FOOD WEB

"The Living Sands of Namib," a National Geographic PBS special

Part of the web: A white lady spider constructs a trapdoor of silk and sand under which she waits for unwitting prey, like this dune cricket.

Mathematical analysis unravels a simple pattern from the complexities of predator-prey interactions

BY JULIE ANN MILLER

From the least to the greatest in the zoological progression, the stomach sways the world; the data supplied by food are chief among all the documents of life.
—J. H. Fabré, 1913

Snakes eat frogs and birds eat spiders. Birds and spiders both eat insects. Frogs eat snails, spiders and insects. No wonder ecologists have been caught up in that tangle of relationships they call a food web.

But among the hundreds of food webs naturalists have reported, each based on painstaking observations of a forest, pond or desert, no persuasive patterns have emerged until now, says population biologist Joel E. Cohen of Rockefeller University. "People were just recording — going out and making observations and putting them down."

Ten years ago Cohen, troubled by the limited analysis of ecological data, began studying a branch of mathematics known as combinatorics in the hope of making sense of food webs. He now reports that the web can be untangled into a straight line, or more technically, into a one-dimensional niche space. His analysis demonstrates that the complexities of food webs do not preclude discovering simple patterns that should stimulate further descriptive and theoretical study.

Cohen's analysis pulls together basic concepts of ecology — the food web and the niche space. "This is really the first time we've found a relation between these two fundamental concepts," he says. In his recently published monograph, *Food Webs and Niche Spaces* (Princeton University Press), Cohen explains, "By a food web, we mean a set of different kinds of organisms, together with a relation that shows the kinds of organisms, if any, that each kind of organism in the set eats." A niche space, on the other hand, is the composite of all the environmental factors acting on an organism in its natural habitat. Each of these factors, such as temperature or altitude, is considered one dimension of the niche.

Cohen has found that most food webs follow a simple pattern. According to his mathematical analysis, they depend on only one dimension of the niche. The challenge remaining is to determine just what that dimension is. To confound the problem, that dimension is probably a different characteristic in different communities of organisms. It may be as obvious as animal size — for instance the bigger a bird's beak, the bigger the food it can swallow. Or the dimension may be more subtle, perhaps the ratio of energy gained by eating a prey organism per unit energy expended in predation.

As an analogy, Cohen suggests that geometers trying to classify circles on the basis of size might record the radius, the diameter and area as three separate dimensions of each. Soon, however, such categorizers should realize that only one of those dimensions is sufficient (the diameter is always twice the radius and the area always *pi* times the square of the radius). Similarly, in categorizing communities on the basis of food relationships, Cohen says, "If you classify niches by pressure, temperature, salinity, altitude, humidity and sunshine, a single dimension is sufficient to account for the information in food webs."

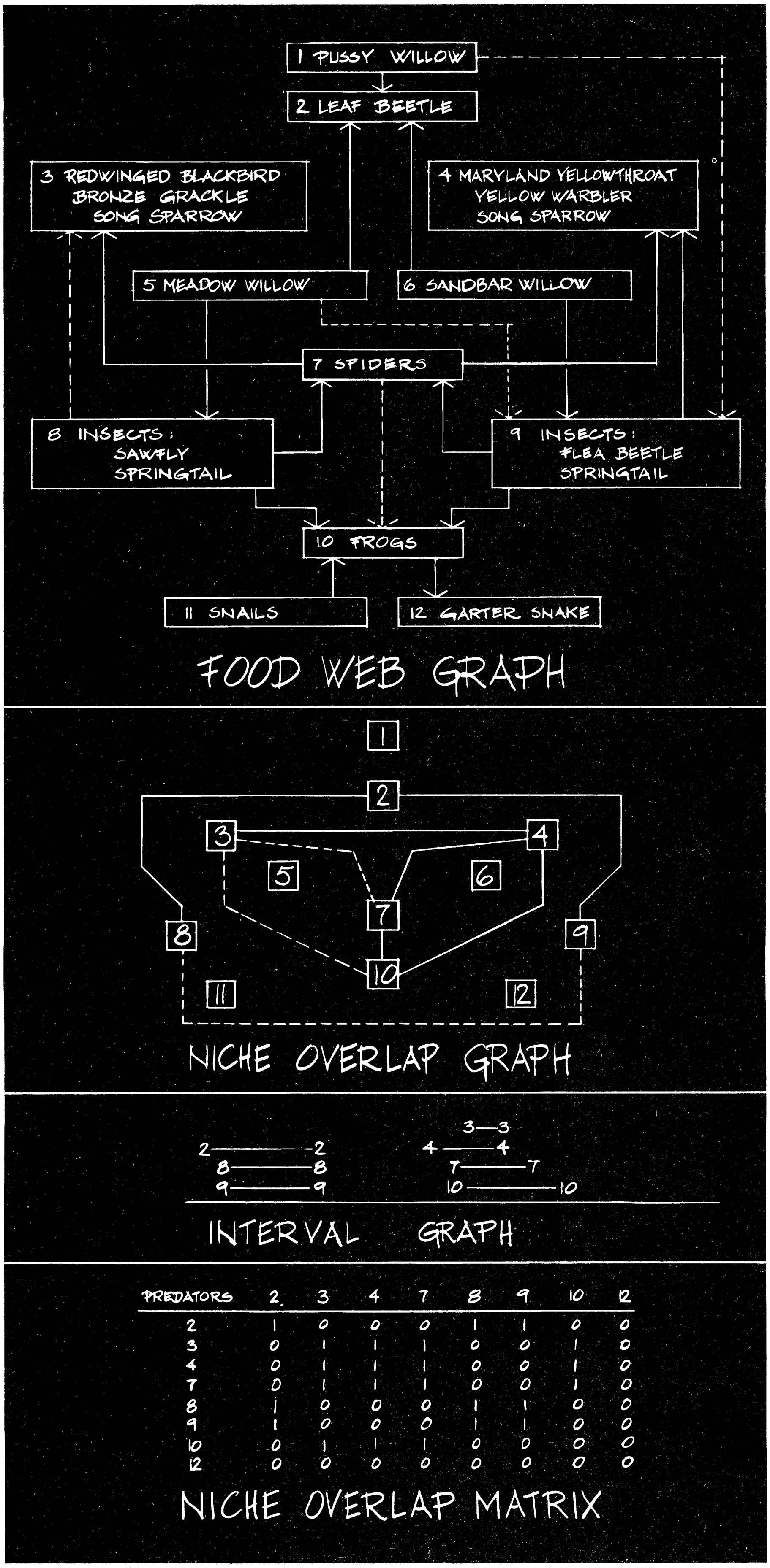
Outside the problem of who eats whom, niches may of course have other aspects. For example, a factor that could influence how a community of organisms functions is need for shelter. Going back to the circle analogy, Cohen points out that if the geometers became interested in the color of their circles, the radius dimension would no longer provide sufficient information.

The mathematical idea Cohen applied to the food webs is called an interval graph. Interestingly, this class of graphs was invented twenty years ago by a biologist faced with a very different problem. Seymour Benzer of California Institute of Technology invented the interval graph in an attempt to study the arrangement of mutations within a gene. He found that mutant viruses missing pieces of their DNA could be analyzed so that all the missing segments appeared as intervals of a line. This analysis made it unlikely that the virus's genetic material was arranged in a branched or circular pattern. In this case, in contrast to the food webs and niche spaces, the one commanding dimension was obvious: It is the physical linearity of a DNA molecule. (Interval graphs were also invented independently in Europe by G. Hajós as a purely mathematical speculation.)

Interval graphs since have also played a role in archeology, in which the important dimension is time. Styles of artifacts can be associated with an interval of history, so the interval graph helps determine the sequence of findings. The technique has also been applied in as far-flung fields as psychophysiology, economics and traffic engineering. The idea of applying it to food webs, Cohen insists, came to him in a dream after he heard a former classmate define interval graphs in a lecture.

Although Cohen has done field work in tropical ecology and primate social behavior, he did not himself collect the food webs he analyzes. He gathered the 31 webs from descriptions in 22 different papers published between 1923 and 1970. Because many published food webs did not contain sufficient information to be included in his study, Cohen bids ecologists to be quantitative in reporting their investigations (for instance, include the actual number of specimens of each kind of prey taken by each kind of predator under specified conditions) and to pay particular attention to regions of overlap among predators. So far, he knows of no field investigations specifically designed to test his niche-space hypothesis. "It takes time for people to digest a new approach," he says.

To explain how he turns a food web into an interval graph, Cohen works through the example of the community of organisms living in a Canadian willow forest, reported in 1930 by Ralph D. Bird. In each box of the food web diagram are organisms that share both predators and prey. The arrows point from the prey to the predator. Cohen derives from the diagram a "niche overlap" graph by drawing lines connecting groups of organisms if and only if both groups have a common prey. For example, spiders and frogs are joined



Volker Zinser/Cohen

Analysis of a Canadian willow forest, from food web to computer format. Dashed lines indicate the more tentative relationships. Arrows point from prey to predator.

because they both eat insects.

The question then is whether all the niche overlaps can be represented by overlapping intervals of a line. For the willow forest there are several arrangements of intervals along a line that adequately reflect the observed niche overlaps. For instance, group 2 (a leaf beetle) overlaps only groups 8 and 9 (different kinds of insects). Thus, if in this community the important dimension was, for example, distance from a stream, there would be an area for predation only by those insects.

Cohen further converts the data to tables of 0's and 1's that are convenient for computer analysis. In these tables, a 1 indicates that the predator of the columns eats the prey of that row. From such tables a computer can determine whether the data fit an interval graph. An example of a noninterval pattern is a hypothetical community including four predators (A, B, C, D) in which the only overlaps in diet are between A and B, B and C, C and D and D and A. Such a pattern could not be represented as overlapping intervals along a line.

Twenty out of twenty-three actual single-habitat food webs that Cohen analyzed were found to be interval; the overlaps between predator groups map on a straight line. To see whether that is a surprising finding, Cohen "pseudorandomly" sampled artificial food webs constructed to meet specific criteria. He concludes that the high frequency of interval graphs among the observed food webs is based on something more than chance.

The finding that niche overlaps in food webs can be described by a single dimension of the niche space has three levels of implications, according to Cohen. "It suggests that life may be simpler than one had reason to suspect previously," he says. It also provides a firm basis for other theories of ecology. For instance, theories on the evolution of niches have assumed a one-dimensional niche space as a matter of convenience. A multi-dimensional niche space is simply too difficult to analyze. "That wasn't totally off the wall," Cohen now concludes.

Finally, the analysis provides a new way of looking at things, Cohen says. It should encourage naturalists to look for simple relationships in the confusing complexity of a plant and animal community. Cohen suggests that many of an animal's physiological possibilities may be restricted by the company of other animals. For instance, a bird may have reflexes quick enough to catch a frog, a beak big enough to engulf it and the physiological machinery to digest it. But that is of little import in a natural setting where snakes always get to the frogs first.

Cohen says that he has focused his analysis on food because it is one of the most fundamental themes in ecology: "How to get the energy to survive is basic to how any community works." □