Chapter 4

Chaos: simple rules can generate complex results

4.1 Ricker model revisited

In Chapter 3 we studied the equilibria $x_e = 0$ and $x_e = c^{-1}\ln b$ of the Ricker model

$$\begin{aligned} x_{t+1} &= b x_t e^{-c x_t} \\ x_0 &\geq 0 \\ b, c &> 0. \end{aligned}$$

We used the Linearization Theorem to prove that

$$\begin{aligned} 0 &< b < 1 \Longrightarrow x_e = 0 \text{ is stable} \\ b &> 1 \Longrightarrow x_e = 0 \text{ is unstable} \end{aligned}$$

and that

$$\begin{aligned} 1 &< b < e^2 \Longrightarrow x_e = \frac{\ln b}{c} \text{ is stable} \\ 0 &< b < 1 \Longrightarrow x_e = \frac{\ln b}{c} \text{ is unstable} \\ b &> e^2 \Longrightarrow x_e = \frac{\ln b}{c} \text{ is unstable.} \end{aligned}$$

We summarized this information in a bifurcation diagram, shown again here as Fig. 4.1.

The equilibrium analysis of the Ricker model begs the question, "what happens to solutions if $b > e^2$?" For these values of b, nonequilibrium solutions

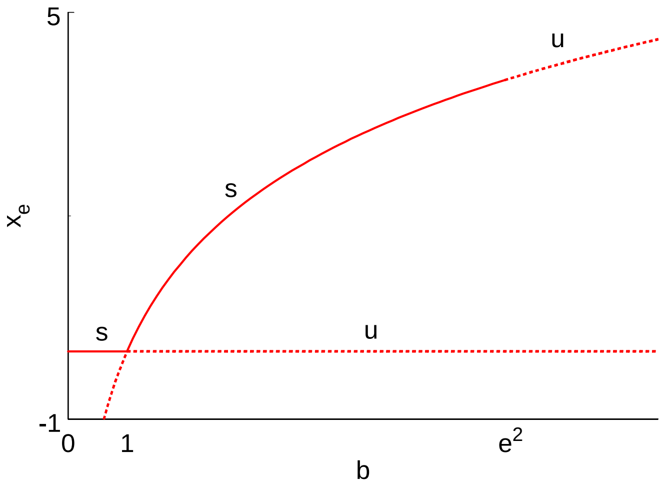

Figure 4.1: Bifurcation diagram of the Ricker map showing stability of equilibria. Dotted equilibria are unstable; solid are stable. Here $c = 0.01$.

cannot equilibriate, for there are no stable equilibria for them to approach. Some exploratory computer simulations are in order.

Let $c = 0.01$ and $x_0 = 75$. We will set b at various values and inspect the resulting time series.

Fig. 4.2 shows the time series that are generated when $b = 0.5$, $b = 1.3$, $b = 3.6$, and 5.7. If $b = 0.5$, solutions equilibrate to zero, whereas if $b = 1.3$, solutions equilibrate to a positive equilibrium $x_e \approx 26.3$. The *attractors* in these cases are the sets $\{0\}$ and $\{26.3\}$, respectively. For $b = 3.6$, the equilibrium is higher, about $x_e \approx 128.1$, and for $b = 5.7$, the equilibrium value is even higher, about $x_e \approx 174.0$. The interesting thing in this last case is that solutions oscillate as they approach the equilibrium. The attractors are the sets $\{128.1\}$ and $\{174.0\}$, respectively.

Fig. 4.3 shows time series for $b = 8$, $b = 14$, $b = 14.6$, and $b = 17$. We know from our linearization that for $b > e^2 \approx 7.389$, the solutions no longer equilibrate. Indeed, when $b = 8$, solutions approach a two-cycle; that is, they begin to oscillate between the two values $x \approx 138.6$ and $x \approx 277.3$. The attractor in this case is $\{138.6, 277.3\}$. Further numerical exploration reveals that as b was increased, the point attractor bifurcated into two points at $b = e^2$. The value $b = e^2$ is called a *bifurcation value*. For $b = 14$, solutions approach a four-cycle attractor, and for $b = 14.6$, an eight-cycle. As b is increased, the periods of these cycles continue to double, until at a critical value of b there is a transition to an aperiodic, complicated dynamic called *chaos*. This sequence of bifurcations is called a *period-doubling cascade to chaos*.

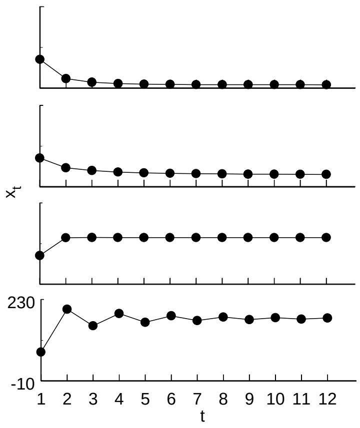

Figure 4.2: Time series for the Ricker map with $b = 0.5$, $b = 1.3$, $b = 3.6$, 5.7. In each case, $c = 0.01$.

If the attractor, also called the *final state*, of each of these time series is plotted against the parameter b, we can continue the Ricker bifurcation diagram beyond $b = e^2$ (Fig. 4.4). Note that unstable equilibria and cycles are not shown in Fig. 4.4, since computer iterations will only identify the stable ones.

Chaos has a complicated mathematical definition which we will not address in this book. For our purposes here we will note three important characteristics of chaos. First, chaos is deterministic. Note that the chaotic time series shown at the bottom of Fig. 4.3 is completely determined by the simple iterative rule $x_{t+1} = 17x_t e^{-0.01x_t}$, where $x_0 = 75$. Second, chaotic dynamics "look" random. Third, chaotic dynamics exhibit *sensitivity to initial conditions*. In Fig. 4.5 we see two time series of the Ricker model. The solid curve was started with the initial condition $x_0 = 75$, while the dotted curve was generated from $x_0 = 75.1$.The time series are close together for several steps, but soon diverge. This is sensitivity to initial conditions: a small error in initial conditions is quickly magnified.

Note: Chaos is a deterministic phenomenon.

4.2 New paradigms arise from chaos

4.2.1 Deterministic unpredictability

Determinism has generally been equated with *predictability.* If a system is deterministic, then the output is completely determined by the input, and is

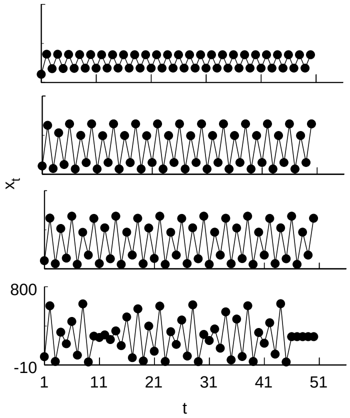

Figure 4.3: Ricker time series for $b = 8$, $b = 14$, $b = 14.6$, $b = 17$. In each case $c = 0.01$.

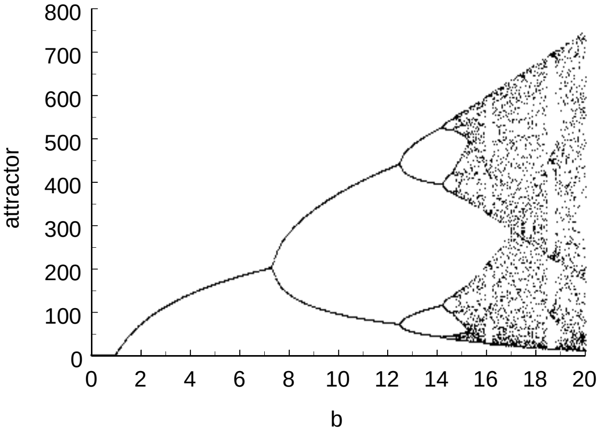

Figure 4.4: Bifurcation diagram for the Ricker model with $c = 0.01$.

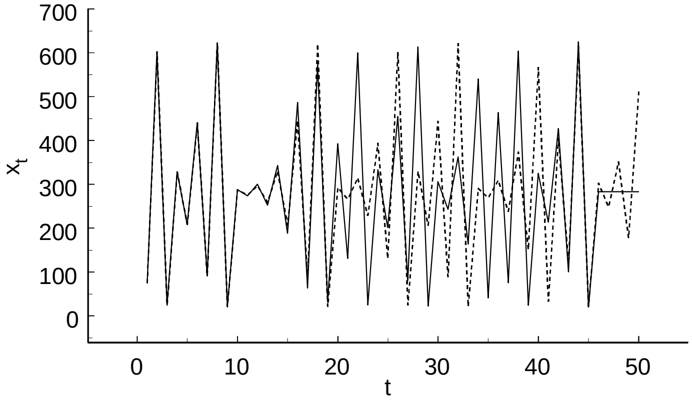

Figure 4.5: Two time series of the Ricker model with $b = 17$ and $c = 0.01$. The solid curve has initial condition $x_0 = 75$, and the dotted curve has initial condition $x_0 = 75.1$. The two solutions soon diverge, showing sensitivity to initial conditions.

thus predictable, given the input. Similarly, *stochasticity* has been identified with *unpredictability*, for obvious reasons.

Chaos, however, significantly alters this classical paradigm. Chaos is deterministic, but has sensitivity to initial conditions. Therefore, if the initial conditions are not known precisely (and they never are in the real world), then the future state of the system is, for all practical purposes, unpredictable. So in a very real sense, there is such a thing as "deterministic unpredictability".

4.2.2 Complex results can arise from simple rules

Another classical paradigm has been that simple causes give rise to simple results, and (equivalently) complex results imply complex causes. Chaos shows emphatically that this is not always the case. The Ricker recursion formula is quite simple, and yet its dynamics are so complicated that a mathematician can spend a lifetime exploring them. Thus, we see that complex results do NOT necessary imply complex causes. Very simple rules can generate very complicated results.

4.3 May's Hypothesis

In 1976, Robert May wrote [1]:

> "Quite apart from their intrinsic mathematical interest, the above results raise very awkward biological questions. They show that

> simple and fully deterministic models, in which all biological parameters are exactly known, can nonetheless (if the nonlinearities are sufficiently severe) lead to population dynamics which are in effect indistinguishable from the sample function of a random process. Apparently chaotic population fluctuations need not necessarily be due to random environmental fluctuations, or sampling errors, but may reflect the workings of some deterministic, but strongly density dependent, population model."

Note: May's Hypothesis: The apprently random fluctuations of population abundances can be explained largely by low-dimensional, nonlinear, deterministic forces.

In 1997, chaos was documented in population dynamics for the first time when it was experimentally induced in laboratory populations of insects [2,3]. We will discuss these experiments in Chapter @. To date, no one knows whether chaos occurs "naturally" in field populations; speculation and argumentation abound.

4.4 Exercises

1. Use the computer to draw a bifurcation diagram for the Beverton-Holt model

$$\begin{aligned} x_{t+1} &= \frac{bx_t}{1+cx_t} \\ x_0 &> 0 \\ b,c &> 0 \end{aligned}$$

   using b as the bifurcation parameter. Set $c = 1$,and let $0 \leq b \leq 10$.

2. Use the computer to draw a bifurcation diagram for the so-called discrete logistic model

$$\begin{aligned} x_{t+1} &= bx_t\left(1-x_t\right) \\ 0 &< x_0 < 1 \\ 0 &\leq b \leq 4 \end{aligned}$$

   using b as the bifurcation parameter. What happens to solutions if $b > 4$?

3. Consider the Ricker model with survivorship:

$$\begin{aligned} x_{t+1} &= bx_t e^{-cx_t} + \left(1-\mu\right)x_t \\ x_0 &> 0 \\ b,c &> 0 \\ 0 &\leq \mu \leq 1 \end{aligned}$$

   Here μ is the fraction of the population that does not survive one time step, and $1-\mu$ is the fraction that does survive one time step.

  (a) Set $c = 0.01$. Use the computer to draw bifurcation diagrams for each of the following values of μ, using b as the bifurcation parameter with $0 \leq b \leq 100$.
    i. $\mu = 1.0$ (Note that this is the usual Ricker model, without the survivorship term.)
    ii. $\mu = 0.9$
    iii. $\mu = 0.8$
    iv. $\mu = 0.7$
    v. $\mu = 0.6$
    vi. $\mu = 0.5$
    vii. $\mu = 0.4$
    viii. $\mu = 0.3$
    ix. $\mu = 0.2$
    x. $\mu = 0.1$
    xi. $\mu = 0.0$
  (b) Set $c = 0.01$ and $b = 80$. Draw the bifurcation diagram using μ as the bifurcation parameter with $0 \leq \mu \leq 1$. Relate this diagram to the sequence of diagrams in (3a).

4. In this problem you will use the computer to further explore the bifurcation diagram of the Ricker model

$$\begin{aligned} x_{t+1} &= b x_t e^{-c x_t} \\ x_0 &> 0 \\ b, c &> 0 \end{aligned}$$

using b as the bifurcation parameter. Let $c = 1$.

  (a) Draw the bifurcation diagram for $0 \leq b \leq 50$.
  (b) Draw the bifurcation diagram for $21 \leq b \leq 26$.
  (c) Draw the bifurcation diagram for $23 \leq b \leq 25$.
  (d) Draw the bifurcation diagram for $24.8 \leq b \leq 25$. Zoom in on the neighborhood of $0.3 \leq x \leq 1.8$ and $24.88 \leq b \leq 24.95$. (In Octave graph, right click, draw zoom box, right click again.) This illustrates the *fractal* nature of the bifurcation diagram, in which patterns are repeated at ever-smaller scales. Fractal structures are another common characteristic of chaos.

4.5 References

1. May, R. M., ed. 1976 Theoretical ecology: principles and applications. Philadelphia: W. B. Saunders.

2. Costantino, R. F., Desharnais, R. A., Cushing, J. M., and Dennis, B. 1997. Chaotic dynamics in an insect population. *Science* 275: 389–391.

3. Dennis, B., Desharnais, R. A., Cushing, J. M., Henson, S. M., and R. F. Costantino 2001. Estimating Chaos and Complex Dynamics in an Insect Population. *Ecological Monographs* 71:277-303.