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BIG FISH, LITTLE FISH

The Search for Patterns in Predator-Prey Relationships

by JOEL E. COHEN

TO CHARLES DARWIN, concluding *On the Origin of Species*, the natural world seemed "an entangled bank" of predators and prey. Since his voyage aboard the H.M.S. *Beagle*, in the 1830s, Darwin had come to realize that predatory relationships are among the important forces that guide evolution—that, in a more immediate sense, one carnivorous species could transform an entire expanse of English pasture. The blossoms of two meadow flowers, heartsease and red clover, he observed, are pollinated by a single species of bee. And the "number of humble-bees in any district depends in a great degree on the number of field-mice, which destroy their combs and nests." Since certain domestic creatures in England have a well-documented taste for mice, "it is quite credible," Darwin proposed, "that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!"

Spurred in part by Darwin's ideas, and in part by the practical needs of agriculture, the American naturalist Stephen Alfred Forbes, in the 1870s, studied another piece of the same entangled bank: the diets of birds and

fishes in Illinois. Cutting open hundreds of specimens and cataloguing the contents of their stomachs, down to the last berry and bug, Forbes quantified the connections between species. To keep track of the predatory relationships in each ecological community, he constructed a simple table, consisting of columns of numbers. At the head of each column, he wrote the name of a predator, and beneath, the number of specimens of each species found in its stomach. A walleyed pike, for example, would be placed at the top of a column containing the numbers of water fleas, crayfishes, and other small invertebrates it had consumed.

Sometimes, Forbes revised his columns so that each one represented a group of species of a particular size: fishes less than one inch long, fishes one to two inches long, and so on. Then, at the left margin of each row, he wrote the name of an organism found in the stomach of at least one of the predators, and, at the intersection of a column and a row, the average fraction of the predator group's diet represented by that prey. Tables such as these, with minor variations, have been used ever since to tabulate predatory relationships. Thus, Forbes's thor-

ough investigations in the fields, lakes, and streams of the Midwest constituted an early step in what has become an international effort to measure the extent to which one species feeds on another.

In 1913, another Illinois naturalist, Victor E. Shelford, came up with a different method of describing the complex feeding relationships that Darwin and Forbes had discerned, using drawings of interconnected boxes. In Shelford's diagrams, the name of each species or group of species in a habitat was placed in a box, and arrows were drawn connecting prey to their predators. At the top of the diagram were creatures, such as sharks, that have no natural enemies (overlooking microscopic parasites and other sharks)—species that eat other species but are not themselves consumed by members of their own habitat. In the middle were species such as mackerels and squids, which hunt other creatures and, in turn, are preyed upon. And at the bottom were species such as algae and phytoplankton, which serve as food for animals but do not themselves eat animals or plants. Because of the profusion of lines connecting the boxes, Shelford's illustration resembled a web, and biologists eventually adopted the concept: the full complement of predator-prey relationships within any habitat came to be known as a food web.

The first diagram of an actual food web (Shelford's sketches were only hypothetical, requiring no hard data) was drawn by an English naturalist, Charles S. Elton. In 1921, Elton explored Bear Island, an Arctic outcrop two hundred and forty miles north of Norway. His diagram of predator-prey relationships included more than thirty-five species, with arrows indicating that common eiders, oldsquaws, and red-throated loons dined on microscopic *Rotifera* and were, in turn, eaten by the arctic fox.

A year later, the English marine biologist Alistair C. Hardy constructed an even more extensive diagram. He presented, at the top of the page, four circles in a row, each containing a species of herring at a particular stage of development. Below these were some forty additional circles and boxes, each enclosing the name of a food that herrings eat: young fishes of other species, sand eels, fish eggs, worms, plankton. Lines connected the herrings and their prey and also indicated which species of prey consume each other (sand eels dine on plankton, for instance). Taken together, the strands of Hardy's web portray the vast variety of ways in which forty-odd species living in the North Sea, off the eastern coast of Great Britain, nourish one another.

In the years since these drawings were made, food-web diagrams have become more prevalent than the kind of tables Forbes used; many biologists find it easier to think in pictorial, rather than numerical, terms, and far less labor is required to sketch a series of boxes than to count and tabulate, as Forbes had done. In short, the food-web diagram is a handy simplification of nature. It ignores the real-life details of species interaction—the variety of diets that individuals within a species may have (one walleye may eat mostly crayfishes; another may prefer water fleas); the effects that such natural disasters as drought or flood may have on numbers of predators and prey—and focuses on the question of what eats what. Like a street map, which pictures where cars can go but ignores the details of how actual traffic ebbs and flows, a food web presents a framework for viewing, in isolation, the con-

nections between species in a habitat. Yet even such a stripped-down view of nature can be remarkably complex. Looking at the welter of boxes and lines in Hardy's diagram, one can hardly argue with Darwin's description: the natural world is "an entangled bank" indeed.

Recently, however, a certain order in networks of predator-prey relationships has come into focus. Through statistical comparisons of more than a hundred of the most detailed food webs that biologists have drawn, and through the use of mathematical models (similar to, but more complicated than, Forbes's tables), have emerged glimpses of regularity in predator-prey relationships. It turns out that food webs from diverse and far-flung habitats—from arctic sea to tropical forest—share some basic properties. Just as the mathematics of Malthus (population grows geometrically, while the means of subsistence increase only arithmetically) pointed Darwin to his key



insight into how the struggle for scarce resources can lead to survival of the fittest, some novel but simple mathematics is now helping ecologists gain insight into the entangled bank.

DURING THE PAST HALF-CENTURY, squadrons of field biologists have sketched hundreds, perhaps even thousands, of food webs, based on their observations of habitats throughout the world. As each new web was published, and it appeared that no two contained the same pattern of boxes and lines, biologists became increasingly awed by nature's complexity. Most presumed that each web, like each snowflake, had its own idiosyncratic beauty. So it is understandable that only a few paused to investigate the possibility that the various networks of predators and prey might have some features in common.

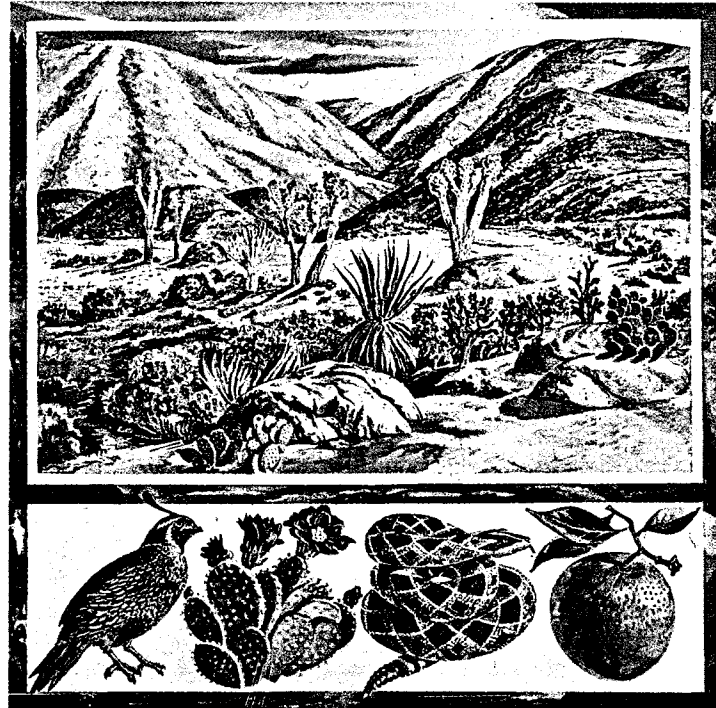
One of those who attempted to make sense of the ap-

parent chaos was an American chemist named Alfred J. Lotka, who, in the 1920s, turned his attention to predator-prey relationships. Accustomed as he was to the ways in which different kinds of atoms have predictable effects on one another, combining in prescribed amounts to yield molecules, Lotka suspected that different species might also interact according to general laws that could be stated mathematically. Therefore, he modified some of the formulas that chemists use to understand how molecules combine, so that they could be used to represent predator-prey relationships.

His calculations indicated that the populations of a predator and its prey fluctuate regularly in a coordinated manner, ensuring the continued survival of both species. A cycle might begin, for example, with a decline in the prey, followed by a decline in the predator species, an increase in the prey, and an eventual increase in the pred-

were unable to consume enough prey to keep the prey in check, so the prey multiplied indefinitely. In most cases, predator and prey refused to interact as Lotka's equations assumed they might.

Another attempt to find order in food webs came in 1942, from the research of Raymond L. Lindeman, a post-graduate student of zoology at Yale. In his last paper, published posthumously, Lindeman observed that a predator assimilates, or uses for its metabolism, only a small fraction of the energy its prey consumes. A human family, for instance, assimilates only a small fraction of the usable calories a cow eats—only the part of the cow's diet that is incorporated into its muscle and fat tissue (most of the rest is used by the cow in respiration; is taken up in the production of such inedible body parts as bone, hide, and head; or goes to waste). Cattle, in turn, assimilate only a small fraction of the total energy from the pastures they



Don Nice, California Quartet: Winter, Summer, Spring, 1988

tor. Theoretically, such a cycle might be explained in terms of each species' biological needs: When the number of prey decreases, the number of predators must drop, because there is a shortage of food. Life, in turn, becomes safer for the prey, and so it flourishes. And its success means prosperity for the predator, which ultimately multiplies, too. But Lotka was concerned only with demonstrating the mathematical basis of such cycles—with showing that population cycles could repeat indefinitely if predator and prey behaved as his equations assumed they would.

To test Lotka's ideas, scientists set up ecosystems in their laboratories—creating miniature habitats in aquariums, for instance. They found that population cycles did occur in some cases, but that, in most, the predators and prey refused to interact as Lotka's equations suggested they would. In some experimental systems, the predators ate *all* the prey and then became extinct; in others, they

graze (much is uneaten or inedible), and the pasture likewise transfers only a small amount of the energy from the sunlight that strikes it to stalks and leaves. Lindeman pointed out that the further an organism is from depending directly on solar radiation, the less probable it is the organism will dine solely on prey that are exactly one step closer to relying on solar energy: in a lake, for instance, pondweeds depend entirely on sunlight for energy; browsers eat pondweeds; benthic (bottom-dwelling) predators eat browsers and pondweeds; and swimming fishes, the least dependent on sunlight, may eat benthic predators, browsers, and pondweeds.

In 1959, G. Evelyn Hutchinson, who had been Lindeman's professor, used this insight to explain why a single food chain (a series of predators and prey stretching from the bottom of the food web to the top, in which each species is eaten by the next one in line) is usually short—typically no more than four or five species long. Hutchinson

believed that so little energy is transferred from link to link in the chain that, after more than four or five steps, not enough energy remains to support another level of life.

More than a decade later, another element of order within food chains was observed. In 1972, the Argentine biologist Gilberto C. Gallopín observed that species near the bottom of a chain rarely prey on those higher up (provided decomposers are excluded, as they generally have been, until recently, in food-web diagrams). It seems obvious enough in hindsight, and it is even implied by the hierarchical arrangement of food-web diagrams: If species A eats species B, and species B eats species C, then it is unlikely that species C will eat species A. (The general pattern Gallopín observed does not rule out cases in which two species prey upon each other. For example, in the Coachella Valley, a desert region of California, black widow spiders catch and eat scorpions by trapping them in strands of silk and lifting them off the ground, and the same scorpions capture black widows traveling on the ground.)

Such glimpses of order did little to disturb the view of food webs as essentially chaotic, perhaps because each observation was confined to a narrow aspect of webs: Lotka's was focused on relationships between individual pairs of species, and those of Lindeman, Hutchinson, and Gallopín were limited to individual chains. The web in its entirety was still thought too complex to be orderly. Arctic sea and island reef were presumed to be distinct worlds, with food webs organized in fundamentally distinct ways. Many scientists seemed satisfied just to study the population dynamics and natural histories of individual habitats—and to marvel at nature's infinite diversity.

IN THE 1960s, a small group of ecologists trained in mathematics began to look for elements of order in habitats—though, initially, they ignored food webs. One of them, Robert M. May, an Australian theoretical physicist now at the University of Oxford, eventually designed a mathematical model that appeared to demonstrate an inverse relationship between the complexity of an ecosystem (the number of species it contains and the number of feeding relationships among them) and the stability of the individual populations within it: if the ecosystem grows too complex, the populations become highly unstable. But most of those who championed this approach to studying nature had little patience for the detailed collection or analysis of real data; they limited their work to hypothetical habitats.

So it was a novel effort when, in the late sixties, I began to gather actual food webs—representing habitats ranging from Antarctic pack ice to Long Island coastal estuaries and Malaysian rain forests—in the hope of finding common features among them. During the next decade, I analyzed thirty webs. Since then, ecologists have studied hundreds of others, and the hope that patterns would emerge has been richly fulfilled.

Simple tabulations demonstrated, almost immediately, that in nearly all webs the ratio of the total number of predator species to the total number of prey species is approximately the same, no matter what the habitat. Initially, this ratio appeared to be about four to three, but that estimate was based on the misleading assumption



that biologists' descriptions of all kinds of predators and prey are equally detailed. In fact, as Stuart Pimm, of the University of Tennessee, in Knoxville, has pointed out, ecologists are more likely to describe furry and feathered creatures than the less familiar insects, plants, and microorganisms upon which those creatures dine. Where an ecologist might distinguish two species of sparrows, the same ecologist might not distinguish the small insects those sparrows eat.



Don Nice, American Totem: Cornucopia Bear, 1981

In 1984, Frédéric Briand, an ecologist now at the International Union for Conservation of Nature, in Gland, Switzerland, and I devised a way of circumventing this problem, by redefining a species (usually thought of as a group of plants or animals with shared genetic traits) as a collection of creatures that behave alike within a food web. For example, if three species of grasshoppers all eat the same food and are, in turn, eaten by the same birds, they can be considered members of the same *trophic spe-*

cies (from the Greek *trophikos*, meaning nourishment). Upon reexamining food webs in this light, we found the ratio between predator and prey trophic species to be much closer to one to one.

Briand and I also discovered that there is typically a balanced distribution in a habitat's numbers of top species (those that are predators but never prey), intermediate species (those that act as both predator and prey), and basal species (those that are consumed but never consume other plants or animals). On average, top species make up about one-fourth of the total, intermediate species about one-half, and basal species the remaining fourth. The precise proportions may vary from habitat to habitat, but none are wholly lopsided such that one type of species makes up an unduly large share of the web.

Another pattern can be found in the number of connections between predators and prey—the so-called links, which are represented by the lines in food-web diagrams. There are four kinds of links: those between top and intermediate species (a shark and a mackerel, for example), those between different intermediate species (a flounder and a clam), those between intermediate and basal species (a duck and *Rotifera*), and those between top and basal species (a man and a carrot). On average, the proportions of the four kinds of links appear to be roughly the same in every habitat, regardless of the number of species the habitat contains: about thirty-five percent of links fall into the first category, thirty percent into the second, twenty-seven percent into the third, and only eight percent into the fourth.

Finally, the comparison of webs has revealed that the number of links in a web is approximately twice the number of trophic species. In one California salt marsh, for example, biologists have observed thirteen trophic species—including terrestrial and marine plants, fishes, herons, migrant shorebirds and waterfowl, passerines (perching birds), and meadow mice and rats—and twenty-six links among them. Naturalists realize that there are hundreds, or perhaps even thousands, of biological species yet to be described in the salt marsh and that, if all of them were lumped into trophic groups, there might be hundreds of trophic species, not thirteen. But given the consistency with which the food webs studied so far have followed the observed patterns, it seems unlikely that the ratios would change dramatically.

THESE INSIGHTS, demonstrating the existence of standard dimensions in most food webs, opened the way for the creation of a remarkably simple but useful mathematical representation of food webs, designed to illuminate other elements of structure in predator-prey relationships. The model (devised by Charles M. Newman, a mathematician at the University of Arizona, and me) uses a numerical table, or matrix, which is a tool for examining relationships between pairs of objects in a collection. All the trophic species in the web are listed down the left side of the matrix, with each assigned its own row, and, again, across the top of the matrix, so that each also has its own column. The boxes in the grid can then be filled in with numbers that represent interactions between columns and rows, assuming that column species always play the role of predator, and row species that of prey. If the matrix were to represent an actual food web,

a numeral one would be entered in the matrix where, say, a shark column intersects a mackerel row, to indicate the existence of a predator-prey relationship, whereas the box where the mackerel column intersects the shark row would hold a zero (since mackerel do not eat sharks). This way, the grid would show only one link between each predator-prey pair.

The mathematical model incorporates three fundamental qualities of real webs. The first is the rarity with which one species preys on another that lies above it in the web. All the trophic species in the web are numbered consecutively, beginning with the most basal species (numbered one) and working up to the topmost species (which has the highest rating), so any species is presumed capable of eating any other with a number lower than its own. Species number one is listed to the left of the topmost row of the predation matrix, species two below it, and so on to the bottom, and the columns are similarly numbered in order from left to right.

Looking at the grid then, one could imagine a diagonal line drawn from the top left box to the bottom right box, running through all the spaces in which the column species is the same as the row species. The boxes along this diagonal would be filled with zeroes, indicating that trophic species never consume themselves. Similarly, the boxes to the left of the diagonal would always be filled with zeroes, because they represent the places where the row species has a lower number than the corresponding column species. Thus, the only numerals one in the entire grid fall to the right of the diagonal. Since this numbering pattern mimics the way predation cascades downward from top species to intermediate to basal, and because it is such an essential feature of the matrix, the model has come to be called the cascade model.

The second fundamental characteristic the model incorporates is the great variability known to exist among food webs. When data from actual webs are plugged into such a matrix, there appears to be no regularity whatever to the way the ones and zeroes are arranged; each web appears to have a unique pattern, because each link is formed independently. (Whether a mole eats a winter moth has no influence on whether the moth feeds on an oak tree.) To mimic nature, then, the cascade model assumes that each box in the top right half of the matrix should receive a one or a zero independently of every other box. So the equations used to generate ones and zeroes are designed to ensure that the existence of a link between species six and species five, say, has no influence on whether a link exists between species five and species four.

Finally, to reflect the discovery that, in real webs there are usually about twice as many links as trophic species, the cascade model assumes that the probability that any box in the upper right half of the matrix will contain a one is equal to four divided by the total number of species in the web. (This formula was arrived at by looking at webs of various sizes and figuring out what kind of arithmetic it takes to produce a two-to-one ratio of links to species over the entire matrix in all cases—given that the bottom left triangle is always filled with zeroes.) Thus, in a web with eight species, the probability that any box in the top right half would contain a one is four divided by eight, or one-half, while in a web with sixteen species, the proba-

bility would be four divided by sixteen, or one-quarter.

In sum, the cascade model assumes nothing more than an ordering of species, independence among predator-prey pairs, and a probability of links that is inversely proportional to the number of species. It ignores how much an individual predator eats of any given prey, surges and declines in the populations of different species, and a host of other factors. Yet, simple as it is, the model has proved capable of constructing hypothetical webs that mimic nature quite nicely. Whether the webs it generates are large or small, all exhibit the same general balance in top, intermediate, and basal species observed in real webs. They all have realistic proportions of the four kinds of trophic links. And the food chains within them are relatively short—usually, no more than four or five species from top to bottom—as has been observed in nature since Hutchinson's day.

BECAUSE the cascade model works so well, it can be used to investigate further the fundamental structure within real webs. It indicates, for example, that the length of the longest chain in a web increases with the number of species, but only gradually. Hypothetical webs containing a hundred species generally have chains with no more than six links; those containing a thousand species, usually no more than nine links; and even in the extremely unrealistic case of webs with a hundred million species, the longest chains are predicted to have fewer than twenty links. (In nature, the existence of relatively long food chains is not unheard of. One tropical plankton community in the Pacific Ocean is reported to have a chain ten links long. But the cascade model suggests that such chains are extremely rare.)

In the future, the model also could be used to investigate how food webs are related to other aspects of natural environments. One goal is to predict how particular habitats may be affected by change. For instance, the model could indicate how the introduction of a new species or the elimination of an existing one might affect the length of food chains within a habitat. Again, the model could be of value in determining the potential risk of dangerous concentrations of toxins in a habitat, because, typically, chemicals spilled into an environment become more concentrated at each successive step along the chain. (A plant or an animal consumes the contaminant but does not easily dispose of it, so each organism gradually collects a concentrated amount of the poison. The further up the food chain an organism is, the greater is the amount of the chemical to which it can be exposed.) One day, it may be possible to predict how an entire food web would be altered by a chemical toxin. And perhaps biologists will come to understand the dynamics of food webs well enough to estimate ideal habitat sizes and thereby improve the design of parks and wildlife reserves. In short, mathematical models of food webs may ultimately serve to protect some of the order among predator-prey relationships that is only now coming to light. ●

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