Population Dynamics and Chaos: A Descriptive Introduction Thomas Caraco

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1. PRELIMINARIES

1.1. Objectives

I want to introduce some significant properties of mathematical, or deterministic, chaos. Deterministic chaos was essentially unknown to science 30 years ago, but today serves a vital role in research across the physical, biological and social sciences. We shall address some basic behaviors of "nonlinear dynamics," the generator of chaos, by exploring a model for the growth and decline of a wildflower population. Our approach will not require excessive technical detail, but we shall demonstrate some nontrivial concepts.

We have a series of objectives. The reader should gain some familiarity with the terms of chaos theory and its objects of study, a terminology increasingly encountered in science, literature and even television commercials. The reader should appreciate that remarkably complex behavior can emerge from simple models of natural processes. That is, we can ask if the complexity we observe around us is produced by equally complex processes, or arises from fairly simple (though perhaps unknown) nonlinear rules. For biological systems, the reader should understand a "cause and effect" problem repeatedly encountered by field workers. Given that a natural population's size changes unpredictiably, is this behavior due to interactions among the individuals within the population ("endogenous" generation of deterministic chaos), or is the unpredictability due to external forces (random change in "exogenous" factors, such as rainfall)? Finally, the reader can prepare for the plenary discussion of deterministic chaos.

1.2. Brief Background: Deterministic Chaos

The term chaos may refer to disorder and disorganization. Physicists invoke the notion of entropy to quantify disorder. Maximal entropy implies complete randomness, absence of order. At this extreme, knowledge of the current state of a system tells us nothing about the system's future states. Chaos, in this sense, means that lack of order and random change make accurate prediction of a system's behavior very difficult.

In 1975, Tien-Yien Li and James Yorke published a paper titled "Period three implies chaos," and the term acquired a new meaning. This type of chaos is deterministic, rather than

random. That is, each current value (or state) of the system determines the next value exactly. Furthermore, the initial (starting) value determines the behavior at all future times. This sort of chaos, then, possesses a high degree of order. However, these chaotic systems also exhibit highly complex behavior (for example, no value ever repeats under chaos). Without knowledge of the mechanism generating the deterministic order, the behavior of the system may appear random, so again prediction can be difficult. We shall refer to this ordered, but complex phenomenon as *deterministic chaos*, to avoid confusion with randomness. Roots of our current understanding of deterministic chaos extend into mathematics, physics, ecology, and atmospheric science. Several references listed at the end of this document recount the rapid development of this understanding.

2. THE PERIOD-DOUBLING ROUTE TO CHAOS

2.1. A Model for a Population of Annual Plants

Consider a population of annual wildflowers. "Annual" means that a new generation appears each year, and different generations do not overlap. Seeds germinate as the growing season begins. Following a short period of vegetative growth, the plants flower and reproduce. The new seeds are dispersed, and the flowers die. For the remainder of the year, seeds lie dormant; when the next growing season arrives, they produce a new generation of flowers. Many plants and invertebrate animals exhibit an annual life cycle, so our example is not excessively artificial.

Since our wildflowers appear only briefly each year, we treat time (t) as advancing discretely, in units of years. That is, time t = 0, 1, 2, ..., a sequence of (non-negative) integers, the same sequence most people use to track their age. Students of calculus may be accustomed to problems assuming continuous (rather than discrete) time. Discrete-time models yield chaos more readily than do models in continuous time, but chaos can occur in continuous time also.

Each year we visit the population during flowering, and measure the fraction of the environment (a field) covered by the plants. We term this number the *population density*, and represent density at time *t* as x(t). Since x(t) is a proportion, it cannot exceed one. Of course, its value cannot be less than zero, since x(t) = 0 implies extinction of the population.

We reasonably assume that the density of wildflowers in any year depends on the number of seeds produced in the previous year. Seed production in any year depends on the density of wildflowers in that year. Therefore, the density of flowers in any given year will depend on the

previous year's density. To characterize this dependence we construct a map, a mathematical function, which gives us next year's population density when we provide this year's density:

Density at (t + 1) = MAP [Density at t]

We represent the map by the symbol *F*. Since x(t) represents density, we have:

x(t+1) = F[x(t)]

This is called a finite-difference equation. x(t) is the *state* of the system at time *t*. The way population density varies as time progresses is termed the *dynamics* of the system. More specifically, the dynamics refers to properties or pattern we discover in the sequence of *x* values.

Our next task is formulating the map F. We expect that crowding impedes each plant's uptake of nutrients and water from the soil. Crowding of plants may further result in shading, so that some plants lack adequate sunlight. Therefore, our model assumes that increasing population density (which increases crowding) will reduce the mean number of seeds per flowering plant. In ecological terms, crowding reduces average reproductive success among individual plants. That is, the number of plants flowering in the generation at time (t + 1), *per plant* flowering at time t, declines as the number of plants at time t increases. Assume that in the absence of crowding, an individual plant at time t produces r plants flowering at time (t + 1); r is essentially the number of offspring. As density, x(t), increases an individual plant experiences greater crowding, and its reproductive success declines with density according to:

Individual Reproduction at time t = r [1 - x(t)]

As density increases, the individual plant's average reproduction declines as a straight line:



POPULATION DENSITY

r = 3.5 in the upper plot, and r = 2.1 in the lower plot. For any value of r, individual reproductive success approaches zero as density approaches one, the assumed effect of crowding.

Next year's population density, x(t + 1), will be given by the product of this year's density and the average reproductive success in this year's population:

$$x(t+1) = x(t) r [1 - x(t)]$$

That is, we multiply a density (plants/area) by individual reproductive success (plants/plant), and obtain the next year's density. Rewriting the above expression yields

$$x(t+1) = r \{ x(t) - [x(t)]^2 \}$$

Note that density x(t) appears as a linear term and as a squared term. The squared (or quadratic) term makes our map nonlinear, and the changes in population density over time are consequently termed *nonlinear dynamics*. Please note that the model is very simple; next year's density depends only on *r* and this year's density. We'll see, however, that the model's behavior can be quite complex.

To investigate our model, we'll change the value of *r*, and observe the resulting dynamics. Since *r* is an average number of plants per plant, it cannot be less than zero. We shall also require that *r* not exceed four. (Try r = 5 on your calculator, and you'll see that x(t) eventually takes biologically unrealistic values. If you begin at x(t = 0) = 0.5, you won't wait long.)

Suppose *r* exceeds zero, but is less than one. Then, even in the absence of competitive crowding, each plant on average does not fully replace itself, and the population should decline to extinction. So, let's try r = 0.75, and we'll plot the dynamics for initial states: x(t = 0) = 0.1, and x(t = 0) = 0.7. We obtain:



For both initial conditions the population approaches extinction within fifteen generations. In this case, the model is simple and so is the dynamics.

To avert wildflower extinction we'll increase *r* beyond 1.0, so that at low density an indivdual can more than replace itself. Let's choose r = 2.9, and observe the dynamics for our first initial condition, x(t = 0) = 0.1:



Next, we'll keep r = 2.9, but use the other initial condition, x(t = 0) = 0.7:



In both cases the population density initially fluctuates a bit, but then reaches a constant value, an "*equilibrium node*." By equilibrium node we mean that two consecutive generations have identical population densities. Note that both initial values lead to the same equilibrium. For this value of r, we would predict a stable population; the simple model again produces simple dynamics.

More generally, for *r* falling between 1 and 3, our model yields an equilibrium node where the steady-state population density equals $x^* = 1 - (1/r)$. For this range of *r*, the equilibrium density depends on the reproduction parameter *r*, but does not depend on the initial population density; hence the equilibrium is termed independent of initial condition.

Now we begin the march from simplicity to complexity. Let's increase *r* just a little, to 3.3, and observe the dynamics for x(t = 0) = 0.1:



A small increase in r results in a striking qualitative change in model behavior. The equilibrium node has given way to a 2-cycle. A *bifurcation* has occurred. In a sense the equilibrium node has split into two points, not the sort of smooth change we find in calculus problems. After the 20-th generation or so, the population density alternates between the same two values forever; we term this behavior *periodic dynamics*. A different initial condition, while holding r at the same value, would eventually reach the same equilibrium, a 2-cycle with the same values. The values of an equilibrium cycle are independent of initial condition.

Increasing individual reproductive potential r has produced a qualitative transition in the dynamics; many scientists find such threshold transitions quite interesting. It's fair to say that the bifurcation has produced slightly more complex behavior; we consider a cycle more complex than a constant. So, let's increase r again.

We next let *r* equal 3.56, keep x(t = 0) = 0.1, and observe our model's dynamics:



Another bifurcation has occurred, and the 2-cycle has been replaced by a 4-cycle. The model still exhibits periodic behavior, but this *period-doubling* bifurcation has increased dynamic

complexity. Again, the equilibrium cycle depends only on r, and so the dynamics will eventually cycle through the same four values from any initial condition.

We can continue to increase the reproductive parameter r, and the *bifurcation cascade* will proceed very rapidly. The periodicity doubles with each bifurcation. We have seen equilibrium behavior of one value, two values, and four values. As we increase r, we quickly see cycles of length 8, 16, 32, 64, ... different density values. Ecologists treat each increase in the length of the period as an increase in complexity, since the population density must visit more values before its behavior is revealed fully.

The cycle length has increased at each bifurcation, but we have not yet made the transition to deterministic chaos. We continue to increase *r* until we reach the "Feigenbaum point," r = 3.5699456... Here, an infinite number of bifurcations have occurred (you can't count them, but they are there), and we enter the chaotic regime. For example, suppose r = 3.93, and x(t = 0) = 0.1. Then:



This is deterministic chaos. For the same r, let's change the initial value x(t = 0) to 0.7:



TIME

Again, we have deterministic chaos, but the dynamics differs from the preceding case. The two graphs serve to remind us the initial conditions did not affect the dynamics before chaos, but within the chaotic regime, changing the first value changes every subsequent value x(t).

By "tuning" the reproductive parameter of our simple model, we have proceeded from simple to very complex behavior. Deterministic chaos looks like random numbers. Computers sometimes use a simple model like ours to provide "random numbers." They are not random, but they are chaotic, and so appear random. Note also that the increased dynamic complexity of chaos causes the population's density to more often visit values near zero, hence near extinction. Without adding details to our model, we can infer that a single population with chaotic dynamics has a higher risk of extinction than a population with simpler dynamic behavior.

2.2. Some General Characteristics of Deterministic Chaos

Let's list some properties of deterministic chaos. Each of these three attributes applies to any case of deterministic chaos; our wildflower model is merely an example.

1. Chaos is *aperiodic*. No state repeats; once the dynamics takes a certain value, that value never occurs again. (A computer may need quite a few decimal places to discriminate the different values of our model.) Aperiodcity is somewhat profound; under chaos what has been can never recur.

2. Chaotic dynamics is **bounded**. This means that the dynamics never approaches $\pm \infty$ (plus or minus infinity). In our model the density can vary chaotically, but stays between 0 and 1. This property is not especially interesting, since the dynamics is similarly bounded before the onset of chaos. Being bounded above and below, however, permits useful applications of chaotic dynamics to real-world questions.

3. Deterministic chaos displays *sensitive dependence on initial conditions*. This defining aspect of chaos makes prediction so difficult. Changing the initial value of the same chaotic system (as we did above) results in a completely different sequence of values. The jargon for this property tells us that "nearby trajectories diverge." Since it can be very difficult to determine the exact value of the initial condition for any realistic chaotic system, we simply cannot predict the system's behavior over long periods of time. Recall that such a system has internal order; each value depends exactly on the preceding value. But the complexity of the system's behavior masks the determinism from the observer outside the system.

Ecologically, we have observed that nonlinear feedback in the dynamics of the population density (the map) combined with an individual's capacity to produce many offspring when the population is small (high r) leads to deterministic chaos. Using the same simple model, we saw complexity increase from equilibrium nodes to cycles and then to chaos as we followed the period-doubling route.

To close this section, let's recall the objectives we stated initially. We have introduced some terms essential to any scientific discussion of deterministic chaos, although we're not quite through. We've seen that the behavior of a nonlinear system can suddenly change at a bifurcation. We've observed that our simple model's dynamics range from very simple to exceedingly complex, but at every level of complexity, we have deterministic order. That is, chance and disorder have nothing to do with generation of the chaos in our wildflower model.

We find complex, quantitative systems all around us: the weather, the stock market, the rise and fall of influenza cases, etc. In some case, the observed complexity may be the result of a large set of interacting forces that drive the system of interest. In lecture, we'll suggest that the chaos of the healthy heart rate arises this way. However, our simple quadratic model teaches us that complexity (chaotic dynamics anyway) can arise from sufficiently strong feedback in a reasonably simple nonlinear mechanism. Consequently, we can explore the possibility that simple (but nonlinear) rules may generate complex system behavior.

Presented with an erratically fluctuating population, the ecologist may wonder whether the changes result from nonlinearity and chaos, or from random variation induced by an unpredictable environment. At a glance, deterministic chaos and a sequence of random numbers look about the same. But there is far deeper order in deterministic chaos. Unfortunately, detecting that order from data can prove quite challenging. To avoid a headache and end our assignment, we'll address a necessary, though not sufficient, condition for deterministic chaos: the fractal.

3. Self-Similarity: The Fractal Signature of Chaos

3.1. A Bifurcation Diagram

Our plan is to construct a bifurcation diagram, explained just below, look at the chaotic region, and find fractal geometry (also explained below). Above, we chose a few values of r and plotted population density as time progressed. For any particular value of r, we noted equilibrium behavior (0, positive node, or cycle), or we observed chaos. Suppose we do the same for a very

large number of *r*-values. Then for each *r*, we plot above it the 1, 2, 4 ... or very many values the dynamics visited. So, we have a graph with a set of density (*x*) values for each *r*-value. The resulting graph is called a *bifurcation diagram*:



When *r* is less than one, the population goes extinct, and x = 0 at equilibrium. When *r* falls between 1 and 3, the density reaches a positive equilibrium node; the bifurcation diagram reminds us that that equilibrium density in this region increases with *r*. For values of *r* between 3 and 3.4, the dynamics equilibrates at a 2-cycle; hence we see two density values in this region. The plot shows the bifurcation at r = 3 very clearly; the node gives way to the 2-cycle. A 4-cycle is visible above r = 3.5. Beyond the 8-cycle, the bifurcations occur so rapidly that we would need a much large figure to show the details. After *r* is increased past 3.5699, we enter the chaotic region, and the number of different densities visited equals the number we choose to plot. But we know all this from our previous observations.

Notice that not every value of *r* beyond 3.7 induces chaos. You can see that "*periodic windows*" appear. The most obvious is the cycle of period 3 (recall the title of Li and Yorke's paper mentioned above) near r = 3.83. A small increase in *r* can suddenly causes dynamic complexity to collapse to periodicity. Further increases in *r* lead again to chaos. Let's magnify the bifurcation diagram around the middle value of this 3-cycle. We'll show the bifurcation plot from about r = 3.81 to about r = 3.86:



Remember, *r* increases as we move to the right, and density increases as we move up. We see the departure from chaos at the left. We see the value associated with the 3-cycle (middle of the figure), and then we see that this point gives way to another bifurcation cascade (like the one in the figure above). The same is true if we magnify the diagram around either of the other two points of the 3-cycle. Next, we note the chaotic region resulting from the cascade at the right, and within it, we identify another cycle of period-3. We could magnify the bifurcation diagram again, and we'll find another such cascade within the periodic window. In fact, we can keep magnifying the diagram, and we'll continue to find the same picture at smaller and smaller scales. The same pattern emerges at every magnification; we can find remarkable order within deterministic chaos.

To characterize this order, we say that the bifurcation diagram exhibits *self-similarity*. Self-similarity implies that the bifurcation-cascade phenomenon is *scale-invariant*; that is, it looks the same at all scales. This geometry, endlessly repeating across scales, is a *fractal*. Fractals are the signature of chaos (although other processes can generate fractals). As a consequence, it turns out that when we see self-similarity in the dynamics of a system of interest – that is, when the dynamics look the same at different scales of time – we can suspect deterministic chaos. We would require much more detail to justify many of the points made above. But we have made sufficient observations here to note that chaos and order are not necessarily inconsistent. In fact, deterministic chaos exhibits the infinite order of self-similarity.

4. Suggested Reading

An enormous number of scientific papers, textbooks, websites, and popular articles are devoted to chaos, nonlinear dynamics, fractals, and their applications in diverse fields. In my own work I find the following four books very helpful; anyone interested in these topics can find other useful sources.

Alligood, K.T., Sauer, T.D. & Yorke, J.A. 1997. *Chaos: An introduction to dynamical systems*. Springer-Verlag, New York.

Kaplan, D. & Glass, L. 1995. Understanding nonlinear dynamics. Springer-Verlag, New York.Lauwerier, H. 1991. Fractals: Endlessly repeated geometrical figures. Princeton UniversityPress, Princeton, NJ.

Peitgen, H.-O., Jurgens, H. & Saupe, D. 1992. *Chaos and fractals: New frontiers of science*. Springer-Verlag, New York.