Ecologists Flirt with Chaos

The jury is still out on whether biological populations exhibit chaos, but the search for this unusual type of order is leading to new ways of thinking about ecology

CHAOS AND POPULATION BIOLOGY have had a frustrating affair over the past 15 years. It began in the early 1970s, when population biologists were among the first scientists to study chaos seriously. Chaos, a strange type of mathematical order that gives the illusion of being random, seemed like a natural candidate to explain the erratic fluctuations in certain animal populations, and population biologists did much of the initial work on the properties of chaos.

Chaos theory has since proved valuable in a number of other fields, ranging from chemistry and physics to medicine and meteorology. Researchers have found chaos in such varied physical systems as chemical reactions and the orbit of Pluto.

Ironically, chaos and population biology have never quite consummated their own affair. After 15 years, no one has provided a universally accepted example of chaos in a biological population, and researchers can only point to data that are "suggestive" of chaos—populations that vary erratically from year to year in interesting patterns. Most ecologists and population biologists have ignored chaos, deeming it an interesting artifact with few applications to the real world.

Nonetheless, a few biologists and mathematicians continue the search, encouraged by mathematical analyses that indicate chaos may be quite common in ecology. "If you have a lot of species interacting, it's hard not to get chaos," as Mark Kot, a mathematician at the University of Tennessee, puts it. Judging from several recent results, including work on a parasite-host system of wasp and beetle and a predator-prey relationship between a protozoan and bacterium, the workers are tantalizingly close to their goal.

This is the second in a series of stories on chaos in various fields of science. Subjects of future articles will include chaos in medicine and physiology and quantum chaos.

And even if chaotic behavior proves to be rare or nonexistent in biological populations, chaos researchers believe they have made a lasting contribution to this field—they have challenged ecological dogma and generated new ideas about how natural populations behave. Whatever else happens, the little romance between chaos and population biology has certainly made life much more interesting.

Chaos and population biology were formally introduced to each other by Princeton ecologist Robert May in a 1974 paper in *Science*. May, who is now at Oxford University, examined a mathematical model for a simple ecological system—a single species with non-overlapping generations—and showed it had an amazing range of dynamical behavior (see box, p. 311). Depending on the birthrate and how the species responded to overcrowding, the population could settle down to a stable equilibrium point; oscillate between two fixed values, or four, or any other number; or jump around seemingly at random—become chaotic.

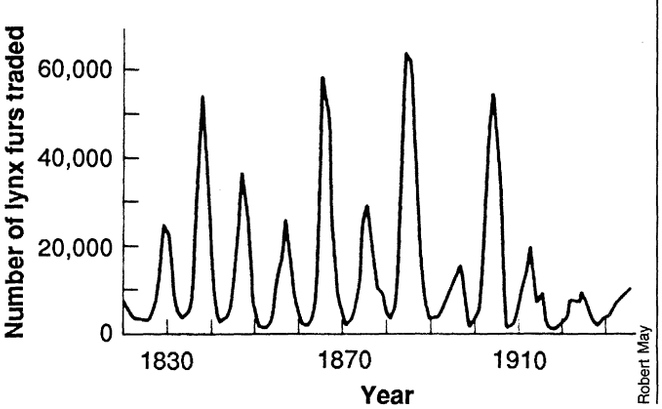
Although chaos is a mathematical concept and somewhat difficult to define precisely, its profile is easy to recognize. To begin with, chaos is deterministic—it obeys mathematical equations. Normally, anything that behaves according to mathematical equations, such as the movement of the earth around the sun, is regular and easy to predict. Chaos is different. A chaotic system is complicated and can look quite erratic. The defining characteristic of chaos is its "sensitivity to initial conditions"—if the initial configuration of a chaotic system is changed even slightly, its future behavior is altered radically. (In contrast, if something pushed the earth a little out of its usual orbit, the result would be a new orbit very close to the original.)

May's work was surprising because at the time most scientists assumed such complicated behavior would arise only in complicated systems, or in systems that had some random component. May showed that simple, deterministic systems could act in complicated, seemingly random manners. (A decade earlier, meteorologist Edward Lorenz had proven a similar result, but it had been almost completely overlooked.)

The implication of May's result was that biological populations have the potential—in theory, at least—to do more than just stay close to some sort of natural equilibrium point, as the old idea of a "balance of nature" implied they should. This might explain some of the fluctuations in natural populations that were traditionally ascribed to random environmental noise—changes in the weather, unpredictable population movements, and the like.

After May's paper appeared, researchers examined various ecological data for evidence of chaos. The promise and the frustration of this search are exemplified by the analysis of the Canadian lynx population between 1735 and 1940, one of the best known data sets in ecology.

Because the lynx was trapped for its fur for more than 200 years, records from fur trading companies provide a history of lynx population much longer than any data collected by scientists. These records show the lynx population fluctuated dramatically (see figure). In the years between 1830 and 1910, the population would hit a peak every 9 or 10 years, fall sharply for a few years, and then climb back up again. The spacing of the



Canadian lynx *populations fluctuated dramatically between 1820 and 1930, hitting peaks every 9 to 10 years and then dropping sharply.*

peaks was quite regular, but their sizes were not—the larger peaks were three or more times the size of the smaller ones.

Researchers originally guessed that an interaction between the lynx and its main prey, the snowshoe hare, was responsible for the pattern. Later work has suggested the approximately 10-year cycle was caused by the dynamics between the hare and its food supply, and the lynx was just along for the ride.

The lynx data are a good place to look for complicated dynamics such as chaos because they are somewhat regular, which implies they are deterministic, but they have erratic fluctuations as well. The standard description of the pattern is a natural 10-year (or perhaps 20-year) cycle with fluctuations caused by random variations in the lynx's environment.

In 1984, William Schaffer of the University of Arizona looked for chaos in the lynx data. To analyze the relationship between populations in succeeding years, he formed return maps—graphs that express one year's population in terms of those of previous years—and studied the return maps for structure that would indicate the presence of chaos. In technical terms, he looked for a strange attractor in the return maps, which would be evidence that the variations in the cycle were not random at all but were deterministic. "The data analyzed here are meager," he concluded. "Determining whether or not a strange attractor lurks in the lynx data is thus probably impossible."

What was true of the lynx data is doubly true for most of the populations that have been analyzed. "The data by and large are horrible data," says Kot, who has checked about 50 sets of data for evidence of chaos. "They're often very suggestive, but they're not the type of data I'm comfortable with."

Part of the problem is the noise level of the data. Trying to pick out a deterministic pattern from data saturated with random environmental effects is worse that trying to make out the words of a radio broadcast overwhelmed with static.

A second part of the problem is that the data sets are usually too short to reveal a chaotic pattern. Kot mentions a beautiful set of data for bugs called coffee-leaf miners, which in their juvenile stage live inside coffee leaves. Researchers recorded the number of adults in the population daily for 9 years. Unfortunately, outbreaks of the insects occurred every 2 to 3 years, which meant the data covered only a few cycles—enough to be suggestive, but not enough to pin down a pattern. "That was the most frustrating data set I'd ever come across," Kot says.

May suggests that chaos may not show up

A Simple Model of Chaos

The following model from population biology provides probably the simplest and best known example of how chaos develops. The model is for a single species with generations that do not interact with each other—a hypothetical insect population, for instance, that hatches in the spring, lives through the summer, and dies after it lays its eggs in the fall. One can count the number of insects alive at one particular time each year and get a yearly record: N_1 insects the first year, N_2 the second, and so on.

The number of insects alive one summer, N_t, will determine the number alive the next, N_{t+1}. The exact relationship between the populations in succeeding years is hard to determine, but the simplest mathematical formula that seems somewhat close to reality is $N_{t+1} = aN_t - bN_t^2$. In this formula, a corresponds to a birthrate, and b is an overcrowding factor, which causes a decrease in population size any time the species gets too populous for its resources. The formula can be made simpler with the mathematical trick of choosing the units of population in the most convenient way. With the right choice of units, a is equal to b, and the model is simplified to read: $N_{t+1} = a(N_t - N_t^2)$. For this choice of units, one must have $0<N_t<1$, or else N_{t+1} will become negative, which implies the population becomes extinct.

This simple equation can have very complex behavior, depending on what a is.

If $0<a<1$, the population dies faster than it replaces itself, and N_t goes to zero.

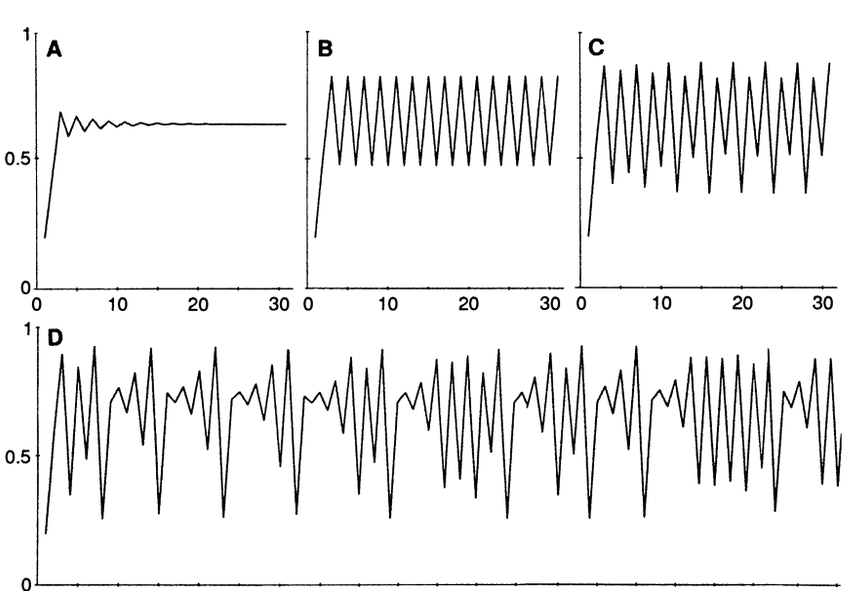
If $1<a<3$, N_t approaches some fixed value dependent on a but independent of the size of the original population. If $a = 2$, for instance, N_t settles down to 0.5.

If $3<a<3.4$, N_t does not approach a single value, but oscillates between two values. For a slightly greater than 3.4, N_t jumps back and forth between 4 fixed values. As a continues to get larger, N_t will oscillate between 8 values, then 16, then 32, and so on, in a process called period doubling.

For $a>3.57$, there are no fixed values. N_t jumps around erratically. It is chaotic.

The defining characteristic of this chaotic behavior is not its random appearance but rather its "sensitivity to initial conditions." In the nonchaotic cases, the long-term behavior of the population does not depend on the size of the original population. For example, if $a = 2$, the population will approach 0.5 within a few years no matter where it started—0.5 is a so-called stable attractor. The same thing is true for other values of $a<3.57$, although the final behavior can get much more complicated.

In the chaotic regime, the behavior of N_t from year to year depends very sensitively on the initial population. Two initial populations that differ by less than 1%, say, will have very different numbers within just a few years, and their long-term behaviors will look completely unalike. ■ **R.P.**



The model shows a range of behavior: (*A*) *A steady state when* a = *2.8;* (*B*) *a two-cycle when* a = *3.3;* (*C*) *a four-cycle when* a = *3.53; and* (*D*) *chaos when* a = *3.7.*

in existing data sets because researchers are more likely to take long-term data on relatively stable populations than on ones that jump around. "The things we have long runs of data for may turn out to be the things that aren't chaotic," he says.

Whatever the reason, no one has unequivocally found chaos in any data set for a natural population. For that reason, several researchers are turning to laboratory experiments. By looking at simple systems that can be easily represented by mathematical models, researchers can compare the behavior of the system with the predictions of the model. If they match, and if the model's behavior is chaotic, the system itself should be chaotic.

Kot has analyzed a mathematical model of a simple predator/prey system that can be set up in a laboratory. The predator is a protozoan and its prey is a bacterium, and they both are kept in a chemostat system—a liquid-filled container with a continuous influx of substrate for the bacteria to live on and a continuous outflow to keep the liquid volume constant.

Kot's analysis predicts that with a constant influx of nutrients, the system should have simple dynamics. No chaos. "But if you vary the substrate periodically to mimic seasonality," he says, "you have no trouble whatsoever picking up all sorts of chaotic behavior." Kot says he and colleagues are setting up a laboratory experiment now to check his theoretical predictions of chaos.

Michael Hassell at Imperial College in London has looked at the interaction of a parasitic wasp and the beetle it preys upon. Short-term studies of the two insects gave Hassell such information as the survival rate of the beetle, and allowed him to develop a detailed model of the wasp/beetle system. Simulations of this model agreed "fairly well" with long-term experimental data taken earlier by another researcher, Hassell says. Since the mathematical behavior of the model was chaotic, the real wasp/beetle system is likely to have been, too.

Hassell says he and May have recently extended the two-species model to three species—hosts, parasites, and pathogens. "When one adds an extra species," he says, "one can get chaos with quite reasonable parameters."

Hassell's mention of "parameters" refers to the key issue in the debate over whether chaos appears in biological populations. No one doubts that mathematical models of ecological systems can exhibit chaos, if they are "tuned" correctly. The question is whether the tuning needed to give chaotic behavior actually corresponds to what is found in nature.

Any ecological model has certain parameters—the birthrate, say, or the variation in survival rate as population density changes—that take on different values depending on the species and its environment. Varying these parameters varies the type of behavior predicted by the model (see box). Generally, increasing certain parameters will take a simulation from very simple behavior, such as approaching a constant population, through progressively more complicated behavior where the population size jumps around somewhat predictably from year to year, to complete chaos. All but the most simple, unrealistic ecological models will turn chaotic if this parameter dial is turned far enough; the question is whether natural populations operate at such high settings.

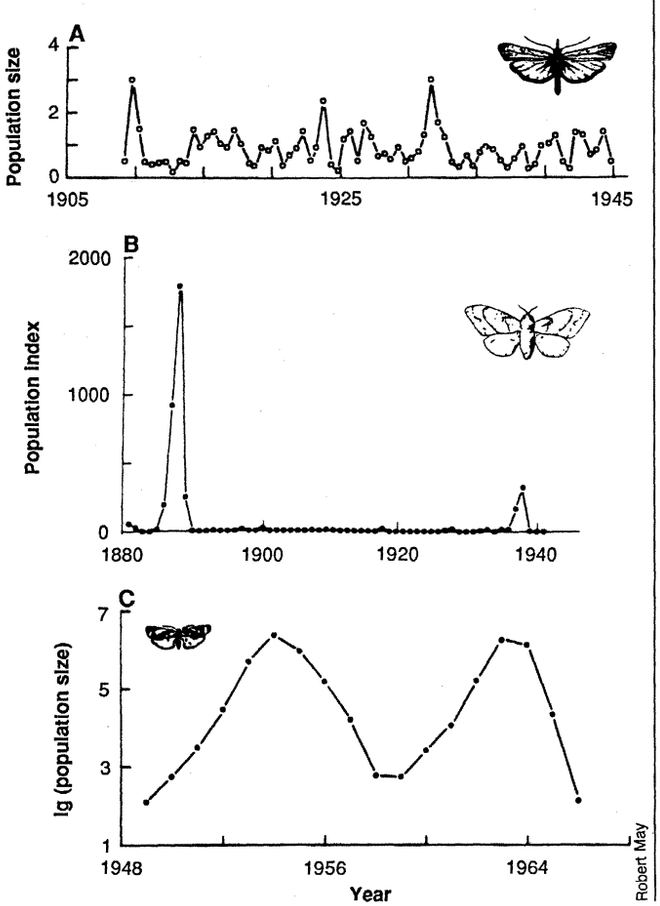
Ironically, May and Hassell played a big part in convincing many scientists that they do not. In 1976, May, Hassell, and John Lawton looked at 28 populations of seasonally breeding insects, some wild and some in the laboratory, and fitted the data to a simple model, estimating the parameters for each population. The three concluded that none of the field populations and only one lab population had parameters high enough to be chaotic.

The study convinced many other researchers that chaos in insect populations was unlikely. It had, as Kot puts it, "an inhibitory effect on studying chaos in population biology."

May says the study was misinterpreted. The models they used were extremely simple, and fitting the data to these models "does a lot of violence to reality."

The simple single-species models used by Hassell, May, and Lawton are also the models that are most difficult to get chaotic behavior in naturally. Although single-species models are the simplest and easiest to analyze, which made them a natural place to begin, the models need fairly high parameters to become chaotic—parameters corresponding to a much sharper reaction to the environment than normally found in natural populations. The researchers who analyze multispecies models report that the more complicated the model, the easier it is to get chaos. "As soon as you move to three or more species, there are hundreds of ways to get chaos," Kot says.

The realization that chaos lurks in nearly every model of ecological systems has led to new ways of viewing population biology, even among some of those who do not believe chaos arises in natural populations. For instance, Alan Berryman and Jeffrey Millstein of Washington State University conclude in a recent paper that "ecosystems do not normally behave chaotically." How-



Moth populations *show a variety of behaviors: (A) The moth,* Chilo suppressalis, *in Japan fluctuates around an average value that remains approximately constant; (B) the large pine moth,* Dendrolimus pini, *in Germany keeps a low population density except for occasional big outbreaks; and (C) the larch budmoth,* Zeiraphera diniana, *in Switzerland oscillates by four orders of magnitude with an approximate 10-year cycle.*

ever, they suggest that even if chaos does not appear in natural populations, human actions may push a population into chaos.

"Although the evidence does not seem to support the notion that natural ecosystems exhibit chaotic dynamics," they write, "we should emphasize that all self-replicating systems possess the seeds of chaos. . . . As all biological systems contain positive feedback processes, it is always possible to force them into the chaotic regime by increasing the value of the positive feedback parameter(s); for example, increasing growth rates through biotechnology, stimulating economic growth, etc." Scientists could look for chaos in insect populations that are being treated with pesticides, for example.

May argues that the study of chaos in population biology indicates ecologists may have been seeing mostly what they expected to see. The assumptions they make about what the systems were doing have influenced the way they collect data: "You can create yourself an imaginary world—get pseudo-data and then apply conventional techniques—but the conventional techniques cannot determine the important factors."

May suggests that ecologists "may have to go back to the drawing board" in order to get reliable data.

The study of nonlinear dynamics in population biology has implications for other fields too, May notes. "Populations aren't just creatures with four or six legs, or viruses and bacteria," he says. Population biology models can be used to study individual cells in an organism, for example, or the components of the immune system. He and Imperial College mathematician Roy Anderson have done just this with a model of how the AIDS virus behaves when it infects the human immune system.

In this model, T4 lymphocytes and AIDS viruses have both a host-pathogen relationship, where the virus infects the immune cells, and a predator-prey relationship, where the T4 cells prey on the virus via the production of B cells and antibodies specific to the AIDS virus. This arrangement, as Anderson points out, implies the system is nonlinear and thus has the capacity for oscillatory and even chaotic behavior.

"The real question, of course, is how relevant it is to practicality," Anderson says, but he adds, "There is some empirical evidence of this type of nonlinear behavior in the immune system." He and May say they plan to publish evidence for chaos in AIDS-infected immune systems in a coming report. It might be that the easiest place to find chaotic populations is not the forest or the plains or the ocean, but in the jungle of the human body. ■ ROBERT POOL

Troubles Encountered in Gene Linkage Land

Why are published data from gene linkage studies of four different mental disorders so difficult to replicate?

A DISCOURAGING REALITY is emerging from the quest to identify chromosome locations for genes that cause various human diseases. It is that the ideal scenario for doing gene linkage studies rarely exists—particularly for mental illnesses. The result is that when one group of researchers reports that a disease-associated gene is located on a specific region of a chromosome, other investigators frequently cannot substantiate the finding. No one is claiming to have found the disease genes themselves; at this point only their chromosome locations are in question.

"The only way to prove heterogeneity is to localize or isolate all the different genes. And that would be tremendously difficult. . . ."

Within the past few years, for example, researchers have reported that a gene locus associated with major depressive disorders is on the X chromosome, a gene for familial Alzheimer's is on chromosome 21, a gene that predisposes Old Order Amish to manic depression is on chromosome 11, and, most recently, that a "susceptibility locus" for schizophrenia is on chromosome 5. But other research groups are unable to confirm these gene locations in their studies of other families with the same disorders.

"The major problem [in this research area] is all the non-replications," says Elliot Gershon of the National Institute of Mental Health (NIMH) in Bethesda, Maryland. "The question is why." Researchers suggest several complicating factors: multiple causes of what appears to be the same mental disorder; the lack of large family pedigrees and large numbers of pedigrees; misdiagnosis of affected relatives; inappropriate statistical methodology; and the sheer complexity of mental illnesses.

One disorder that affects brain function and behavior and appears to have an undisputed chromosome location is Huntington's chorea. Huntington's is a rare neurodegenerative disorder caused by a dominant gene located on the short arm of chromosome 4, and it has become the gold standard for gene linkage analysis.

"Huntington's is very clear cut," says James Gusella of Massachusetts General Hospital in Boston. "You find an individual with the classical symptoms and you know that these symptoms are caused by the gene." In addition, researchers can trace the pattern of the gene's inheritance because affected family members usually show signs of the disease before the age of forty. "That's the opposite of other neuropsychiatric disorders," says Gusella.

For most mental illnesses it is still not well established that a genetic cause even exists. Diseases such as schizophrenia and major affective (mood) disorders often tend to run in families, but that does not necessarily mean they are genetically caused. So, in some cases the current search is for genes that may predispose an individual to a particular mental disorder rather than cause it directly, thus adding another level of obscurity to the process.

Major affective disorders such as depression are prime examples. "There are now a number of studies in the literature [including his] that have reported linkage on the X chromosome in major depressive illness and a number of other studies that have reported something different," says Miron Baron of Columbia University College of Physicians and Surgeons and the New York State Psychiatric Institute. The discrepancies could result from any of several factors, he suggests. One, for instance, is genetic heterogeneity, meaning that the same group of disorders has different genetic causes. Another is misdiagnosis of certain people in the families under study. The diagnostic criteria for mood disorders keep changing and each group of researchers tends to use slightly different criteria when they define the affected people in their study.

Given these vagaries, it may not be surprising that the data from different research groups suggest different chromosome locations for a gene associated with major de-