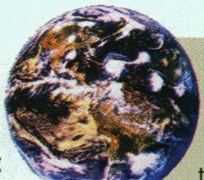
# When Rigor Meets Reality

**Ecological experiments have become quite good at isolating causes and effects. But there's a debate brewing over whether these results reveal anything about the natural world**



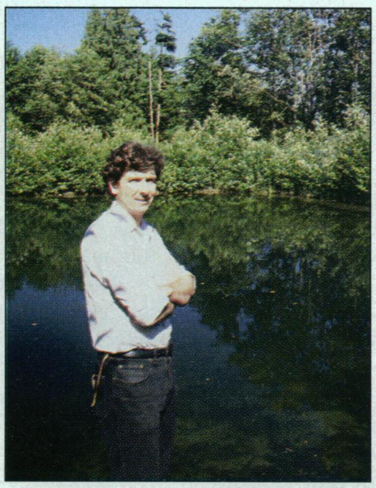
Ecologists use many tactics in their attempts to understand how organisms relate to one another and to their surroundings. In the News section of this special issue on ecology, our lead story deals with one of those tactics, experimentation, and an emerging debate over how ecologists design these tests of the natural world. This is followed by stories on how small organisms have large influences, two hugely ambitious conservation plans, and the value of a biological survey in Hawaii.

Articles, beginning on page 324, start with an exploration of the value of large- and small-scale manipulations of ecosystems. Other topics discussed include strategies for assessing climate-driven effects on ecosystems, world biodiversity, the impact of human population growth, land restoration programs, public opinion on the environment, and the effects of environmental discontinuities and synergisms.

When ecologist Andrew Blaustein linked vanishing amphibians to disappearing ozone last year, he made a splash in the popular press. Alarming field studies showing big drops in frog and salamander populations all over the world have had scientists scrambling for explanations. One controversial idea was that a thinner ozone layer—produced by global atmospheric changes—was the culprit. And Blaustein and his colleagues at Oregon State University had what looked like dramatic experimental data suggesting the amphibians are suffering from higher levels of ultraviolet radiation—a result of thinner ozone. The scientists had placed UV filters over some frog and salamander eggs and left other eggs uncovered. Survival rates in the uncovered eggs were markedly lower. And media attention suddenly became higher. *The New York Times* editorialized that "the Oregon team has provided suggestive evidence that wildlife is affected by the thinning ozone layer. Those vanishing frogs are telling us something."

But some of Blaustein's colleagues aren't sure what that something is. "The study was very poorly grounded in long-term, quantitative field data," says Joseph Bernardo, an ecologist at the University of Texas. The Oregon team failed to investigate whether UV levels had actually risen over the last 10 years—the period in which, according to Blaustein, amphibians have become more difficult to find—nor did they test other possible explanations for frog egg mortality, Bernardo says. For instance, a fungus known to be spreading through some frog populations in the Northwest could have killed enough of the eggs to provide a more mundane solution to the mystery of the attenuated amphibians.

Although Blaustein insists that "we've been doing natural history on these animals since 1979," and "we studied UV because we can't find any other reason why they are dying," Bernardo is not impressed. The "inferential chain to what's going on in nature" is weak in this work, he says.



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**Natural design?** Experiments to test evolutionary theories, such as ecologist Dolph Schluter's artificial fish pond *(above)*, have some wondering if the tests are too artificial.

And there are too many such experiments being done, he and others charge. For 3 decades, ecologists have been replacing assumptions about natural systems with testable theories and rigorous statistical analyses, says William Resetarits, an ecologist for the Illinois Natural History Survey. While this effort has been key to the field's progress, Resetarits says it's gone a bit too far, and experiments often reduce nature to oversimplified caricatures that have little to do with the real world. "Experiments can do something for ecology that no other approach can do: establish cause and effect. But they don't tell you what questions to ask, or whether you are testing your questions appropriately," Resetarits says.

Now, says Bernardo, "there is a little bit of a backlash from people like me, younger folks who are fed up with that kind of artificiality." And at the annual meeting of the American Society of Zoologists in St. Louis in January, in a 2-day symposium called "The State of Experimental Ecology," these new experimentalists held an organizational rally of sorts. They argued that only by combining careful experimental design with long periods spent observing ecosystems and their inhabitants—what field researchers call "muddy-boots biology"—can ecologists come up with truly meaningful results. "We wanted to provide a framework for the next paradigm in experimental ecology," says Resetarits.

### Ecology's evolution

This budding revisionist movement is a reaction to what, 30 years ago, was a revisionist trend of its own: controlled lab and field manipulations. Now comprising at least 60% of the studies published in ecology's three major journals, according to a 1994 survey, such research was rare throughout most of the discipline's history, says Robert Holt, a community ecologist at the University of Kansas Museum of Natural History. "People would observe patterns in nature consistent with their theories, then conclude that this proved the theories right," Holt says. Beginning in the 1960s, however, "ecology went through a very critical phase where it was realized that in order to actually nail down that a particular process is taking place, you have to go out and kick the system."

Trailblazing investigations published by ecologists Joseph Connell in 1961 and Robert Paine in 1966 did much to convince their colleagues of the power of experiment. By removing, enclosing, or transplanting small populations of the barnacle *Balanus balanoides* along the intertidal zone of the rocky Scottish coastline, Connell proved that the distribution of another barnacle species, *Chthamalus stellatus*, was regulated mainly by competition with *Balanus*. Paine, by contrast, was able to show that the removal of a "keystone" carnivore, the starfish *Pisaster ochraceus*, from patches of Washington shoreline allowed its favorite prey, the mussel *Mytilus californianus*, to edge out most other local invertebrates, drastically altering local species diversity (see p. 316). Although ecologists had long suspected the importance of mechanisms like competition and predation in shaping species distribution, never before had these forces been so explicitly demonstrated.

These and similar experiments spawned "an incredible maturation and intellectual momentum" in ecology, says David Tilman, director of the University of Minnesota's Cedar Creek Long Term Ecological Research area. "In the intervening 3 decades, ecology has gone from not even considering the possibility of being able to predict patterns in nature to having an understanding of some broad general principles," Tilman says. Contemporary ecologists conduct experimental manipulations in nearly every accessible habitat and on every practical scale, from Rutgers University ecologist Peter Morin's laboratory investigations of food webs among bottled algae and bacteria to Tilman's own studies of changing species diversity within dozens of square-meter plots, each seeded with up to 54 local plant species, on the Minnesota prairie.

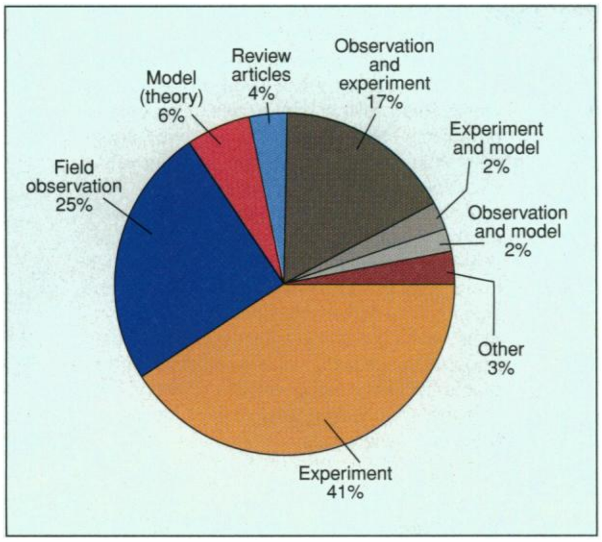
And ecology journals, full of differential equations and multiple regression analyses, are growing more and more difficult to distinguish from their counterparts in "hard" sciences like geophysics or applied mathematics. "The push toward experimentation beginning in the 1960s was the result of 'physics envy,' " says Resetarits. "We wanted to be a hard science."

### A disconnect with nature

But this effort to transform ecology into an experimental science has had a downside, say critics. "Now that we've infused people with the need for rigor, we've perhaps drawn them a bit too far from the roots of ecology," says Resetarits. Authors can have difficulty persuading journal editors to include tables of field observations germane to their experiments, he says. And unlike Connell's and Paine's pioneering field experiments, which were based on prolonged observation of local population dynamics, Bernardo argues that many experiments conducted by today's ecologists evidence no such intimacy with nature. "The problem is that ecologists threw out the proverbial baby with the bath water," Holt says.

One instance of this estrangement, Bernardo and other critics say, was the Oregon team's work on amphibians and UV radiation. Blaustein and co-workers found that frog and salamander eggs inside UV-protected enclosures had a much greater chance of developing into tadpoles than those in unfiltered enclosures. They also discovered that eggs from a frog species with high natural levels of photolyase, an enzyme that repairs UV damage to DNA, survived better in all the enclosures than did those with lower photolyase levels. Human activity, they concluded, may be depleting Earth's ozone layer faster than many amphibian species can evolve new defense mechanisms against UV radiation [*Proceedings of the National Academy of Sciences* **91**, 1791 (1994)].

Bernardo, however, dismisses Blaustein's study as a "science fair experiment" whose central variable, UV radiation, was chosen with no strong grounding in local field conditions. "Has UV influence over those lakes changed over the same period that frog egg mortality has changed? He has no data," Bernardo states. "Suppose Blaustein had decided to manipulate temperature instead of UV—then the story he's weaving in the press would have been that global warming is causing [the amphibian decline]."




**Hard science.** Experiments have taken on a dominant role in ecology, indicated by this breakdown of observational techniques used in studies published in the journals *Ecology*, *Oecologia*, and *Oikos*, from 1987 to 1991.

SOURCE: *BULLETIN OF THE ECOLOGICAL SOCIETY OF AMERICA*, JUNE 1994, PP. 117–121.

David Reznick, an ecologist at the University of California, Riverside, adds that some amphibian populations—such as one Central American tree frog species that inhabits dense foliage—are declining even though they live beneath UV radiation's reach, indicating that some other mechanism must be at work. Says Reznick, "These global patterns don't lend themselves to a single easy explanation."

Blaustein agrees with this last point, saying "UV is definitely not a universal explanation for amphibian declines," and adds that new experiments are already under way to test for a possible synergism between UV radiation and a fungal disease now spreading quickly through amphibian populations in the Oregon Cascades. But while he admits there are no data showing that UV incidence has increased at the team's field sites, he notes "there are absolutely no long-term data on UV anywhere, let alone in our area ... so that can be a criticism of any UV study." Further, he says his team searched hard for other environmental changes that might be harming amphibians, such as acid rain, heavy metals and other pollutants, and habitat destruction, but found nothing. "What we've seen in about 15 different field sites is that the eggs that are dying are right out in the open," where they are most exposed to solar UV, Blaustein says.

Bruce Menge, a community ecologist also at Oregon State University, calls the lack of long-term UV data to back up Blaustein's findings irrelevant. "If we followed [Bernardo's] arguments, we wouldn't do much of anything relevant to these pressing problems" like ozone thinning, Menge says. Blaustein is "an outstanding naturalist" who "doesn't go out and do experiments without having a natural-history basis to do them," Menge adds.

### Designing reality

Whatever the truth of the amphibian puzzle, being disconnected from nature isn't the only factor that can throw off an ecological experiment, the revisionists say. Many studies are also undermined by basic flaws in their design. It's on these grounds that Bernardo, Resetarits, and University of Pennsylvania ecologist Arthur Dunham have attacked an influential study of "character displacement" published in *Science* last year. Character displacement is the theory that competition for an ecological niche can force species that initially have similar characteristics to evolve in slightly different directions—in effect to keep out of one another's way. In the study, Dolph Schluter, an ecologist at the University of British Columbia in Vancouver, filled both halves of each of two divided artificial ponds with "generalist" three-spine stickleback fish (*Gasterosteus aculeatus* complex) that feed both high and low in the water columns of their native glacial lakes (*Science*, 4 November 1994, p. 798). To one half of the pond, he added a second stickleback species that feeds exclusively on plankton near the water's surface.

After 3 months, Schluter began recording the generalists' growth. Fish in the untreated halves of the two ponds grew normally. But in the presence of the top-feeders, he found, the quickest growing generalists were those whose mouths and gill shapes most resembled those of a third, bottom-feeding type of stickleback. Schluter's conclusion: Natural selection was starting to favor the generalists with more bottom-feeding capabilities. If the trend had been allowed to continue through subsequent generations, the initial generalist characteristics would have been be displaced because they are heritable.

Says Resetarits, "It's a sexy result, and it's gotten a lot of play, but it's a very bad experiment." Resetarits was so skeptical of the results that he, Bernardo, and Dunham challenged them in a recent Technical Comment (*Science*, 19 May, p. 1065). The experiment's fatal flaw, they say, was that Schluter failed to control for the possibility that plain overcrowding in the treated halves of the two ponds—rather than the specific presence of the top-feeders—gave the bottom-feeding generalists a growth advantage over their competitors. One simple way to establish such a control, says Resetarits, would have been to add an equal number of generalists to the untreated halves of the ponds, thus keeping the sticklebacks' densities in the two halves equal.

In addition, the critics point out, Schluter artificially increased the frequency of extreme characteristics among the generalist sticklebacks by using hybrid fish with genes from both top- and bottom-feeding species. As a result the generalists were swimming in a far richer gene pool, so to speak, than could be drawn on by individuals in a natural lake.

Schluter responds that extreme phenotypes are so rare in nature that his experiment could not have been done within a reasonable research budget without priming the genetic pump. "If you wanted to [test character displacement] with purely natural variation in those same traits, you would need a much larger sample size and a greater number of ponds," says Schluter. "It's doable in principle, but in practice it would be very daunting."

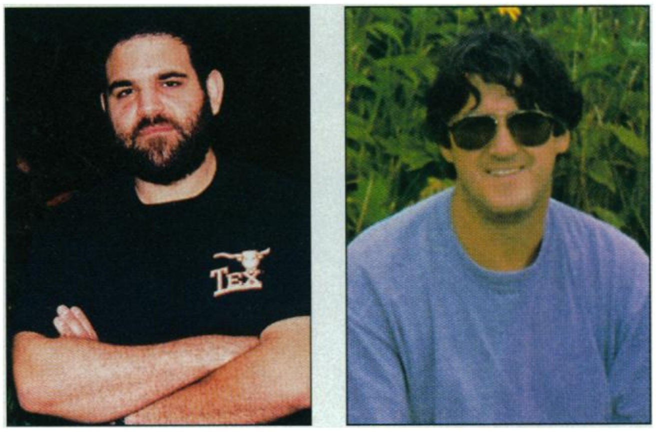
He acknowledges that his experiment did not strictly rule out density as a contributor to morphological changes. He says he chose the design described in the *Science* paper over the alternative Resetarits outlines because the alternative design would not have yielded any information about selection pressures.

In this, Schluter has allies. "I strongly respect the call for ecological realism in the design and conduct of field experiments. But Bernardo and his colleagues have argued the hard line a little too strongly," says Peter Grant, an evolutionary ecologist at Princeton University. "Not only does the stickleback experiment demonstrate a phenotype-specific effect of a competitor on individual growth rates of another—in a manner expected from the hypothesis of character displacement—but it is solidly grounded in 30 years' worth of knowledge of the animals in nature."

Bernardo, however, says the gospel of good experimental design can never be reinforced too strongly, as "there are still plenty of young [ecologists] doing mindless, stupid experiments." Too many researchers, Bernardo and Resetarits say, fail to identify explicitly the biological questions they are trying to address or to translate these questions into a set of precise, statistical tests that unambiguously distinguish between alternative hypotheses. In addition, they say, too many ecologists let their interpretations stray beyond the theory being tested or the natural system under investigation.

Such experiments carry risks that go beyond ecology, says Dunham. "When you overgeneralize your results—particularly when there is a need for applied ecological principles in conservation and biodiversity protection—then you run the risk of having bad science accepted by resource managers, with potentially disastrous results," he says.

The remedy, says Bernardo, is to "allow more complexity and multiple causality to enter into our designs." The revisionists point to ongoing field studies by James H. Brown, an ecologist at the University of New Mexico, as an example of experimental ecology done right. On two dozen quarter-hectare plots in the Chihuahuan desert of southeastern Arizona (a hectare is 2.47 acres), Brown and colleagues have spent the last 18 years manipulating one factor after another in an attempt to explain predator-prey relationships and species composition among seed-eating rodents, ants, and seed-producing plants (*Science*, 10 February, p. 880). At times Brown has fenced out certain ant species to study the effects of decreased competition; at other times he has fenced out certain rodent species to study resulting changes in grass cover and cascading effects on other species. Says Bernardo: "The experiments have been tedious, costly, and difficult, but very realistic."



**Hard questions.** Ecologists Joseph Bernardo *(left)* and William Resetarits *(right)* have challenged some of their colleagues' methods. Says Bernardo: "There are still plenty of young [ecologists] doing mindless, stupid experiments."

### The limits of description

Many researchers believe, however, that Bernardo and his fellow critics are setting unrealistic standards. They argue that complex problems like the ecological effects of global environmental change will never be untangled without help from the most reductionist of experiments: computer simulations and lab-based ecosystems. John Lawton, an ecologist at the U.K.'s Imperial College, has used a terrarium-like enclosure called the Ecotron to measure plant productivity and carbon dioxide uptake as functions of species diversity. He advocates such "controlled environment facilities" as "halfway houses between the simplicity of mathematical models and the full complexity of the field" (see p. 316 and Article by Lawton on p. 328). Adds Rutgers' Morin, "There are some ecologists who put down [lab experiments] because we have abstracted things so much. Our response is that if you don't start with a simple system, you won't understand what's going on anyway."

Other ecologists say critics like Dunham, Bernardo, and Resetarits sometimes make too much of the occasional flaws in published experiments. "It's possible to do anything badly," says Nelson Hairston, an emeritus ecologist at the University of North Carolina, Chapel Hill, and author of the 1989 volume *Ecological Experiments*.

But many ecologists not in the thick of the debate, such as Minnesota's Tilman, say participants in the St. Louis symposium are prescribing a necessary antidote to the excesses of experimentalism. Continuing generational change will reinforce this message, he believes. "Twenty or 30 years ago, most ecologists were either theorists or experimentalists or natural historians. But as younger generations are drawn in, an increasing number of individuals are acquiring skills in all three disciplines." Tilman says this has fostered "a trend in the whole field … toward the realization that ecology will advance most rapidly through a balanced combination."

That advance won't be easy, notes Gary Polis, a community ecologist at Vanderbilt University in Tennessee. Understanding the natural variability in conditions at most field sites and detecting subtle, infrequent, or hidden ecological processes takes studies much longer than the usual timescale of ecological experiments. Restoring natural history to ecological experiments will also mean broadening their spatial scales, Polis says, because many natural processes like mobility, dispersal, and species interactions can create patterns visible only from a macroperspective.

All that will take money, and although funding is scarcer than ever, many ecologists think it's worth the effort to try. "I think we're at a very early, embryological stage in the ontogeny of ecology," says Polis. "There are lots of really neat questions out there for the picking. It's just a question of recognizing them." And asking them in the proper manner.

**–Wade Roush**