Complex Dynamics Link Islands' Predators

In recent years ecologists have turned more and more to direct experimentation in trying to understand the mechanisms that shape the assembly of communities

"THE mission of community ecology . . . is to detect the *patterns* of natural ecosystems, to explain the causal *processes* that underlie them, and to generalize these explanations as far as possible." This very reasonable statement, penned by John Wiens of the University of New Mexico, is in fact very difficult to achieve, simply because the patterns and processes of the natural world are often so very complex.

Once the province principally of field observers, who attempted to infer process from perceived pattern, ecology has during recent years become much more oriented towards manipulative experimentation as a way of teasing out the mechanisms that underlie community structure and dynamics. A very good example is reported on page 949 of this issue, in which Thomas Schoener and David Spiller of the University of California, Davis, removed lizards from circumscribed Caribbean island habitats and observed the effect on orb-weaving spider populations.

Competition between species for limited resources (such as food or space) was until quite recently considered by many ecologists to be the primary force in shaping community structure. For instance, whether certain species might be able to coexist in a particular habitat was regarded as the outcome of competition, as were other biological measures, such as the relative size of coexisting species and the relative shape of structures such as beaks in coexisting bird species.

However, other factors, such as predation and physical environment are now widely recognized as being of equal or even greater importance, depending on prevailing circumstances. "One of the most important aspects of Schoener and Spiller's paper," says Stephen Pacala of the University of Connecticut, "is the way they have tried to tease apart the separate effects of competition and predation in the interaction between the lizards and spiders." It now appears that spiders and lizards are linked by a complex series of ecological interactions, which include the effects of both predation and competition.

In an earlier paper in *Science*, Schoener and another colleague had reported a tenfold greater abundance and a higher species diversity of orb-weaving spiders on a series of Caribbean islands that lacked lizards as compared with islands that carried lizard populations. Ecologists refer to this kind of observation as a "natural experiment." Although this pattern "strongly suggests that lizards reduce spider abundance and species diversity," Schoener and Spiller now comment, it is merely correlative and does not reveal the underlying mechanism. "Is it predation, competition, or both?" they ask. Hence the need for manipulative experimentation.

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In fact, Pacala and Jonathan Roughgarden, of Stanford University, did a limited lizard removal experiment in 1984, and observed an increase in spider abundance. "We saw this primarily in terms of predation," Roughgarden now says. "We didn't have evidence for competition." Schoener and Spiller's current results show that competition too is important in shaping the interaction between spider species and lizards: they both prey on flies.

"The importance of these new results," notes Roughgarden, "is that they reveal a complex network of strong interactions between different levels in the trophic web." Previous ecological theory tended to depict a simpler view of the world, with, for instance, competitive interactions occurring among species on the same trophic level but not between levels. "That neat geometry is not being confirmed." In this case, the top carnivore in the habitat—the lizards—are not only preying on species on lower levels—spiders, for instance—but also are competing with them. "It was simply not predictable that this set of strong interactions would be operating," says Roughgarden.

Schoener and Spiller's results also point up an important difference between marine ecosystems and this particular terrestrial ecosystem. Based on work on marine systems, principally of Robert Paine of the University of Washington, it had become something of a rule of ecology that the presence of predators in an ecosystem maintains a diversity of prey species. The reason is that the predator effectively prevents any one prey species from dominating the community. Remove the predator, therefore, and although the number of individuals in the community might rise, the number of species falls because the ecosystem is now dominated by a few very successful species.

This is not true in the lizard/spider case, however: both the abundance and diversity of spider species increase in sites where lizards are experimentally removed. This study, therefore, "appears to be the first study having terrestrial arthropods as prey, and it goes against the prevailing trend," observe Schoener and Spiller.

The reason for the difference is that in marine ecosystems space is usually a limiting resource, thereby sharpening competition among prey species and allowing the possibility of the most successful competitors to dominate the ecosystem in the absence of predators. By contrast, space appears not to be limiting in the terrestrial ecosystem occupied by the spiders and lizards, so the same equation does not apply. The situation is made more complicated by two factors.

First, the lizards are competing with spiders as well as preying on them, which may exclude some spider species in the face of tough competition. Second, predation of spiders by lizards apparently is so intense that in their presence some spider species become locally extinct. Remove the top predator (and top competitor), therefore, and both the abundance and species diversity of prey increases.

According to Schoener and Spiller, their study "illustrates the complementarity between 'manipulative experiments,' . . . and 'natural experiments'." The "natural experiment" had revealed the pattern in nature while the "manipulative experiment" gave an insight into the processes underlying the pattern. ■ ROGER LEWIN

ADDITIONAL READING

T. W. Schoener and C. A. Toft, *Science* **219**, 1353 (1983).