Eco-Evo Effects Up and Down the Food Chain

A decade ago, few ecologists factored evolution into their studies. How species changed over time was important, but it happened too slowly to be worth considering as they sought to understand ecosystem processes today. That attitude, however, is changing. Using guppies living in natural streams (see main text, p. 904) and other organisms, researchers are exploring links between evolution and ecology in a number of different settings, documenting interconnections that extend down to genetic changes. "It's a very dynamic field," says Andrew Hendry, an evolutionary biologist at McGill University in Montreal, Canada. "Everyone is getting involved."

In one notable example, David Post is focusing on how the alewife, a fish that lives in lakes in eastern North America, shapes and is shaped by its freshwater ecosystem. The community ecologist from Yale University and his colleagues have shown how these so-called eco-evo effects can ripple across a food web in unexpected ways. "It's one of the best examples of how ecology and evolution interact in a contemporary time frame," Hendry says.

Post's work follows in the footsteps of two other Yale researchers, John Langdon Brooks and Stanley Dodson. In 1965, they showed the key role that alewives (*Alosa pseudoharengus*), which grow to 25 centimeters, play in determining the makeup of lake zooplankton, particularly *Daphnia*, tiny crustaceans commonly known as water fleas. Typically, alewives are anadromous: They spend their adult lives in the Atlantic Ocean. Each spring, the fish swim up coastal streams from Nova Scotia south to the Carolinas into lakes for a few weeks to mate and spawn. The young spend the summer and fall in fresh water before they head out to sea again.

That cycle has profound implications for a lake's population of *Daphnia*, which are usually the dominant zooplankton. The newly arrived alewives and their young are hungry and feast on the water fleas. "They are a slash-and-burn fish," Post says. *Daphnia* populations are not restored until the following spring, when eggs resting in the lake bottom hatch.

Ripple effect. Both prey and predator, *Daphnia* affect lake food web dynamics.

About 300 years ago, however, the building of dams stranded some alewives in lakes, creating landlocked populations. More than 40 years ago, Brooks and Dodson showed the *Daphnia* had all but disappeared from those lakes. The landlocked alewives were left with smaller prey and, consequently, have evolved smaller mouths and smaller gill rakers inside their mouths that are better suited to catching those prey. That shift itself likely reflects how ecological change imposed by the alewife led to an evolutionary change in the fish.

But Post and postdoctoral fellow Matthew Walsh decided to go a step further: They looked at whether the ecological impact of the alewife on the *Daphnia* had evolutionary consequences for the *Daphnia* as well. Walsh collected eggs from the sediments of lakes with landlocked alewives, as well as lakes that were still connected to the sea and those that had no alewives at all. Then, he raised several generations of *Daphnia* in the lab. He found genetically based differences: *Daphnia* from lakes with anadromous alewives grew faster, matured sooner, and produced many more offspring than *Daphnia* from landlocked or alewife-free lakes. "There was an overall shift in life history evolution," says

and in 2006 won a $5 million grant from the U.S. National Science Foundation's (NSF's) Frontiers in Integrative Biological Research program to carry out the experiments. His plan: to mimic natural migration patterns by transplanting guppies into stream reaches that didn't previously harbor the fish. "I'm taking the results from theory and lab studies and asking, 'Are they important in nature?' " Reznick says.

Eco-evo test bed

At the end of the potholed road, Reznick parks the Jeep and walks along an old plantation trail, overgrown to a narrow path and flanked by tall cocoa and coffee trees. It ends on the banks of the Guanapo River, whose tributaries are at the heart of his eco-evo test bed. Reznick starts sloshing his way upstream. "We wind up walking in the rivers," he says. Boots with studded soles are the shoe du jour. At times the water is chest deep. Some places require the researchers to clamber up small waterfalls, often with two butterfly nets and a backpack full of water bottles in tow. (The bottles are used to take live guppies back to the lab.)

The Taylor is one of four streams that Reznick and his colleagues picked from more than a dozen candidates for their study, which began in 2008. Each has a 100- to 180-meter stretch of relatively flat water between two waterfalls that serve as barriers to fish migration. Prior to the experiment, the stream segments had no guppies, just killifish.

Before seeding each stretch with 40 male and 40 female guppies derived from a high-predation site downriver, ecologists carefully documented the ecosystems. They characterized the killifish and invertebrates, looked at primary productivity, measured the standing algal crop, and even took into account the organic contributions of leaves falling into the stream. At two streams, they also removed some of the overhanging canopy, increasing the amount of available light, potentially an important ecological variable. Then, every month, they began repeating their measurements—and capturing and releasing the guppies in order to monitor changes in both individual fish and the populations as a whole.

It's a laborious process. Three days before the Jeep trip, field manager William Roberts and several interns had trekked up to the Taylor River on a fishing expedition. Using a tape measure, they marked off distinct pools, riffles, and side pools. Then, with butterfly nets, they caught every fish they could see in each section and transferred the fish to marked Nalgene bottles filled with river water for the 2-hour trip back to the lab. The anglers had to stay out of the water to avoid disturbing the stream's ecology, so the netting took some creativity. "You have to contort your body into funny positions," Roberts says. It's not unusual, he says, to find someone draped over a rock reaching into a pool. And, 2 years ago, the collectors had to scramble to rescue their bottled fish from a flash flood that threatened to sweep away their research subjects. "Now we pay

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Walsh, who is now based at the University of Texas, Arlington. In undammed lakes, the strategy allows *Daphnia* populations to thrive in early spring and deposit plenty of resting eggs before hungry alewives arrive, Walsh and Post reported in 2011.

This ecologically induced evolution in turn has another ecological effect. The spring population explosion of *Daphnia* takes a serious toll on the algae the water fleas eat, in turn shaping overall ecosystem function, Walsh and his colleagues reported in the 23 May issue of the *Proceedings of the Royal Society B.* Walsh grew *Daphnia* in large 56-liter tubs stocked with algae and monitored the growth of both the algae and the *Daphnia*, as well as the primary productivity of the tubs. In the tubs with *Daphnia* from lakes that harbored seasonal alewives, there was a rapid and sharp decline in the phytoplankton population that also caused the clarity of the water to improve. At the same time, primary productivity dropped by 32%. Those changes did not occur in tubs with water fleas from landlocked and alewife-free lakes. "More and more studies are showing that evolution can have strong effects on ecology," says Patrik Nosil, an ecologist at the University of Sheffield in the United Kingdom. Whether these ecological changes in turn affect evolution in the phytoplankton remains to be determined, Walsh says.

Opportunist. Chain pickerel have moved offshore in lakes with landlocked alewives.

Meanwhile, Post and postdoc Jakob Brodersen have now looked in a different direction along the food web. Chain pickerel are a native predator in eastern North American lakes, lurking close to shore to catch other fish. For a year, Post and his colleagues intensely sampled 10 lakes, three with landlocked alewives, three with seasonal alewives, and four with none. To their surprise, they found pickerel in the middle of landlocked lakes, far from their usual shoreline lairs. These fish were not just passing through, either. They tended to have a deeper body and a slender head compared to their counterparts close to shore, and their stomachs were full of alewives. Carbon-isotope ratios in the pickerels' tissues, which can differ depending on whether the fish has an offshore or inshore diet, indicated that these pickerel are offshore residents, Post reported last month at the First Joint Congress on Evolutionary Biology in Ottawa. That's important because it suggests that the change in the alewives' life history—to a landlocked population—has rippled out to affect the pickerel.

Voracious youngsters. In lakes, young alewives devour all the *Daphnia*.

"We believe they are undergoing a novel niche shift," Post says. Pickerel probably don't hang out in the middle of lakes with seasonal alewives, he notes, because the prey disappear each fall. But in landlocked lakes, there appears to be an advantage to heading out to the lake's middle: Offshore pickerel had a higher fat content than inshore pickerel, suggesting they have found a better way of making a living.

Hendry says the alewife system is a "particularly elegant example" of "how evolutionary and ecological effects cascade throughout the food web." **–E.P.**

more attention to the weather," Roberts says.

Once the collecting was done, the researchers hauled the now-25-kilogram packs back to the lab, a covered veranda in the back of the house where they live. There they transferred the fish to a series of aquaria lining a wall. Now, however, processing the fish is delayed. As rain pours down outside, army ants invade the lab, covering the floors and walls in black streams and devouring termites that have flown into the room the night before as part of their breeding migration. An unlucky gecko that strays into the ants' path is also gobbled up. By midmorning, the ants are gone without a trace and the interns set up an assembly line.

Reznick, eager to help, anesthetizes each fish and then hands it off to an intern, who puts it under a microscope to check for identifying tattoos. (When a guppy reaches 14 millimeters, the researchers inject two microscopic dots of colored plastic under its skin. There are 12 colors and eight possible injection points, creating enough combinations to give thousands of fish a unique tattoo.) Fish that aren't yet marked get a tattoo, and workers take three scales for DNA sequencing. They weigh and photograph the fish, and add information on any distinguishing characteristics to a master data sheet. There is a sense of urgency, as the researchers try to minimize their handling of the fish and get them through the process quickly before they wake up. Finally, the researchers are ready for a return trip to the Taylor, where they will release the fish into the same sections where they were caught.

Guppy boom

Early on, the grand guppy experiment almost became a victim of its own success. At first the numbers were manageable—populations in each stream grew to about 300 the first year. But by 2009, one stream had 1600 fish and by 2010, it had 2600. Populations in other streams were also exploding. Reznick got a panicked call from Andrés López-Sepulcre, the postdoc in charge of the census. "We didn't have the means to deal with that scale of fish," Reznick recalls. But they scrambled to hire more people and developed the high-speed production line. Now, the team has dossiers on 30,000 fish (about 15% of which are currently alive). For each, "We have a personal history, where it lives, who it lives with, what its weight gain is," Reznick says.

The rich database is giving the researchers a detailed look at how the eco-evo script is playing out for the Trinidad guppies. The guppy population explosion, for example, meant fish numbers in the test streams reached densities 10 times higher than those in the high-predation stream where the guppies originated. The denser populations led to changes in the amount and type of available food, and within three generations, the fish had begun to shift to different reproduction and growth patterns. For example, instead of growing fast and maturing young, as guppies in high-predation streams do, males are now older and larger

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