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Just Lookin' for a Home
Like the boll weevil in the old folk song, a mother goldenrod gall fly is determined to give her young a good start in life.

By Arthur E. Weis and Warren G. Abrahamson

A parent struggling to stay awake for the 2:00 A.M. feeding of her month-old baby on a tree swallow staring into the gaping mouths of his five featherless, pint-size chicks might be tempted to envy insects, whose parenting duties generally end with the laying of the last egg. But the life of an insect parent, or rather parent-to-be, is not carefree. Ecologists have found that for many insects, actions taken by the mother before the birth of her young are as vital to their survival (and ultimately their reproductive success) as is postnatal care in mammals and birds. Over the last twenty years, in the course of studying the goldenrod gall fly, *Eriosoma sulphureum*—one of North America's most abundant but least-noticed insects—we have observed just how important these maturing preparations can be. Along the way, we have uncovered a complex web of relationships involving the insect, the plant on which it lays its eggs, and its several predators and parasites.

Perhaps it is misleading to say the goldenrod gall fly goes unnoticed. The quarter-inch-long fly itself is rarely seen, but any observant person driving through the countryside of the eastern or midwestern United States or walking through a weedy vacant lot in winter is likely to spot the insect's conspicuous trademark: a gall on the stem of its host plant, goldenrod. A curiosity of nature, galls are abnormal growths of plant tissue induced by the larvae of various species of aphids, weevils, and flies. The insect's relationship to the plant is parasitic, for while the tumorlike growth supplies the larva with food and shelter, the plant receives no benefit in return; in fact, it produces slightly fewer seeds than an unaffected plant and grows more slowly.

The bright green gall induced by *Eriosoma* is a prominent spherical swelling, typically about an inch in diameter, halfway up the goldenrod stem. Inside, a single fly larva feeds on the gall's inner tissues and lives its time. It pupates in early spring and emerges in May as a twain, spittle-winged white, quite handsome as flies go. The male seeks out the tip of a nearby, newly growing goldenrod stem, where he clips its wings in a way females find irresistible. After mating, the female goes off in search of her own goldenrod plant. When she finds a suitable stem, she invades her ovipositor (an egg-laying structure that works much like a hypodermic needle) into the stem's terminal bud and injects a single egg. Over the course of her adult life—which lasts, at most, two weeks—a female goes without food and may lay a hundred eggs. Each egg hatches four to seven days later, and the tiny larvaburrows its way down through the bud and into the stem. There it stimulates the plant to begin producing a gall, which comes from an inner tissue rich in protein and starch and an outer, protective tissue that soon becomes dry and corky. (Just how the fly induces a gall is unknown.) As the larva grows on the nutritious inner tissue, the host produces more of it, guaranteeing a steady food supply. The developing insect remains in the gall's small central chamber for the next fifty days, emerging as an adult fly to begin the cycle all over again.

An emerging adult female *Eriosoma* fly has some crucial decisions to make. First, she must find a goldenrod plant, and not just any one will do. Throughout the Eastern United States, the fly lays its eggs on *Solidago altissima*, or tall goldenrod. Four related, similar-looking plants—the Canadian, rough, early, and late goldenrods—also grow in this region. A gall fly mother, as we learned from a series of experiments, will land on other species of goldenrod, but a quick walk over the...
developing flower is enough for the “false buds” on her host to persuade her to move on. We found that when we wrapped leaves from S. altissima around the bud of another species of goldenrod, we could trick a female into inserting her ovipositor into the bud, but she would quickly realize her mistake, microscopic receptors on the tip of her ovipositor enable her to “taste” potential hosts with her reproductive organs as well as with her feet. Additional experiments showed that this was correct to be choosy: when we fed a few females into injecting eggs into the wrong goldenrod, nearly all the resulting larvae failed to induce galls.

Not all galls on goldenrods are created equal, however, so mother gall flies must be even more discriminating. Some plants in our study area never carry more than a few galls, year after year, while others only yield away consistently many. We could still that females had investigated the seemingly resistant plants; their exploratory probes left small scars on the buds. To find out how these plants managed to discourage the flies, we first cloned closed colonies of resistant and susceptible plants. Experiments showed that newly hatched larvae stimulate both types of plants to begin producing galls, but the resistant plants soon kill off the abnormal tissue. The larva, left without food, dies. A mother gall fly can detect—at least some of the time—the plants that are likely to starve her young. In our experiments, females probed resistant plants less often than they did susceptible ones. And the probes into resistant plants were less likely to end with the injection of an egg.

Gall or no gall, that’s one question. Beyond that lies the question of gall size. This, too, is a complicated issue, with equally significant ramifications for the larva. The gall’s inner chamber is fairly constant in size, but the thickness of its outer tissue varies, determining the gall’s eventual girth. This corky covering is all that separates the defended larva from a challenging set of predators that includes insectivorous wasps, beetles, and birds. Big galls can provide complete protection from one of the Euonyma larva’s worst enemies—the parasitic wasp Euonymus gracilis. Despite its Latin name, this wasp is minute in comparison with the gall fly. It makes its living by infecting its own eggs into goldenrod galls. After hatching, the wasp larva consumes the fly larva and then eats the inner gall tissue as well. If the outer layer is thick enough, however, the wasp’s epipositor cannot reach the central chamber, and the developing fly is spared.

Unfortunately for the little fly larva nestled in its corky house, large gall size is no protection against some other predators. During the winter months, thedowney woodpecker comes out of the woods in search of food. Pecking a narrow hole in a goldenrod gall and extracting the larva inside is easy work for this master excavator. In fact, woodpeckers and, in some areas, black-capped chickadees (whose efforts leave behind a cruciform-shaped hole) show a marked preference for big galls. This preference is understandable, since the smaller ones are likely to contain the parasitic wasp larva, which—after oneenth of the size of Euonyma larva—are a much less rewarding meal.

For other predators, gall size is simply not an issue. The beetle Modellina comata, which evolved from stem-boring ancestors, lays its eggs on the outside of the gall. The larvae then chew their way through the gall to get at the nutritious meal inside. And some of Euonyma’s enemies don’t even wait for the goldenrod gall to form. Euonymus ovalis, another species of parasitoid wasp, seeks out goldenrod galls with Euonymus eggs and injects its own egg into the fly embryo before it hatches. Like a time bomb, the tiny wasp larva waits inside its developing host until the end of summer, by

A female goldenrod gall fly investigates a goldenrod bud. When she finds a spot to her liking, she will insert her needlelike ovipositor (inserting from the rear of her abdomen) and inject an egg.
Gender Matters

Like most wasps, a female Eumenes gigasna can store sperm after mating and thereby determine the sex of her offspring if she withholds sperm from an egg, the offspring is destined to be male; if she fertilizes an egg, it will be female. The diminutive mother lays her fertilized eggs in the largest galls she can manage (all much smaller than the galls preyed on by birds) to provide her daughther with as much food as possible. Unlike its gall fly host, the wasp larva is unable to stimulate growth of the protein-rich tissue lining the gall and, once it has eaten the fly, must rely on however much of the nutritious lining was there at the time of the attack. The mother’s actions help ensure that female larvae will develop into big adults with long ovipositors of their own, enabling them, when the time comes, to reach all the way into the central chamber of a gall to lay their own eggs. Size is less important for males (all they have to do is find a female and mate with her), so a mother wasp can safely delegate her sons to the smaller, less nutritious galls.—A. L. W. and W. G. A.

Above, left: Stimulated by a fly larva, a pre-gall wasp excavates a hollow gall, providing shelter and food for the developing wasp. Above, right: Thirteen days later, a pre-gall wasp injects an egg into a gall’s control chamber. After hatching, the wasp larva will consume the resident fly, which time the fly larva will make a good-sized meal.

With so many enemies, what is an Eumenes mother to do? If she injects her eggs into galls with a weak response to the larva, small galls will result, and her offspring are liable to be eaten by wasps. If she injects her eggs into a highly reactive plant, the resultant large galls are attractive to birds. If the decision process is controlled by genes—as has been shown in many other insect species—the mother that happens to make the right choice will pass those “decisions” on to the next generation. Selection usually favors gall fly mothers that choose reactive plants, since in most places, and in most years, wasp attack is more prevalent than bird attack. This may explain why most mothers prefer fast-growing goldenrods, which on average produce slightly larger galls. But natural selection can be capricious, and where goldenrods grow near woodlots, birds can be a bigger problem. Slightly different “decision” genes may be favored in these locations.

A wise parent knows that, ultimately, a child is responsible for its own success. Goldrood gall fly mothers can get their eggs to the right place, but the larvae must stimulate the galls by themselves. Selection acts here, too. We have found that genes expressed in the larva can alter gall size. This means that where wasp attack is heavy, more of the larvae that stimulate big galls will survive to become adults and pass on those “stimulus” genes to the next generation. Where woodpecker and chickadee presence is heavy, larval fortunes, and the attendant selection pressures on gall site, are
Backyard Biology

Our work with goldenrod gall flies showed that natural selection usually favors larva that produce big galls. Readers can check this for themselves. Sometime between February and April, collect 100 or more goldenrod galls (by sponging, the green galls base faded to pale brown). Measure the diameter of each gall, either with calipers before opening it or with a ruler after splitting the gall down the middle. Use pruning shears to cut partway through the gall, then twist to break it open; don’t cut all the way through or you will clip the larva in half and will never know if it survived. It is easier to cut in the same direction as the stem—from pole to pole, rather than around the equator.

Once the gall is open, identify its contents. Full-grown gall fly larvae have an oval shape and are about a quarter of an inch long and almost an eighth of an inch wide. Score galls with a Dremel laser as “survived.” Galls that contain other kinds of insect larvae (for example, the one-eighth-inch-long, tear-drop-shaped larva of a European gall wasp, the small, white, cylindrical larva of a Melittobia beetle, or the brown pupal case of an E. abnormis wasp) should be scored as “dead.” Galls with woodpecker or chickadee holes also obviously count as dead. Calculate the average size of the survived and the dead galls. Can you tell which size galls casual selection favored in your area this year?—A. E. W. and W. C. A.

from the two species of goldenrod looked identical, but analysis of their mitochondrial DNA showed clear differences. At the very least, Eusoria has split into two races. The split appears to be driven, at least in part, by mutations of genes controlling host-plant choice. The adults that emerge from tall goldenrod galls overwhelmingly seek out that species as a host for laying and later for egg laying. Flies emerging from late goldenrod display the same sort of fidelity to their chosen host plant. These strong plant preferences, combined with a ten-day difference in the emergence dates of the two flies, virtually eliminate genetic mixing of the two populations.

Given sufficient time and the maintenance of barriers to interbreeding, a truly new species of fly may emerge. It is, we hope to be around to document it. This small ecological community, centered on an inconspicuous insect and a coarse plant growing in undistinguished habitats, continues to offer opportunities to explore a broad slice of evolution in nature. If we ever find ourselves wondering why we have spent so many years investigating such a seemingly mundane system, all we have to do is remember Charles Darwin. His few months on the Galápagos Islands may have set in motion much of his thinking about evolution, but he refined those thoughts during many subsequent years of observing and experimenting with earthworms and bumblebees in his own backyard.