

Five weeks later, the researchers found that the sex ratios had reversed. The formerly male-dominated colonies that were now headed by queens from female-dominated colonies were biased toward females, and the previously female-dominated colonies with their new queens now had excess males. Furthermore, an examination of the DNA in the eggs revealed the reason for this change. More than half the eggs laid by queens from male-dominated colonies were haploid—or male. The queens—not their worker daughters—were influencing the sex ratio, by laying either more male or more female eggs. Most likely, they controlled the number of eggs fertilized by their internal stores of sperm.

The researchers still don't know why some colonies are nonetheless biased toward females. Older females may simply be less efficient at fertilizing eggs and thus produce male-biased colonies, or they have a genetic disposition to produce mostly one sex over another. "We need to look at a colony to see if a queen's rate of fertilization is stable through time," says Ross.

The Keller team hopes to do those experiments and look at other species, too. When they do, entomologist Madeleine Beekman of the University of Sydney, Australia, predicts that they will find a variety of scenarios based on "which of the conflicting parties can exert power over the other parties." The outcome, she adds, "is likely to depend on the idiosyncratic details of [each species'] biology."

—ELIZABETH PENNISI

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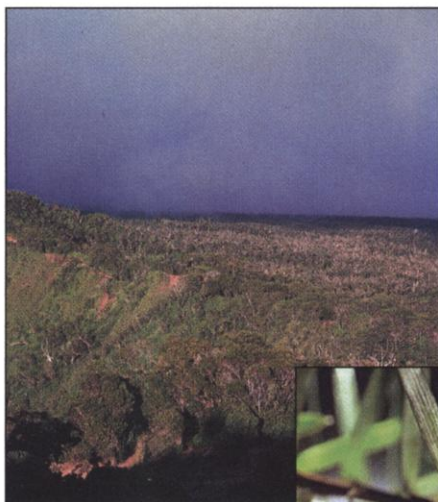
Parasitic Wasps Invade Hawaiian Ecosystem

Like specialized shock troops, insects have frequently been drafted to fight invasive weeds and pests. But these so-called biological control agents also have the potential to run amok, attacking innocent native species. Now comes the most detailed example yet of how deeply a control agent can infiltrate an ecosystem.

On page 1314, ecologists M. Laurie Henneman and Jane Memmott of the University of Bristol, U.K., report that parasitic wasps from Texas and China that were introduced into Hawaii more than 50 years ago to prey on sugarcane pests are now dominant players in the food web of a remote native forest. Use of parasitoid wasps, which kill other insects by laying eggs in them, is a popular strategy for trying to control pests. And although there have been hints that such wasps—for instance, those introduced to combat the gypsy moth—can harm native species, "we had no idea that the nontarget impacts that exotic parasitoids had on native invertebrates could be so great," says biocontrol expert Pauline

Syrett of Landcare Research, a government-funded institute in Lincoln, New Zealand. "The results will shock many ecologists and managers of natural areas."

Syrett and others suggest that the finding justifies more stringent prerelease evaluations of biocontrol agents, including mandatory tests to assess the number of species they attack. "It's a call for safer practices" and for narrower specialists that will target only pests, says Robert Pemberton, an entomologist and botanist at the U.S. Department of



Agriculture's (USDA's) Invasive Plant Research Laboratory in Fort Lauderdale, Florida.

To study how the biocontrol insects interact with native species in the Hawaiian food web, Henneman and Memmott went to Kauai's Alakai Swamp—a boggy forest much higher, cooler, and wetter than the lowland fields where more than 122 parasitoids have been released in the last 100 years. Because the swamp is an extreme environment for Hawaii, the researchers reasoned, any effects from the parasitoids would be a minimum estimate of effects elsewhere.

In the swamp, Henneman collected moth caterpillars from each of two 200-meter-by-25-meter plots, while keeping track of which of 52 kinds of plants the caterpillars were feeding on. Back in the lab, she reared 2112 caterpillars, carefully feeding them leaves she brought to the Kauai Agricultural Research Center and watching to see if parasitoid wasps would burst from the caterpillars.

The vigil paid off; parasitoids emerged from 216 caterpillars, and an equal number of dead caterpillars contained wasp larvae. All told, Memmott and Henneman estimate that about 20% of the caterpillars had been parasitized. Of the wasps, 3% were native and

14% had been accidentally introduced to Hawaii; a whopping 83% were biocontrol agents. "The parasitoids have an amazing ability to move into a pretty difficult environment," says Pemberton.

The biocontrol wasps belonged to three species, and when Henneman and Memmott looked up their release dates, they learned that all three had been set loose more than 50 years ago. This makes it difficult to assess whether the wasps have damaged the swamp ecosystem, because little is known about the original community. Memmott says that the native moths have most likely been attacked for decades and can sustain the rate of parasitism. However, she notes, the most vulnerable moths could have been driven extinct soon after the biocontrol parasitoids arrived in the 1940s and '50s, and there would be no way to detect that.

There is some good news, however. A large population of biocontrol caterpillars, released to control exotic blackberry species, has also reached the swamp, and had it been a target of the parasitoids, it



Overrun. Alien wasps have reached a remote swamp (top) and are now the main parasites of the larvae of native moths (above).

could have increased the number of wasps, thereby exacerbating their effect on native caterpillars. But Henneman and Memmott found that the wasps don't parasitize the biocontrol caterpillars.

Also encouraging is the absence of more recently released parasitoid wasps. "It means that biological control is much safer today," Memmott says. Peter Follett, an entomologist at the USDA's Pacific Basin Agricultural Research Center in Hilo, Hawaii, agrees. "We're definitely more cautious [about releases] now than we were in the '40s, and even in the '80s," he says.

But others aren't sure that the absence of more recent releases is significant. Frank Howarth, an entomologist at the Bishop Museum in Honolulu, points out that these insects simply may not have arrived yet at Alakai Swamp. If they do, the swamp moths will have to face even more renegade mercenaries.

—ERIK STOKSTAD