vinyl monomers and their derivatives. In hindsight, the concept outlined by Fréchet is relatively simple. In principle, this new polymerization method is quite versatile as it should be compatible with the wide range of chemistries associated with vinyl monomer polymerizations, although this first report (*1*) is focused on cationic processes. The method involves the activation of an AB vinyl monomer by an external stimulus, which in this case involved the addition of a Lewis acid to the monomer, which generates a B* moiety that is capable of initiating the polymerization of a vinyl monomer (Fig. 2). The self-condensing then begins with the addition of the B* moiety across the double bond of another AB* monomer unit to afford a dimer that contains one conventional propagating center and one B* center capable of further initiation. At this stage, this dimer now contains two active centers possessing essentially equivalent reactivities and one double bond. As such, this AB monomer has now been transformed into an AB_2-type monomer, which is known to give rise to hyperbranched "dendritic" polymers. Subsequent condensations lead to highly branched polymeric materials with high molecular weights through simple vinyl additions.

Considering the universality of self-condensing vinyl polymerizations, it will not be long before we see a plethora of new materials based on this innovative achievement. It should not be too difficult to extrapolate to such new materials as dendritic perfluoropolymers, liquid crystalline polymers based on simple vinyl monomers (*9*), thermoplastic elastomers, and perhaps even a new version of PE.

The challenges that now remain include the extension of this work to mechanisms other than propagating carbocations, such as radicals; the use of light and thermal energy as external stimuli; the development of synthetic methodologies for the creation of new "self-condensing" monomers from other readily available monomers; and the creative combination of "self-condensing" monomers with conventional monomers to generate unique materials with significantly new properties.

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Snowshoe Hare Populations: Squeezed from Below and Above

Nils Christian Stenseth

All ecologists favor long-term studies and in this respect differ from chemists, physicists, most other biologists, and all politicians. But, like other scientists, ecologists prefer to do experimental work. … We must combine these two approaches to solve the major ecological questions (*1*, *p. 3*).

The cyclical population density of the Canadian snowshoe hare (*Lepus americanus*), with high densitites occurring every 9 to 11 years, is a classic example of the multiannual cycles in many vertebrate populations of the boreal zone (*2*–*4*). Although the cycles in the hare population are cited in almost all introductory biology texts, their cause has been obscure. Food, predators, disease, and sunspots have all been put forward as essential, but there has been no agreement as to which factors best explain the cycles. Now, Krebs and his co-workers, on pages 1112 to 1115 of this issue (*5*), report a technically unique and important experiment indicating that the hare population cycle results from a food-hare-predator interaction.

The new results show that the effects of food and predation on population density are nonadditive. Food augmentation and exclusion of mammalian predators separately caused about a twofold increase in the abundance of individual hares, whereas combined addition of food and reduction of predation increased the population density by a factor of 10. Krebs and co-workers therefore argue that neither plant-herbivore nor predator-prey interactions are by themselves sufficient for cycling. Although this notion is consistent with the earlier suggestion of Keith (*4*) that the periodic fluctuations in the hare population are due to a dynamic interaction between predators and food shortage during winter, the new results do not necessarily support Keith's proposed sequential two-level interaction that assumes food shortage to be temporarily followed by predation.

The validity of the proposed three-trophic-level hypothesis may be tested independently by examining long-term monitoring data of snowshoe hare populations (*6*). If a three-level interaction is truly responsible for generating and maintaining the observed dynamics, the relevant time series should exhibit dimension (*7*) three or higher. Indeed, the structure of the hare time series is consistent with dimension three (*8*) and is therefore consistent with the proposed three-level hypothesis. In theory, a three-dimensional structure in the time series could also arise because of several other three-factorial explanations; however, the extraordinary consistency between the experimental and the time-series data greatly strengthens the plant-hare-predator hypothesis. This consistency is emphasized by the facts that (i) the experimental and the time series data are independent sources of information; (ii) by combining these two data sources, insights derived from experimental manipulation can reinforce insights from statistical analyses of observed patterns; and (iii) the new experimental results allow a biological interpretation of the estimated dimensional structure of the time series.

Indeed, this synthesis is an example of the integrated, dual approach to ecology advocated by Krebs in 1991 (*1*). I agree with Krebs (*1*, p. 3) that "monitoring of populations is politically attractive but ecologically banal unless it is coupled with experimental work to understand the mechanisms behind system changes." Further, the utility of experimentally deduced mechanisms, like the new work of Krebs *et al.* (*5*), is greatly enhanced if these mechanisms can be shown, as I have attempted above, to generate the patterns they are supposed to explain.

Many Northern microtines—lemmings and voles—also exhibit periodic fluctuations in their population densities (*10*). The estimated dimension of the time series for small rodents is typically two (*11*), suggesting that the microtine cycle may be caused by fewer processes than are involved in the snowshoe hare cycle. Krebs favors a structurally simpler hypothesis—the so-called Chitty hypothesis (*12*)—for the microtine cycle, consistent with the estimated lower dimensionality of the microtine time series. This hypothesis assumes that some population-intrinsic factor by itself causes the density cycle. But much experimental and theoretical evidence suggests that the Chitty hypothesis cannot explain the cycle (*10*, pp. 70–73); extrinsic factors also seem essential (*10*, *13*). Perhaps

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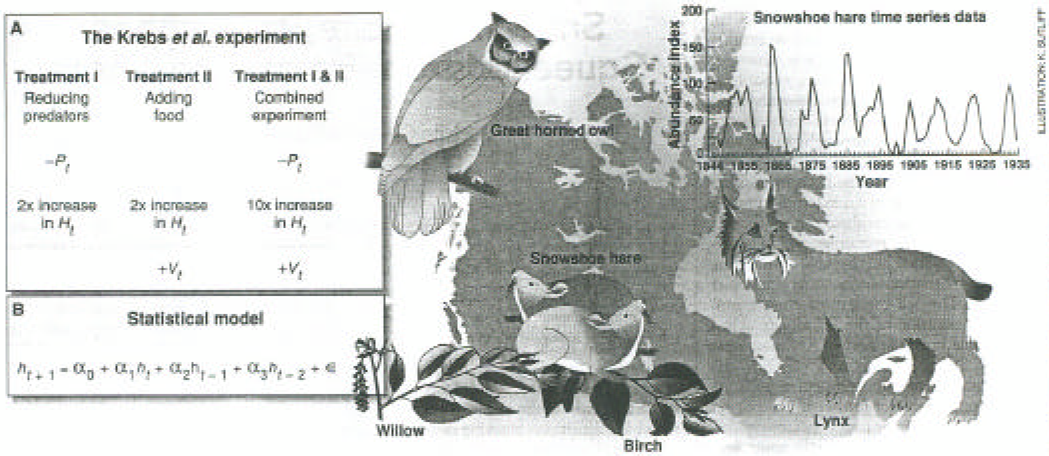

ILLUSTRATION: K. SUTLIFF

Understanding population dynamics by combining experimental and modeling approaches. The structure and dynamics of ecological systems (such as the snowshoe hare of the Canadian boreal forest) may be deduced through a pluralistic approach. (**A**) Experimental manipulations like those reported by Krebs *et al.* in this issue of *Science* (*5*). Assuming H_t to be the abundance of the hare at time *t*, the statistical modeling has been done using $h_t = \ln[H_t]$. (**B**) Statistical modeling of long-term data (*6*, *8*) [as well as mathematical modeling (*7*)]. The snowshoe hare cycle may result from a dynamic interaction between the food supply of the hares [willow (*Salix glauca*) and birch (*Betula glandulosa*)], the hares, and the mammalian predators on the hares [lynx (*Lynx canadensis*), coyote (*Canis latrans*), and great horned owls (*Buteo virginianus*)] (*9*). If the food supply, the hare population (*h*), and the predators each can be modeled as one entity, a system of three difference equations is a plausible mathematical description of the system, implying an expected three-dimensional structure of long-term time series data on the hare, which in fact is observed (*8*). [In the statistical modeling $h_t = \ln(H_t)$ has been used as the transformed variable in the analysis.]

either food or predators may be responsible for the microtine cycle, accounting for the estimated dimensionality of two of the small rodent time series. This two-trophic-level hypothesis for microtines awaits experimental testing, such as has now been provided for the snowshoe hare.

The hare cycle and the microtine cycle will continue to fascinate ecologists as they have since Elton's classic 1924 paper (*2*). Thanks to the new study by the Krebs team, ecologists are now able to pose their questions more sharply, and some pieces in the jigsaw puzzle are falling into place.

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ECOSYSTEM RESEARCH

Taking a New Look at Life Through a Functional Lens

In the mid-1970s, ecologist Robert Steneck began to see a curious pattern of continuity in the face of drastic change among algae floating off the coast of St. Croix, an island in the Caribbean. The species within the algae clusters—mats—fluctuated wildly in abundance, recalls Steneck, who is now at the University of Maine: "Almost none of the dominant species I'd find in one season would I find as dominants in the next." But what was going on in the mats varied little: They consumed nutrients at a fairly constant rate and resisted similar types of predators. Different algae, apparently, were performing the same biological role. "Certain species were ecologically equivalent to one another," Steneck says.

And with the recognition of that equality comes awareness that small organisms in a system can wield a surprising amount of influence. Since the early 1960s, Steneck and dozens of other scientists have shown that in the plant and microbial kingdoms in particular, there are whole suites of organisms with equivalent functions, or what have come to be known as "functional groups." These investigations are forcing researchers to reassess the value of a long-cherished concept: that ecosystem integrity often depends on a single critical top predator, or "keystone," species.

The keystone concept, a notion championed by population biologists who saw the often drastic effects on such systems when a top predator was removed, dominated ecological thought for 3 decades. Removing a single starfish species from a stretch off the Washington state coast, in one classic example, led to the invasion of hundreds of new organisms. But, says Princeton University ecologist Simon Levin, "focusing on particular species often misses a great deal of what's important in an ecosystem."

Indeed, a growing body of work on functional groups, Levin and others say, is giving ecologists a more complete view of ecosystem processes, looking from the ground up as well as the top down. Take the lowly tussock plants in the Arctic tundra: These plants function as a group to create a "microtopography" above the permafrost that provides a home for insects and bacteria, says Gaius Shaver, an ecologist at the Marine Biological Laboratory in Woods Hole, Massachusetts. Functional similarity could also make life easier for ecosystem modelers, because they can perform one calculation for a whole group rather than for each species. "The concept of functional groups is very widely used and implicit in the thinking of most ecologists," says Shaver.

Beyond functional groups, a broader view of ecological processes is also allowing scientists to reassess the role that individual smaller, nonpredatory species have in shaping their communities, such as the way snails breaking down rocks into soil alter the habitat for the rest of the denizens of that particular ecosystem.

The keystone concept, however, is far from dead. Ecologists are trying to integrate it into the new view by formally expanding the definition of keystone species to include creatures not at the top of a food web, such as viruses, that have a big impact on their environment. "For years we've had population biologists who worry about keystone species and food webs doing their thing, and ecologists who worry about other ecosystem processes doing their thing," says Stanford University ecologist Harold Mooney. The goal now is to bring process and species together.


BOB EVANS/PETER ARNOLD INC.

Rugged individualist. Classic keystone species, such as this starfish (*Pisaster ochraceus*), can make or break an ecosystem.

Star species. The keystone species concept took the field by storm in the late 1960s, when University of Washington marine ecologist Robert Paine described removing dozens of *Pisaster ochraceus* starfish from the rocky intertidal zone. The starfish was the main predator of mussels, which took advantage of the absence to invade and occupy the area. These new mussel beds were fertile ground for more than 300 species of organisms, such as sea cucumbers, worms, and smaller starfish that had been scarce when *Pisaster* was around. Other starfish species and carnivorous snails, limited by size in what they could eat, could not produce this dramatic effect. Based on these observations, in 1969 Paine formulated the concept of a keystone species: one that determines "the integrity of the community and its unaltered persistence through time."

Scientists soon described other keystone species, such as the charismatic sea otter. In the early 1970s, ecologists James Estes, John Palmisano, and Charles Siminsted found that after Aleut islanders hunted the otters or otherwise drove them away from certain Aleutian islands off the coast of Alaska, sea urchins—a favorite otter food—began to proliferate. That was bad news for Pacific giant kelp forests and the myriad fish living in them. The urchins gnawed on the kelp roots, killing the huge plants and leaving fish-free "urchin deserts" behind on the sea floor.

The major thrust of the keystone concept has been to identify how the presence of certain predators determines the abundances of prey and competing organisms in an ecosystem. The effects ripple down the food web, and in this way, says University of Montana ecologist Jack Stanford, "a keystone species can identify the boundaries of an ecosystem."

Yet even as ecologists' attention was being captured by the dramatic effects of top predators, a small countermovement was taking form among scientists who had begun to notice that little creatures, too, exerted a large amount of collective power and influence. "As we move lower in the food chain, the concept of keystone species becomes less important," says Levin.

Looking beyond the species. Instead of finding keystone species of bacteria, for instance, ecologists are finding influential clusters: the functional groups. The concept has deep roots, emanating in part from efforts in the 1930s to look at functional similarities among species, such as how desert plants from Africa and North America look alike and conserve nutrients similarly even though each belongs to a different genus.

Microbiologists then picked up the thread in the 1960s and 1970s, with studies on bacteria indicating that vast numbers of species perform similar functions. One example is bacteria of the genus *Rhizobium*: Although many types of *Rhizobium* have not even been identified at the species level, it appears that all the species cataloged so far can fix nitrogen and many can substitute for one another in an ecosystem, says microbiologist Rita Colwell, president of the Maryland Biotechnology Institute. Thus, scientists believe, if a particular *Rhizobium* species were to decline or die out in a system, other species could take over the job of nitrogen fixation. In effect, plants that depend on legumes and symbiotic *Rhizobium* to fix nitrogen for survival have a safety net.

Steneck's continuing investigation of algal communities has produced similar results, pointing to at least seven discrete functional groups among the algae. For instance, one group, microalgae, can form mats close to shore that are highly photosynthetic and highly susceptible to predation by sea urchins and other organisms. Any one of several species of microalgae can form mats with these characteristics [*Oikos* **69**, 476 (1994)]. "You remove one member of a group, then another takes its place: It's like ecosystem insurance," says Mooney.

Today many ecologists are eager to put this insurance policy to practical use. Instead of simply describing functional similarities in an ecosystem, they are attempting to quantify them in order to get a better handle on ecosystem health and to make predictions about how ecosystems will change over time. The notion of functional groups aids such efforts by allowing ecologists to treat many different species as a single group.

One effort where this simplification is paying off is in the development of patch models, small plots of land on which rates of photosynthesis and carbon flow can be measured for all members of the species present. Patch models, on which Levin and Paine did pioneering work in the early 1970s, are now becoming "a marriage between demographics and systems," in that data on nutrient flow can be combined with data on how processes such as forest fires influence germination rates, says Tom Smith, an ecologist at the University of Virginia. A problem that has plagued this type of modeling, says Smith, is that researchers—and their computers—can be overwhelmed by the attempt to chart all the interactions between every species and every nutrient in an ecosystem. But he and his colleagues are hoping functional group data can help them simplify some of their calculations.

The traditional focus on how top predators affect the food web has also obscured the role that single, less dominant species play in shaping their environment, says ecologist Clive Jones of the Institute of Ecosystem Studies (IES) in Millbrook, New York. But as ecologists pay more and more attention to function and process within ecosystems, those roles are becoming more clear. Beavers building dams, microalgae absorbing light and reducing the strength of sea ice, and blind mole rats digging and tunneling are all species that can have a profound effect on the existence of the organisms around them. In an article last year in *Oikos* (vol. 69, p. 373), Jones, John Lawton of Imperial College in Berkshire, U.K., and Moshe Shachak of Ben Gurion University of the Negev in Israel outlined this idea. "Every ecosystem we looked at, we found a species modifying the environment in a manner important to the integrity of the ecosystem," says Jones.


ROBERT STENECK

Mob rule. Although individually not influential, clusters of functionally equivalent species, like these articulated algae (about 3 centimeters tall), can also have powerful effects.

Keystone revisited. Ecologists have not turned their backs on keystone species completely, however. "You can't get around the fact that some individual species are going to have much larger effects than others on their ecosystem," says Lawton. As a result, some researchers are trying to tie species and process together in a broader sense than was used in the traditional keystone concept.

One such attempt is to look at what IES ecologist Rick Ostfeld calls "keystone processes." He and IES colleague Charles Canham have found that population fluctuations of meadow voles can determine the species of trees gaining a foothold in agricultural land now slowly reverting to forest in upstate New York [*Ecology* **74**, 1792 (1993)]. The researchers have found that the voles ravage seedlings of red maples, sugar maples, and white ash, as well as tree of heaven, an aggressive Chinese invader. A healthy vole population "can eliminate an entire cohort of tree seedlings," he says, which clears the way for the growth of tree seedlings the voles eschew, such as acorns, oak, and pine.

A major attempt to refine the keystone concept took place at a meeting in Hawaii last December, where 15 prominent ecologists, including Paine, met to discuss how the notion of a keystone species might be extended beyond creatures sitting atop a food web. One way, says University of Minnesota ecologist David Tilman, a conference participant, might be to define a species as a keystone based on the ratio of its biomass to its effect on an ecosystem. A high ratio would merit a keystone classification.

The advantage of this definition, says Tilman, is that it encompasses the effect of a species on any ecosystem process. For instance, ecologists could identify keystone viruses. In the past, no ecologist would dream of describing a distemper virus that kills lions as a keystone species in the African plains community. But the virus does have large effects on the ecosystem considering its biomass. In line with this idea, the "keystone cops," as the Hawaii group called themselves, drafted a new definition of keystone species: "a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance."

Even a more traditional notion of a keystone species can be put to valuable use in conservation biology when linked to a basic understanding of ecosystems processes, says Stanford. He suggests such an approach could be useful in the effort to bring back two fish in the upper Colorado River, the Colorado squawfish and the humpback chub, which have been on the federal endangered species list for more than 20 years. There are myriad roots of the fishes' decline, Stanford says, including tourist traffic, overfishing, exotic species, and increased ultraviolet radiation that all reduce the food web supporting the fish. But which of these is most important, how many other factors there are, and which would yield the greatest payoff from remediation are open questions.

So Stanford envisions a two-pronged approach. While neither the chub nor the squawfish is a classic keystone species, a real keystone fish, such as a salmon, can be used to define the limits of the food web enmeshing the two endangered species. Once those limits are set, researchers can begin to investigate the processes occurring within those limits. "People lost sight of the very complex interactions that must be preserved to bring the fish back," he says.

Keystone species "may not be important in every ecosystem," says Michigan State University ecologist Gary Mittelbach, but "ecologists should not be too quick to abandon the idea entirely." The bottom line, he and other ecologists say, is not to cordon off research on these "gifted" organisms. If scientists can place keystone biota in the context of the processes that maintain an ecosystem, says Levin, they can "begin to understand what maintains ecological functioning." And that, after all, is what ecology is all about.

–Richard Stone