Box 4.1: Chaos

The fact that deterministic equations can lead to seemingly unpredictable dynamics was first discovered by Edward Lorenz in 1961 (see Lorenz 1963). As a meteorologist working at MIT, Lorenz was developing computer simulations to predict weather patterns using a complex model involving twelve differential equations. One day, he took the predicted weather from a printout of a previous simulation and started a new set of simulations from these values, holding everything else constant. Soon thereafter, however, he noticed that the predicted weather was completely different from his previous results. He later realized that he started the second simulation at a very slightly different position because he had rounded a variable when printing it out. While the initial position was off by just 0.000127, the long-term weather predictions were entirely different. A defining characteristic of chaos is this *sensitivity to initial conditions*, such that two trajectories that start near one another grow apart over time until they are no nearer than two trajectories that started far apart. This sensitivity to initial conditions has become known as the "butterfly effect:"

> The flapping of a single butterfly's wing today produces a tiny change in the state of the atmosphere. Over a period of time, what the atmosphere actually does diverges from what it would have done. So, in a month's time, a tornado that would have devastated the Indonesian coast doesn't happen. Or maybe one that wasn't going to happen, does.
> Stewart (1997), p. 141.

The emergence of chaos from entirely deterministic equations led Lorenz to conclude that there was little hope of predicting long-term weather patterns.

In 1974, the biologist Robert May (1974) published the simplest equation known to exhibit chaos: the logistic equation in discrete time. The logistic model involves a single variable and describes population growth as a quadratic function of the current population size (equation 3.5a). Because the population size can overshoot the equilibrium, chaotic fluctuations around the equilibrium are observed when the growth rate is large (e.g., $r = 2.7$ in Figure 4.2). Because the dynamics are chaotic, the dynamics are sensitive to initial conditions. For example, two populations whose initial sizes are very similar (e.g., 10,000 and 10,001) eventually become as different in population size as a population whose initial size is dramatically different (see Figure 4.1.1).

In the continuous-time logistic model, however, chaos is not observed (see Figure 4.3). Indeed, continuous-time models with only one or two variables never exhibit chaos. This does not mean that continuous-time models are always nicely behaved. In fact, continuous-time models with three or more variables can exhibit chaos. Indeed, chaotic dynamics are a common feature of food webs involving more than two species (Hastings and Powell 1991; Klebanoff and Hastings 1994; McCann and Hastings 1997). Interestingly, these models have been used to show that some forms of species interactions (e.g., linear food webs) are more prone to exhibit chaos than other forms of species interactions (e.g., omnivory).

We have mentioned that a defining feature of chaos is sensitivity to initial conditions. There are other clues that a model might exhibit chaos. One of them is that the system tends to oscillate between a number of states that doubles ("bifurcates") repeatedly as a parameter in the model is altered. This sort of behavior is observed in the logistic model as we increase the intrinsic

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Box 4.1 *(continued)*

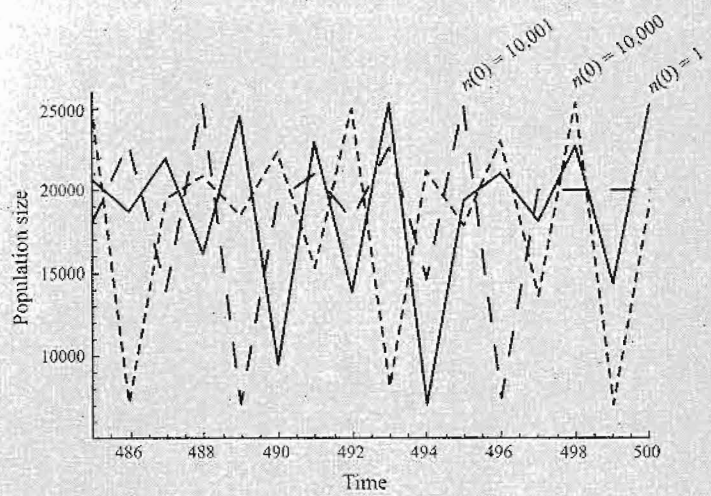

Figure 4.1.1: Sensitivity to initial conditions. A diagram of the population size versus time for the logistic equation (3.5a), starting from three different population sizes. After a few hundred generations, the population size dynamics of the two trajectories whose initial sizes were $n(0) = 10{,}000$ (short dashed lines) and $n(0) = 10{,}001$ (long dashed lines) are no closer together than they are to the population size dynamics starting from $n(0) = 1$ (solid lines). The parameters used were $r = 2.7$ and $K = 20{,}000$. Only time points 485 to 500 are shown to help see the differences between the trajectories.

growth rate, r (Figure 4.2). For low values of r, the population size approaches a single value K (e.g., $r = 0.7$ in Figure 4.2a). For higher values of r, the population size approaches an oscillation between two values, one above and one below K (e.g., $r = 2.1$ in Figure 4.2a). As r is increased further, the system settles down to a cycle involving four population sizes (e.g., $r = 2.5$ in Figure 4.2b). And as r is increased even further, the number of points through which the cycle passes (the *period*) doubles again and again. This period-doubling behavior is easiest to visualize using a *bifurcation diagram*.

Bifurcation diagrams illustrate the eventual states of a system on the vertical axis as a function of a parameter of interest on the horizontal axis. In the logistic model, the dynamics of the logistic model are quite sensitive to the intrinsic growth rate r, but not to other parameters such as the carrying capacity K (Problem 4.3). Thus, we use r as the parameter of interest in our bifurcation diagram (Figure 4.1.2). To produce this diagram, we iterated the recursion equation (3.5a) for a large number of generations (200) until the dynamics approached an equilibrium, a cycle, or showed no tendency to settle down. We then took the last 20 time points and plotted their values on the vertical axis. For small growth rates ($r < 2$), these last 20 time points were always very near the carrying capacity ($K = 1000$). The first period doubling occurred at $r = 2$, above which the population size cycled between two values (e.g., with $r = 2.1$, the population size

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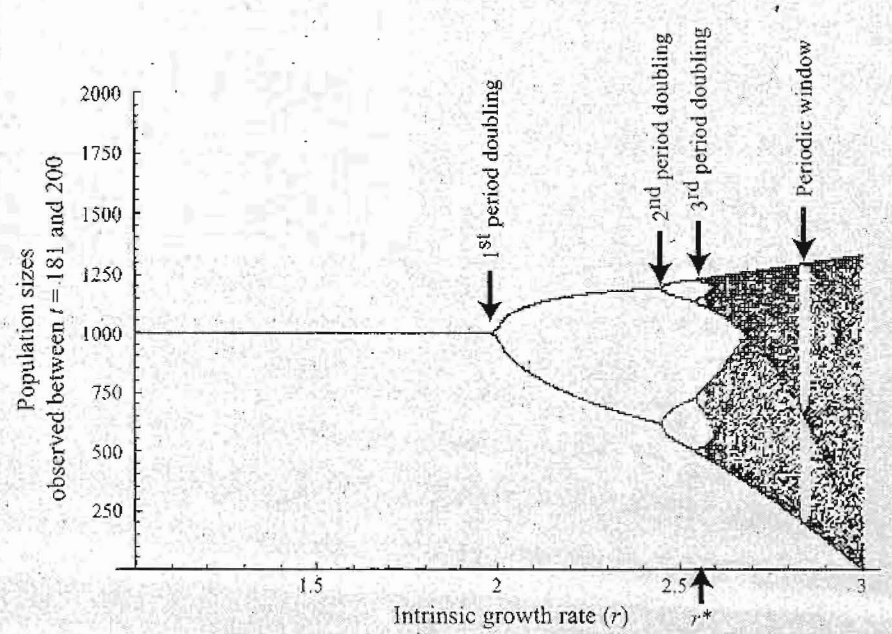

Figure 4.1.2: A bifurcation diagram for the logistic model. The recursion equation (3.5a) was iterated for 200 time steps, the last 20 of which are plotted on the vertical axis over a range of r values along the horizontal axis (r was increased from 1 to 3 in steps of 0.001). In every case, the initial population size was $n(0) = 10$, and the carrying capacity was $K = 1000$.

cycled between $n = 823$ and $n = 1129$, which give the vertical positions of the two points on the bifurcation diagram for $r = 2.1$). These two values grew further apart from one another until about $r = 2.45$, where the next period-doubling event occurred. Each subsequent period-doubling event occurred after shorter and shorter intervals in r. Eventually, the period doublings occurred so rapidly as r increased that the dynamics passed through a point at which an infinite number of period doublings had occurred. It is at this point that the dynamics become chaotic (at about $r^* = 2.569944$).

Period doubling is one route to chaos, and bifurcation diagrams allow us to visualize this process. If the bifurcation diagram for a model exhibits a forklike shape with tongs that divide faster and faster as the parameter of interest increases (as in Figure 4.1.2), expect to see chaos in the model.

A bifurcation diagram also illustrates that chaos does not imply a complete lack of order. In fact, for r values slightly above r^*, the population size remains within a fairly narrow region around the carrying capacity. This region expands as r increases and eventually includes zero at $r = 3$. Between the onset of chaos at r^* and extinction at $r = 3$, "periodic windows" appear, where the population size no longer fluctuates chaotically but cycles once again between a limited set of values. For example, a cycle among three points is observed at $r = 2.84$. Forklike bifurcations also occur within these periodic windows as r is increased further until, once again, the dynamics become chaotic.