WINGS

ESSAYS ON INVERTEBRATE CONSERVATION

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Turning the Tables: Plants Bite Back

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In our orderly world—where plants harvest sunlight and carbon dioxide to make sugars and starch, herbivores eat plants, and carnivores eat herbivores—the idea that plants might eat meat sends us reeling into the topsy-turvy world of science fiction novels, horror films, and Broadway shows. However, not only do carnivorous plants exist on every continent except Antarctica, but they grow in a wide variety of environments—in bogs, fens, and outwash plains, on mountain tops and in valleys, on stream banks, and in lakes and ponds. They thrive wherever light is abundant and conventional soil nutrients, especially nitrogen, phosphorus, and potassium, are scarce. In addition to moving up the food chain and turning the tables on arthropods and the occasional vertebrate in order to meet their nutritional needs, carnivorous plants are central players in a wide range of fascinating interactions involving an array of invertebrates.

Since Charles Darwin first conclusively demonstrated that plants could eat insects in his 1875 work *Insectivorous Plants*, more than six hundred species of carnivorous plants have been described. In all four orders of the true dicotyledonous flowering plants in which carnivores have evolved—the heathers (Ericales), carnations (Caryophyllales), sorrels (Oxidales), and mints (Lamiales), —plants with more complex traps (bladders, snap traps, and pitchers) descended from ancestors that used simple hairs

Unlike the mirid shown on the front cover, this long-legged fly (family Dolichopodidae) could not evade the sticky spines of the sundew (*Drosera auriculata*). Photographed in Australia by Jim Frazier; © 1992 Densey Clyne.

When an insect—here a flesh fly (family Sarcophagidae)—triggers a hair at the base of the Venus' fly-trap (*Dionaea muscipula*), the trap closes within a tenth of a second. Photograph by Densey Clyne.

or adhesive glands to attract, ensnare, and ultimately digest their prey. And although the morphological diversity of many other plant groups reaches its zenith in the tropics, the broadest range of carnivorous plants is in North America, in particular in North Carolina, where all types of traps can be found within a day's journey from the coast.

As sit-and-wait predators, carnivorous plants must use a variety of lures to attract and capture their prey. And, unlike the man-eating Audrey, Jr., in *The Little Shop of Horrors*, the majority of them thrive on a catholic diet of insects, spiders, and other small arthropods. Sundews (*Drosera* spp.), rainbow plants (*Byblis* spp.), and butterworts (*Pinguicula* spp.) all have flypaper traps, sticky leaves that filter passing gnats and flies from the "aerial plankton," while their glistening glandular hairs attract foraging ants and small beetles. The more deliberate pitcher plants secrete nectar from a specialized roll of extrafloral nectaries surrounding the rim of their pitfall traps. These traps—which are modified from leaves (in the New World species of *Sarracenia*, *Darlingtonia*, and *Heliamphora*), tendrils (in the Asian species of *Nepenthes*), or petioles (in the Australian *Cephalotus follicularis*)—are lined with waxy-coated cells and downward-pointing hairs that prevent fallen insects from escaping.

The vacuum traps of the bladderworts (*Utricularia* spp.) and the snap traps of the Venus' fly-trap (*Dionaea muscipula*) and the waterwheel plant (*Aldrovanda vesiculosa*) are the most intricate and active carnivorous plant organs. The thin, transparent bladders of *Utricularia* have an inward-opening door at one end, sealed with mucus. When a passing protozoan, zooplankton, or aquatic larva touches the trigger-hairs just outside the door, it swings inward and the vacuum sucks in the prey with the surrounding water. The door snaps shut; the water is pumped out; the prey is digested; and, in less than half an hour, the trap is reset and able to capture more prey. The snap traps of the familiar Venus' fly-trap close when potential prey stimulates a trigger-hair at the base of the trap. Within one-tenth of a second—one of the fastest movements ever recorded for any plant—the hinged leaves snap shut and begin to digest the captured insect. Remarkably, it was not until 2005 that the mechanism by which these snap traps work—the physical release of elastic energy stored in the leaves—was discovered.

Although bladderworts, fly-traps, and waterwheel plants all use sensitive hairs to trigger their traps, they evolved separately. Bladderworts share a common ancestor with the sticky-leaved butterworts, whereas the Venus' fly-trap and the waterwheel plant share a common ancestor with the sundews and the Asian pitcher plants. As a group, carnivorous plants provide one of the best examples of convergence, the evolution by unrelated organisms of similar biological solutions to similar environmental problems.

The traps of most, but not all, carnivorous plants are lined with specialized cells that secrete enzymes to digest the chitin and protein of their prey and release essential nutrients for the plants' consumption. Lacking these cells, two of the North American pitcher plants—*Sarracenia purpurea* and *Darlingtonia californica*—and many species of *Nepenthes* in Asia instead host in their water-filled pitchers food webs of bacteria, protozoa, rotifers, mites, and fly larvae that break down the prey and release the nutrients for the plants' consumption. The rotifers, mites, and flies in these food webs are obligate inhabitants of pitcher plants; they complete all or part of their life cycles within the pitchers. The sun-pitchers (*Heliamphora* spp.), which grow only on the Venezuelan and Guyanan tepuis (sandstone massifs), rely on bacteria alone to process captured prey.

The South African species of *Roridula*, which resemble sundews but are actually more closely related to *Sarracenia*, also do not produce any digestive enzymes. Like sundews, *Roridula* captures insects on sticky, hair-covered leaves. The predatory *Pameridea*, a true bug, walks among these glandular hairs without getting stuck as it picks prey off the leaves and eats it. The plant, in turn, absorbs the bug's nitrogen-rich excretions. Each of the two species of *Roridula* has

Unlike most insects, caterpillars of the distinct Quaker moth (*Achatia distincta*) can crawl out of the northern pitcher plant (*Sarracenia purpurea*). Photographed in Massachusetts by Aaron M. Ellison.

its own specialized species of *Pameridea* engaged in this curious mutualism, an ecological interaction in which both partners benefit.

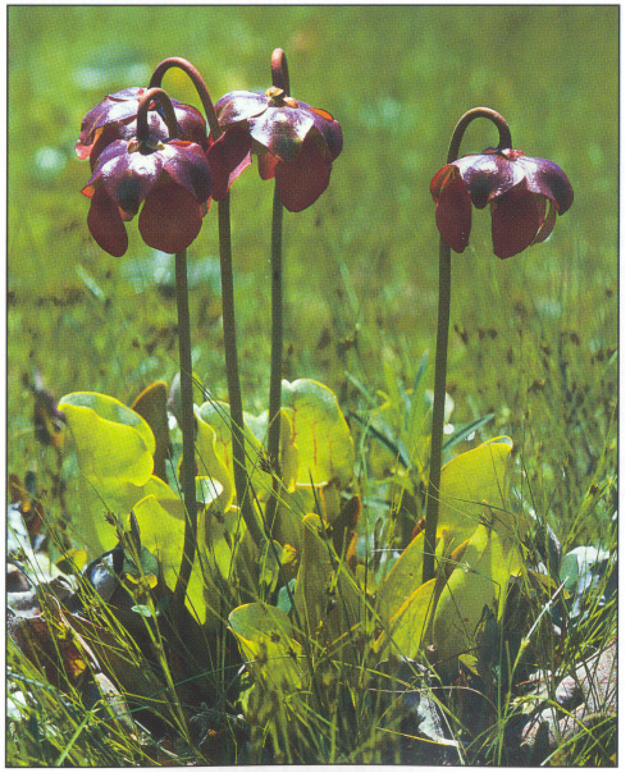
As evolutionary biologists have repeatedly shown, mutualisms are a short step from the slippery slope leading to deceit and cheating. Swimming ants (an undescribed species of *Camponotus*) and the two-fanged pitcher plant *Nepenthes bicalcarata* from Borneo are such slippery mutualists. This *Camponotus* species nests in specialized structures called domatia within the hollow tendrils of the pitcher plant and regularly removes prey from the pitchers. On one hand, removal of excess prey prevents the prey-filled soup within the pitcher from becoming putrid; on the other hand, the plant is continually deprived of much-needed nutrients. Are the ants mutualists, cleaning out pitchers in return for housing? Or are they kleptoparasites, stealing prey from the plant that protects them? Many such interactions are equally ambiguous. Ants and slugs regularly steal gnats and other small prey from butterworts, and frogs will perch on the lips of *Sarracenia*, snatching passing flies before they fall into the pitchers. Is the cost to the plant of losing prey outweighed by some unknown benefit?

Perhaps the most important competitors with pitcher plants for prey are spiders. The linyphiid spider *Frontinella communis* builds its "bowl-and-doily" webs throughout the vegetation in close proximity to *Sarracenia* pitcher plants at or above pitcher height. Clarisse Hart, Callan Ordoyne, and I found that removing *Frontinella* webs allows *Sarracenia purpurea* to capture much more prey, especially springtails, flies, and ants. Other linyphiids—including *Linyphia clathrata*, *Hypselistes* spp., *Centromerus denticulata*, and *Bathyphantes pallidus*—build sheet webs over pitcher openings, taking advantage of the pitcher's extrafloral nectaries to attract prey and steal it from the plant's gaping maw.

Spiders also interfere with the success of sexual reproduction of pitcher plants. Sac spiders (Clubionidae) and crab spiders (Thomisidae) sit on or in *Sarracenia* flowers and capture halictid bees (*Augochlorella aurata*) and flies (*Fletcherimyia fletcheri*), specialist pollinators that come to collect nectar and thus cross-fertilize the plants. By capturing adult flies, *Clubiona obesa* may reduce fruit set and seed production. In an especially ironic twist, these spiders also may limit the efficiency of the food web that processes prey for the pitcher plant. The larvae of the pollinator *Fletcherimyia* are the top predators in the aquatic food web that digests prey for *Sarracenia purpurea*. The adult flies roost overnight in the umbrella-shaped flowers, emerging during the day to forage and lay eggs in newly opened pitchers. The cannibalistic larvae eat each other until only one remains in each pitcher. But if the spiders eat the mature flies that pollinate the plants, the flies' larvae are not available to feed the plant.

On the other hand, spiders may play a more positive role in the pollination of a related carnivore, the cobra plant (*Darlingtonia californica*). Rebecca Austin, a self-taught botanist who made extensive observations on *Darlingtonia* in the late 1800s, observed spiders in most of this species' flowers in her study areas in the Sierra Nevada and concluded that they were its pollinators. More than a hundred years later, Susan Nyoka of Southern Oregon University revisited Austin's hypothesis. She observed few insects visiting *Darlingtonia* flowers in the Siskiyou Mountains, but, inside the flower heads, she found species of eight families of spiders carrying *Darlingtonia* pollen. Although pollination by spiders is rarely reported in the plant world, if plants can eat animals, why shouldn't spiders pollinate flowers?

Of course, pollinators themselves are at risk of becoming prey. Carnivorous plants need to eat insects but also need insects to pollinate their flowers. Because of these conflicting needs, there has been strong selection for plants to evolve mechanisms to avoid eating their pollinators. Many carnivorous plants flower early in the growing season, before new traps are produced. Others produce flowers that are physically much taller than the traps. As an extreme example, bladderwort traps are either submerged underwater or buried in the soil, while their flowers project up into the air, reaching an environment completely different from that of the vacuum traps. Regino Zamora of Spain's University of Grenada has shown that when flowers and traps are not separated in space or time—as in the butterwort *Pin-*



To avoid eating their potential pollinators, carnivorous plants such as this northern pitcher plant (*Sarracenia purpurea*) grow their flowers high above their traps. Photographed in Massachusetts by Aaron M. Ellison.

Carnivorous plants are pollinated by a variety of invertebrates, including this syrphid fly (*Sphaerophoria* sp.) visiting a thread-leaved sundew (*Drosera filiformis*). Photographed in Massachusetts by Aaron M. Ellison.

guicula vallisneriifolia—many potential pollinators, especially thrips and beetles, end up as prey. Thus, the appetite of its leaves limits successful reproduction of this carnivorous plant.

All plants need nutrients but only a few—less than one tenth of a percent of the flowering plants—have evolved the ability to attract, capture, and directly digest animal prey in order to obtain them. In sunny yet nutrient-poor habitats, many non-carnivorous plants grow side-by-side with carnivorous ones. Why aren't more plants carnivorous? Carnivory has its costs. It takes a lot of carbon and energy to produce traps, and, despite the plant's desperate need for nutrients, the traps are remarkably inefficient at capturing prey. For example, more than 99 percent of insects foraging for nectar around the sweet lips of the northern pitcher plant (*Sarracenia purpurea*) escape with their sugary rewards. Similarly, only 1 percent of the vespulid wasps that collect nectar from the cobra plant (*Darlingtonia californica*) are actually captured. Carnivorous structures also contribute little to photosynthesis, and so leafy, non-carnivorous plants can easily out-compete carnivorous ones as soon as nutrients become just a little more plentiful or if there's just a little less light. So rest easy. Audrey, Jr.'s children won't be lurking behind every bush any time soon.

Aaron M. Ellison is a senior research fellow in organismic and evolutionary biology at the Harvard Forest, a field station of Harvard University and a long-term ecological research site supported by the National Science Foundation. He and his colleagues use pitcher plants and their associated insects as model systems for studying plant and animal population dynamics, the structure of food webs, nitrogen cycling, and the impacts of acid rain on wetland ecosystems.

XERCES NEWS

Publications for Land Managers, Scientists, Conservationists

This past spring the Xerces Society produced the *Red List of Pollinator Insects of North America*, a searchable CD-ROM that identifies threatened, endangered, and vulnerable pollinator species and their habitats. In October, we presented information on the Red List to the National Academy of Sciences.

In the fall we published *Logging to Control Insects: The Science and Myths Behind Managing Forest Insect "Pests," A Synthesis of Independently Reviewed Research*. This book summarizes over 150 scientific papers and Forest Service documents and proposes a refocusing of current forest-management strategies to work with nature and not against it. Former U.S. Forest Service Chief Mike Dombeck calls the report "the most useful publication on the topic of forests and forest pests that I have seen."

For more information on these publications, please visit www.xerces.org or call 503-232-6639.

Salt Creek Tiger Beetle Finally on Endangered List

Thanks to the efforts of scientists, conservationists, and Xerces members, the Salt Creek tiger beetle will finally get Endangered Species Act status. Recent surveys show that the beetle's population numbers about 150. ESA listing will provide for habitat protection and will also increase funding for conservation measures. With luck, this species may now have a chance.

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