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 nine-month-old baby in a tree swallow trying to gap the mouthful of his five featherless, pincushion chicks might be tempted to envy insects, whose parental 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, Enostis solida—one of North America’s most abundant but least noticed insects—we have observed just how important these maternal preparations can be. Along the way, we have uncovered a complex set 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 goll on the stem of its host plant, goldenrod. A curiosity of nature, galls are abnormal growths of plant tissue induced by the larva of various species of aphids, weevils, and flies. The insect’s relationship to the plant is parasitic, for while the tomato-like goll grows 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 Enostis 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 andicides its time. It pupates in early spring and emerges in May as a tawny, speckle-winged whal, quite harmless to flies go. The male seeks out the tip of a nearby, newly growing goldenrod stem, where he flicks his 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 inserts 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 in four to seven days later, and the tiny larva burrows its way down through the bud and into the stem. There it stimulates the plant to begin producing a gall, which contains 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 grases 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 weeks, emerging as an adult fly to begin the cycle over again.

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

The beetle *Melissotrix combata*, 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 to the nutritious meal inside. And some of *Eusarca*’s enemies don’t even wait for the goldenrod gall to form. *Eusarca emotissima*, another species of parasitoid wasp, seeks out goldenrod buds with *Eusarca* 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 which time it is fully grown and ready to hatch.

Unfortunately for the little fly larva nested in its corky home, large gall size is no protection against some other predators. During the winter months, the downy 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 cruder, coeval-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—about one-tenth the size of *Eusarca* larva—is a much less rewarding meal.

For other predators, gall size is simply not an issue.
Gender Matters

Like most wasps, a female Eurytoma gigas 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 (still 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 predesigned groove in a tottallan gall provokes shelter and food for the developing insect. Above, right: With fly long, the adult wasp, a parasite: A 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 a Eurytoma mother to do? If she injects her eggs into plans 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 it has been shown in many other insect species—the mothers that happen 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 goldenrod grows 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. Goldened 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 size, are
Backyard Biology

Our work with goldenrod gall flies showed that natural selection usually favors larvae that produce big galls. Readers can check this for themselves. Sometimes between February and April, count 100 or more goldenrod galls (by winnowing; the green galls fade 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 pathway through the gall, then twist to break it open. Don’t cut all the way through or you will strip the larva in half and will never know if it survived. It is easiest 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 galls 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 knife to larva as “survived.” Galls that contain other kinds of insect larvae (for example, the one-eighth-inch-long, teardrop-shaped larva of a Chrysopa ginseng wasp; the small, white, cylindrical larva of a Machilius beetle; or the brown pupal case of an E. chlorinum 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 natural selection favored in your area this year?—A. E. W. and W. C. A.

A ladybird beetle nears a goldenrod flower head, probably looking for insect prey.

The Eusoria plot thickened still more when we began looking at the flies in other parts of the country. In the mid-Atlantic states, where we have done most of our research, the gall fly lays its eggs exclusively on gall goldenrod. Across the northern tier of states, however, from New England to the Great Plains and up into Canada, galls are also found on late goldenrod. Evidence suggests that we may be witnessing one insect species beginning to split into two. Working with post-doctoral colleagues, we investigated some gall flies from Minnesota and New England. The adults that emerged from the two species of goldenrod looked identical, but an 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 resource for mating 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, however, quite possible to understand the evolution of 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 evolutionary biology. 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 in the Galapagos 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.