sprouted bamboo shoot (left), extracting plant sap through elongated mouthparts in much the same way a mosquito sucks blood. Exuding a snowy dusting of wax, they belong to a group known as woolly aphids.

Scattered among plump winged and wingless aphids are soldiers. These slender females are actually nymphs (immature aphids) of unusual appearance. Compared with other nymphs in the colony, which grow to adulthood after molting several times, aphid soldiers grow little if at all. Trapped in juvenile bodies, they cannot reproduce.

Although aphids are gregarious, colony members in most species show no social behavior. However, samurai species are comparable to termites, ants, and some wasps and bees—there is a division of labor, with some individuals devoting their lives to protecting the colony. Scientists believe this cooperative behavior may be the result of close family ties within the group. The soldiers' altruism ranks samurai aphids among the most social of animals.

ACTUAL SIZE OF APHID CLUSTER AT LEFT

Confronted by predators, aphids of other species try to flee—or they may kick an enemy or smear it with sticky secretions. Many predators larger than the aphids are not deterred by such feeble actions.

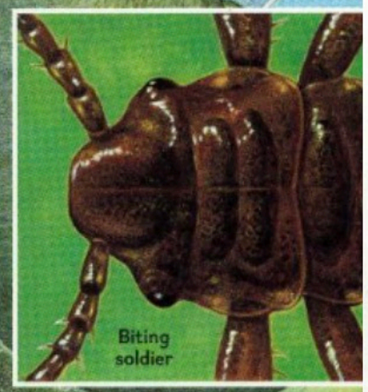
Perhaps the best line of defense for most aphids is reproduction—generating individuals so quickly that colonies grow and spread to new places, and predators simply cannot keep pace. Without soldiers the huge colonies of *Pseudoregma* would be extremely attractive to predators. Piled one on top of the other in dense mats of tens of thousands, the aphids could be devoured at will. Yet the soldiers successfully defend the colony from many predators.

Defense among samurai aphids is aggressive. I pluck a maggot, or larva, of the *Allograpta* flowerfly from a non-samurai colony of aphids and transfer it to a *Pseudoregma* colony. These maggots are ordinarily able to move unhindered among their aphid prey, but they are unprepared for soldiers. Two climb onto the maggot—more than ten times their length—and grasp it near its head with their forelegs. The soldiers butt it with their heads, puncturing its body with their needle-sharp horns (above). They jam in their horns again and again while rocking back and forth. The bleeding larva gyrates frantically, then plummets from the bamboo, still in the soldiers' tenacious grip.

Because they are masters at combating soldiers, a few insects successfully prey on samurai aphids. Fortunately for these predators, soldier defenses often are inept compared with the bites and stings of termites and ants.

Zoologist MARK W. MOFFETT's "Life in a Nutshell" appeared in the June 1989 magazine.

Life cycle of the woolly aphids



The life cycle of the samurai aphids is poorly known, but it is probably complex, like that of most woolly aphids. Typically an egg is laid in autumn on a primary host—a tree or shrub (1). Hatching in the spring, the founder (2) of a new colony seeks a good feeding site and begins to reproduce wingless aphids (3)—which in some species produce more of the same (4). These aphids, such as *Ceratoglyphina bambusae* (inset above), make their home inside a gall on the host, gradually formed when the insects inject saliva into the plant, altering its growth pattern. In spring or summer the colony produces winged "migrants" (5), which fly to a secondary host plant, such as grass or herbs. Here a migrant gives birth (6) to wingless aphids (7), which in turn may reproduce themselves (8) as the colony grows on the plant's surface. In rare instances more migrants may be produced (9) to spread the colony to other secondary host plants. *Pseudoregma* aphids (inset left), however, depend on wingless newborns, which are light enough to be carried by the wind; if one happens to land on bamboo, she may start a new colony. In autumn winged migrants (10) return to the primary hosts and give birth (11) to dwarf males and females (12). They mate, and the females each lay a single egg. They soon die and the cycle begins again.

PAINTING BY JOHN DAWSON. SOURCES: DR. SHIGEYUKI AOKI, LABORATORY OF BIOLOGY, RISSHO UNIVERSITY, SAITAMA, JAPAN; DR. MANYA B. STOETZEL, U. S. DEPARTMENT OF AGRICULTURE

Almost all aphids are females that reproduce by parthenogenesis—without sex. This results in offspring genetically identical to their mothers. Aphids lack the larval and pupal stages of many insects, and for most of the year they also skip the egg stage. Thus live birth is a common sight in an aphid colony.

Emerging from her mother, a *Pseudoregma* soldier reaches down with her legs to pull herself free (top). Moments later the mother seems to cradle her offspring (middle), but in fact she provides no parental care. Her next birth may be either a normal aphid or another soldier; how an offspring's caste is determined is not known. In fact, the non-soldier embryos inside her body already contain her developing grandchildren. This is one reason why aphids reproduce so rapidly.

Different types of soldiers are found on primary and secondary host plants. The primary host soldiers of *Ceratoglyphina bambusae* lack horns—they bite their enemies rather than pierce them. These soldiers develop from nymphs who have molted once. *Pseudoregma* typify most secondary host soldiers, armed at birth with pronounced horns and massive forelegs.

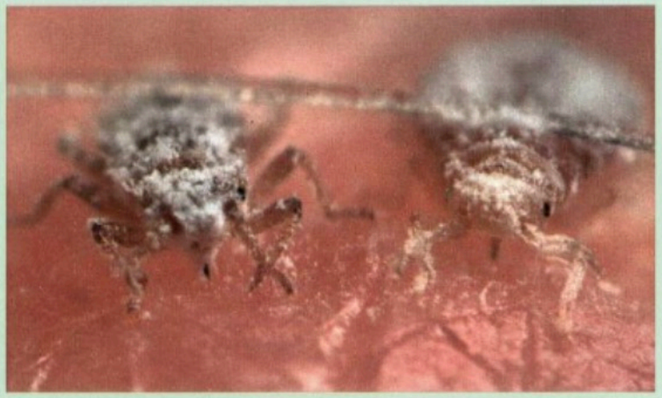
Scientists believe that the behavior of the Taiwanese aphid *Astegopteryx bambucifoliae* provides clues to the evolution of soldiers. This species—a relative of samurai aphids—lacks a distinct soldier caste. However, all of these aphids possess some warrior characteristics, such as diminutive horns that are too small to be lethal. Fighting over a feeding site, a hungry *Astegopteryx* aphid uses her horns to butt another drinking plant sap. The aggressor is shoved back by her colony mate, who swings at her with her body (right).

Ceratovacuna lanigera represents a more advanced stage in samurai aphid evolution. This species also lacks soldiers, yet any newborn can use its horns to crush a predator's eggs.

By developing specialized soldiers, samurai aphids have taken on a far more dangerous function: killing large and aggressive predators. Still, even samurai aphids sometimes use their horns for their original function—contests over food. Biting soldiers have evolved along a different pathway.

In subtropical and tropical areas many species—including samurai aphids—have colonies that last for more than a season. For example, *Pseudoregma* aphids are found on bamboo year-round. Yet Japanese biologists Seiki Yamane and Tsukasa Sunose have discovered the percentage of soldiers in a colony varies; it is nearly 20 percent in late autumn, when soldiers can protect the growing brood of winged migrants.

Attack of the samurai aphids



Scanning a tree with binoculars, Kurosu detects a white bell-shaped gall several centimeters wide on a branch high in the canopy. Galls of the *Ceratoglyphina bambusae* aphid are found only in *Styrax suberifolia,* commonly called snowbell trees.

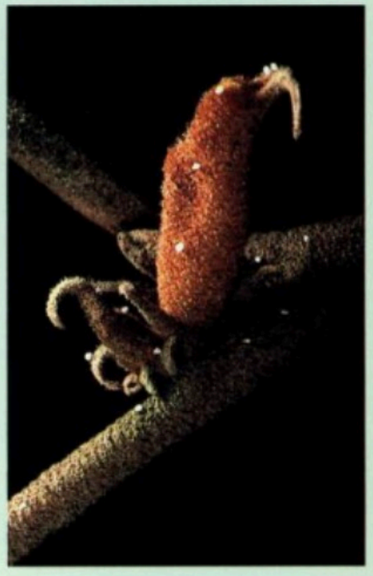
To gain a closer perspective, Kurosu cuts down a large gall (bottom far right). She handles it cautiously—at its current size its powdery surface is guarded by thousands of soldiers. Slicing into the soft cauliflower-like growth reveals a labyrinth of tiny channels where the colony resides (top right).

Kurosu has found that galls can last for more than a year. A single gall may hold in excess of 200,000 aphids, of which about half are soldiers. A young gall (right), shown here at twice its actual size, is patrolled by just a few pale guardians.

Disturbing these galls is unpleasant business. Only about half a millimeter long, the soldiers are too small to be seen as they rain down and bite anyone disrupting their colony. While not actually dangerous, they do a pretty good job at dissuading visitors.

Taking on someone two billion times their size, the soldiers bite my knee as if they were drilling into a plant (above). Each leaves a minute bloody spot, where a welt later forms that itches for two or three days. One particularly heavy attack leaves me with a rash on my leg that rages for three weeks.

Although people are often victims of the *Ceratoglyphina* soldiers' bite, squirrels and monkeys, which find galls appetizing, may also meet with the soldiers' wrath. Soldiers also ward off caterpillars and other insects that invade galls.

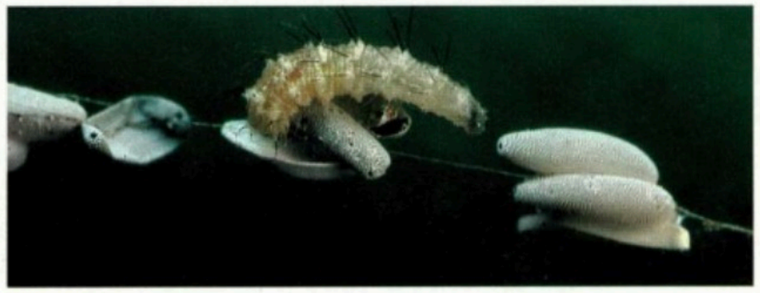


Commonly mistaken for bees, flowerflies are harmless and feed on nectar. Their larvae, however, are fierce predators.

When ready to lay her eggs, the Asian flowerfly *Metasyrphus confrater* seeks out clumps of bamboo. Starting near the top, she glides along a stalk in search of a colony of *Pseudoregma* aphids, sole prey of this fly's larvae in Japan. When she finds a colony, her fanning wings arouse the aphids like a breath of air. The bamboo surface shimmers as hundreds of aphids lift their hind legs and wave them about, as if to keep the fly at bay.

However, the fly avoids the aphids, homing instead on silk threads near the colony that were abandoned by ubiquitous wandering spiders. Maneuvering along a strand, the fly apparently finds it acceptable if she can trace an uninterrupted path from thread to bamboo. She then alights on the silk and deposits her eggs (top).

Eggs from other flowerflies often accumulate on a single thread, as is the case here. Perhaps the presence of previously laid eggs signals other females that the site is safe.



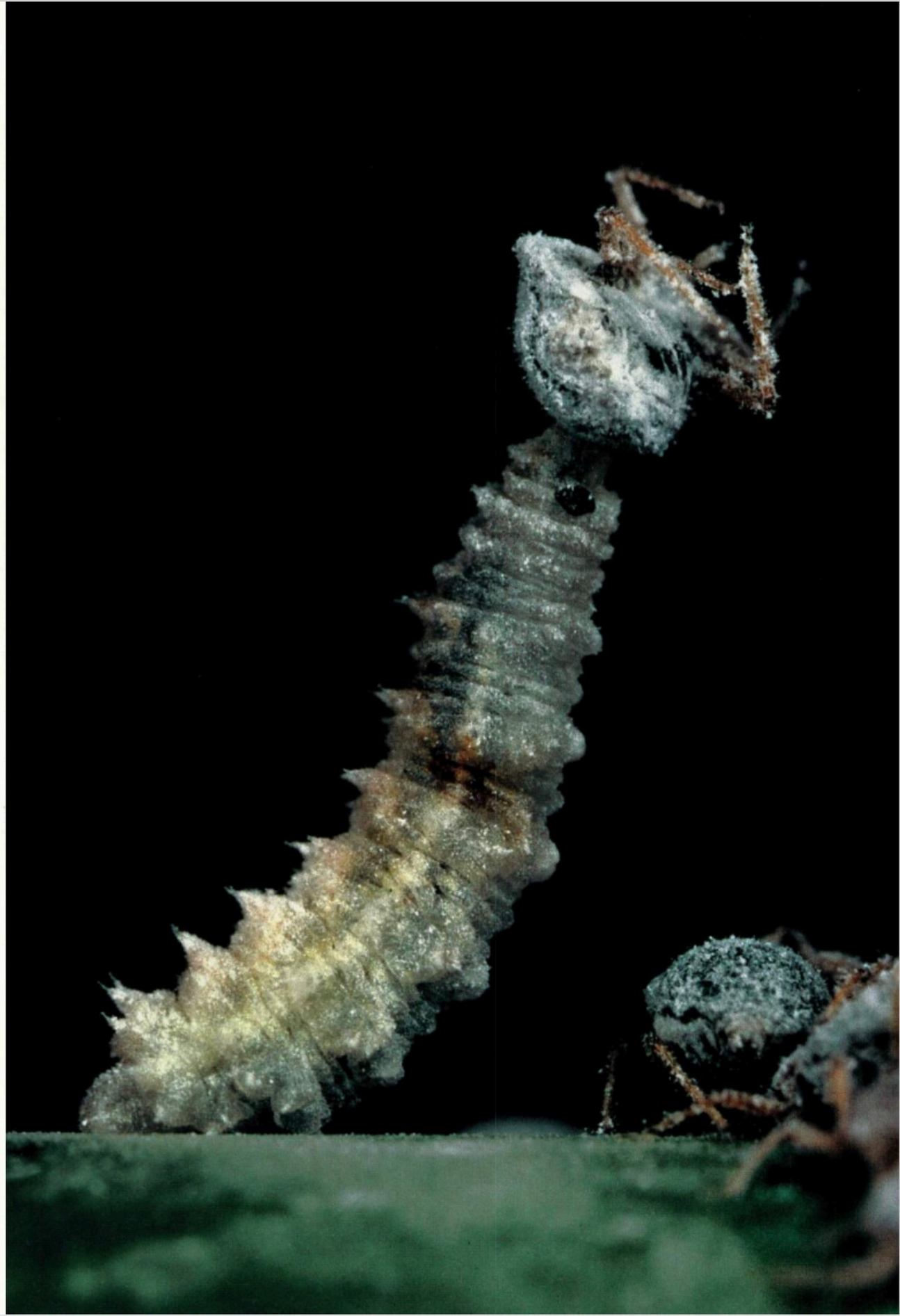
Days later a hatched larva emerges from an egg and struggles along the silk line to the aphid colony, using other eggs as stepping-stones when available (above).

Growing to a length of 1.5 centimeters, the legless maggots tower over the aphids. They move like leeches through the colony each night, often feasting in groups.

At the edge of one colony a maggot lifts its meal high in the air (right) so that the aphid's struggle to grasp the ground and free herself is in vain. Mouth hooks slice into the aphid's body, and the maggot drinks its fill of insect blood (lower left). The small orange spot on the eyeless maggot's head is a spiracle, or breathing hole. The empty carcass will be tossed away, and the maggot will ravenously seize its next victim.

Soldiers that fight back are unable to pierce the maggot's tough body and are only a minor irritant to this ultimate aphid-killing machine. In fact, any soldiers even attempting to attack invariably fall dead within minutes—apparently from poisons in the maggot's skin.

Japanese entomologist Kenji Ôhara discovered that the soldiers can successfully attack only newly hatched larvae so small that soldiers can throw them from the bamboo.



The safety usually afforded Asian flowerfly eggs by the fragile silk thread has its price: The journey a young maggot is forced to make to reach the aphid colony is extremely dangerous. It is perhaps for this reason that the egg-laying habits of the fly change with temperature.

In the autumn virtually all eggs are bound to silk, which is impossible for soldiers to traverse unless it becomes coated with enough aphid wax to offer better footing. During the cool winter days typical of southern Japan, the soldiers become sluggish or completely immobilized.

With the colonies left undefended, the flies shift to depositing their eggs at less precarious sites—on other objects near the bamboo, on the bamboo itself, or even directly on a hapless aphid such as this winged migrant (bottom right, at top). The maggots can now begin feeding almost immediately after hatching.

During a November visit to Kagoshima I saw favored egg sites change as the temperature fluctuated. Surprisingly, after one chilly afternoon of aphid-watching I discovered I had been holding myself so still that several flies had attached eggs to my shoelaces!

Another predator, *Dipha aphidivora,* has a simpler solution for preserving her eggs. This dull brown moth flutters around bamboo at night, laying eggs in or near a colony. But the eggs are too flat for the aphids to grip and so are left unmolested (bottom, far right).

Small *Pseudoregma* colonies often attract ants like *Crematogaster osakensis,* which pluck droplets of honeydew from the aphids (top). This is the same sweet libation that lures ants to aphid colonies around the world, which explains why aphids are commonly called ant cows.

Honeydew is plant sap that has passed through an aphid's body after needed nutrients are absorbed. If ants don't take a droplet, the aphid flicks her hind legs to shake it loose, and it drops from the plant. Fallen honeydew of aphids and their relatives—the "manna" of the Old Testament—was once a human delicacy in various parts of the globe.

In return for this "candy," most ants protect the aphids. For example, when an ant locates fly eggs, she releases a tiny droplet from the tip of her stinger (right). It apparently contains a pheromone that diffuses and alarms her colony mates. Worker ants responding to her call tear up the eggs or carry them away. The ants even build protective walls of soil around small aphid colonies.

If ants can ward off predators, why are soldiers necessary? Perhaps a *Pseudoregma* colony grows so large that it produces more honeydew than the ants can deal with. Most of it falls to the ground, where ants can drink their fill without helping the aphids. Larger colonies thus depend on their own soldiers for protection.

Unlike ordinary caterpillars with a taste for leaves, pale green carnivores hungry for aphids hatch from the eggs of the *Dipha aphidivora* moth. Highly skilled predators, they weave tunnels of silk on the bamboo, extending them directly through aphid colonies. Such nests provide a safe haven from soldiers, which can't tear through the tough fiber. A tunnel may contain several caterpillars; when two meet in a passageway, the walls shake briefly as they appear to fight.

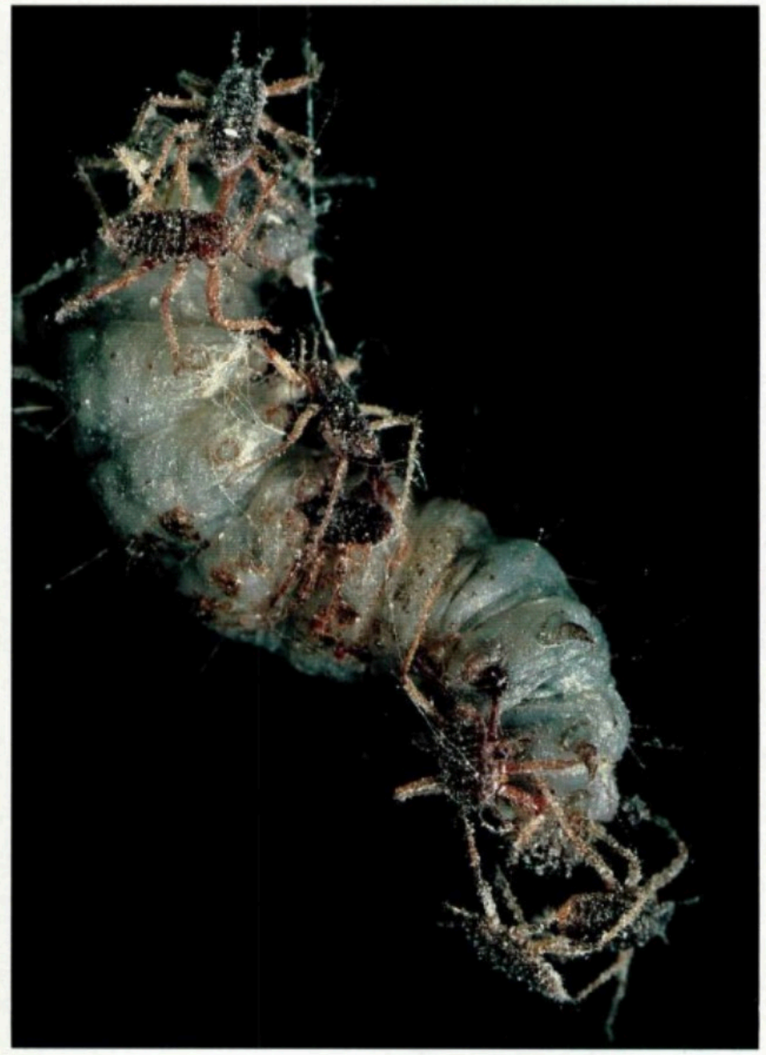
Catching these predators in the act is difficult. Eventually, I resort to a marathon stakeout of a nest. During a 27-hour watch at one swampy spot in Okinawa, I document six kills from start to finish.

A hungry caterpillar cuts a slit in the tunnel or uses gaps already present in the silk. At first it peers out as if to consider its best target (top left), then it lunges forward to grab an aphid (top right).

While the aphid is dragged toward the lair, black droplets ooze from two glands near the back of her body (bottom left). In some species this fluid repels enemies or warns other aphids of danger. Here I suspect it attracts soldiers when caterpillars are slow at retrieving meals.

An attacked caterpillar drops from the bamboo on a silk line and swiftly weaves it around the soldiers (below). After tying them up, it plucks them off and climbs the silk to its nest. If the soldiers' attack forces it to fall to the ground, it will die.

Most often a caterpillar moves swiftly enough to avoid soldiers. Once safely hidden within its tunnel, it can feed in peace. When finished, it leaves the carcass outside its lair among the remains of past prey.

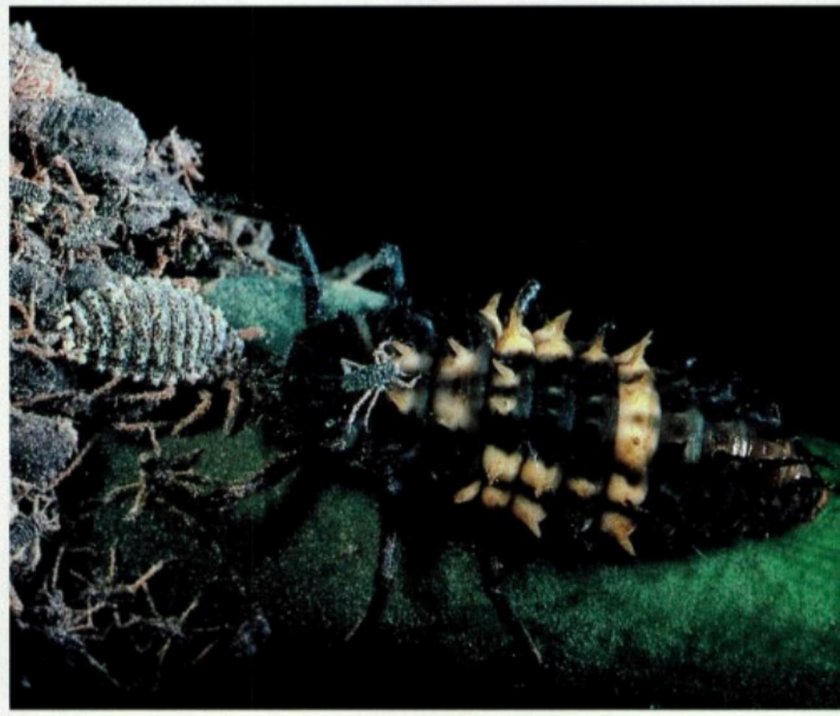


The dwarf ladybug is common at *Pseudoregma* colonies in Taiwan. Though its body is black, its pale hairs pick up aphid wax until the whole insect turns aphid gray.

Watching one of these *Pseudoscymnus amplus* ladybugs magnified by a camera's lens, I see an awesome form rise from the background (above). It lumbers toward the dwarf beetle until, at the last moment, the 3.5-millimeter ladybug waves a foreleg upward and smacks it in the face. Instantly the mammoth creature draws back, retracting its head and legs like a frightened turtle.

It's a brave act for this shy little ladybug, which normally drops from an aphid colony at the slightest disturbance. However, this insect face-off is with another, much larger species of ladybug, *Synonycha grandis*.

Both compete for *Pseudoregma* aphid prey, but they adopt almost opposite methods of pursuit. The dwarf adult and its larvae spend most of their time within the aphid colony. Dully colored, they blend in so well with the aphids that they wander freely among their prey and are difficult to detect by the human eye. Why they should mimic the appearance of the aphids is unclear. It seems unlikely that the latter could be fooled, since they depend more on smell than vision. In any event their camouflage appears to work; inserting themselves among the aphids, the dwarf larvae devour them freely, ignored by soldiers. Perhaps the ladybugs even fool their own predators.



In contrast, the larger species of ladybug is brilliantly colored and about 13 millimeters long. It usually stays near the edges of the colony, where it looms conspicuously.

A giant ladybug consumes hundreds of aphids every day. A female munches insatiably on one aphid after another during hours of mating, while her partner can only look on (lower left). Although soldiers cling to the female's legs, they are ineffective against her tanklike body. Occasionally she pauses to groom her forelegs, swallowing soldiers in the process.

The spiny larva of the giant ladybug is black with yellow splotches (above), resembling ladybug larvae commonly found in backyards. The larvae prey on aphids but have trouble consuming their meals because they are regularly attacked by soldiers. This ambushed larva forces blood from its joints, then beats a quick retreat. The blood's adhesive quality may slow the soldiers' attack.

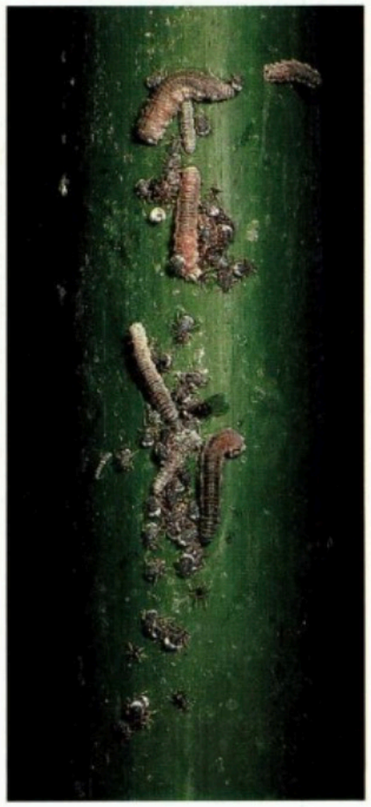
A giant ladybug lays egg clusters beneath leaves far enough from the colony to be safe from patrolling soldiers. Another ladybug species goes to greater extremes to protect her eggs—she disguises them with a layer of her feces.

Ladybug hatchlings must find food fast to ensure their survival; the first larvae to emerge often cannibalize neighboring eggs before heading off in search of an aphid feast.

New samurai aphid predators are still being discovered. In Taiwan I found brown lacewing larvae emerging at night from a bamboo leaf joint, using their tails like a fifth leg to aid rapid scurrying. When they approach one another, they slap their tails like fighting reptiles.

Compared with the chewing mandibles of most aphid predators, a lacewing's sickle-like pincers are unique (above). After puncturing an aphid with its pincers, the larva injects her with paralyzing fluid. The hollow pincers then work like straws to drain her body, leaving only a shell behind.

Under constant siege by maggots, caterpillars, ladybugs, and lacewings, whole *Pseudoregma* colonies are eventually destroyed. After sighting one vigorous colony, I return a week later to find that almost nothing



remains (left). The few surviving flowerfly maggots have almost no food. By the next day even these have starved, their corpses scattered at the base of the bamboo.

The aphids and their enemies show us ecology in a microcosm. Tranquil at first glance, this community is in fact caught in a delicate balance between life and death. On the one hand predators are in a race to eat and reproduce before food runs out; on the other the aphids must survive long enough for some to disperse to new sites. There the race begins anew.

This is a battle played out with aphids everywhere. Large *Pseudoregma* colonies, tempting targets for predators, differ only in the intensity of the struggle. Although soldiers may seem ineffective, they slow down enemies enough for the species to survive. □