

MA 137 — Calculus 1 with Life Science Applications

Difference Equations: Stability

(Section 5.7)

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First-Order Recursions (Review)

In Chapter 2 we saw that an important biological application of sequences consists of models of seasonally breeding populations with nonoverlapping generations where the population size at one generation depends only on the population size of the previous generation.

The discrete exponential growth model fits into this category.

To this end, we introduced first-order recursions [\equiv difference equations or iterated maps] by setting

$$x_{t+1} = f(x_t), \quad t = 0, 1, 2, \dots$$

where $f(x)$ is a function (\equiv updating function) that describes the density dependence of the population dynamics.

The name *difference equation* comes from writing the dynamics in the form

$$\frac{x_{t+1} - x_t}{(t+1) - t} = g(x_t)$$

[where $g(x) = f(x) - x$], which allows us to track population size changes from one time step to the next.

The name *iterated map* refers to the recursive definition.

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Fixed Points (\equiv Equilibria)

In Chapter 2, we were able to analyze difference equations only numerically (except for equations describing exponential growth, which we were able to solve).

We saw that fixed points (or equilibria) played a special role.

A **fixed point** \hat{x} satisfies the equation

$$\hat{x} = f(\hat{x})$$

and has the property that if $x_0 = \hat{x}$, then $x_t = \hat{x}$ for $t = 1, 2, 3, \dots$

We also saw in a number of applications that, under certain conditions, x_t converged to the fixed point as $t \rightarrow \infty$ even if $x_0 \neq \hat{x}$.

However, back in Chapter 2, we were not able to predict when such behavior would occur.

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Example 1: (Neuhauser, Example # 1, p. 274)

Find the equilibria of the recursive sequence

$$x_{t+1} = \frac{1}{4} - \frac{5}{4}x_t^2, \quad t = 0, 1, 2, \dots$$

What happens to x_t as $t \rightarrow \infty$ if $x_0 = -0.9$?

(You could use for example an Excel spreadsheet.)

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$$x_{t+1} = \frac{1}{4} - \frac{5}{4} x_t^2$$

To find the fixed points we need to solve

$$x = \frac{1}{4} - \frac{5}{4} x^2 \iff 4x = 1 - 5x^2 \iff$$

$$5x^2 + 4x - 1 = 0$$

We can factor it as: $(5x - 1)(x + 1) = 0$

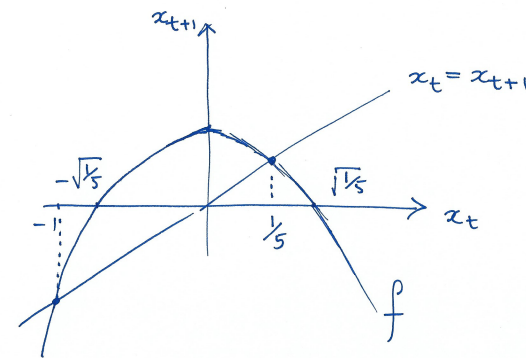
and we obtain after inspection:

$$(5x - 1)(x + 1) = 0$$

$$\therefore \boxed{\hat{x}_1 = \frac{1}{5}} \text{ and } \boxed{\hat{x}_2 = -1}$$

Notice that $x_{t+1} = \frac{1}{4} - \frac{5}{4} x_t^2$
 $= f(x_t)$

where $y = f(x) = \frac{1}{4} - \frac{5}{4} x^2$ parabola



graphic interpretation
of fixed
points

Note that $x_{t+1} = \frac{1}{4} - \frac{5}{4} x_t^2$ implies

$$x_0 = -0.9 \quad x_1 = -0.7625 \quad x_2 = -0.4767$$

$$x_3 = -0.0341 \quad x_4 = 0.2485 \quad x_5 = 0.1728$$

$$x_6 = 0.21268 \quad x_7 = 0.1935 \text{ etc....}$$

Exponential Growth

Exponential growth in discrete time is given by the recursion

$$N_{t+1} = R N_t, \quad t = 0, 1, 2, \dots$$

where N_t is the population size at time t and $R > 0$ is the growth rate.

We assume throughout that $N_0 \geq 0$, which implies that $N_t \geq 0$.

The fixed point of our recursion can be found by solving $N = R N$.

The only solution of this equation is $\hat{N} = 0$, unless $R = 1$.

If $R = 1$, then the population size never changes, regardless of N_0 .

What happens if we start with $N_0 > 0$ and $R \neq 1$?

In Chapter 2, we found that

$$N_t = N_0 R^t$$

is a solution of our recursion. Using this fact, we concluded that

$$N_t \rightarrow \begin{cases} 0 & \text{if } 0 < R < 1 \\ \infty & \text{if } R > 1, \end{cases}$$

as $t \rightarrow \infty$.

We can interpret the behavior of N_t as follows:

If $0 < R < 1$ and $N_0 > 0$, then N_t will return to the equilibrium $\hat{N} = 0$;

if $R \geq 1$ and $N_0 > 0$, then N_t will not return to the equilibrium $\hat{N} = 0$
 (more precisely, if $R = 1$, N_t will stay at N_0 ; if $R > 1$, N_t will go to ∞).

Terminology

We say that $\hat{N} = 0$ is **stable** if $0 < R < 1$ and **unstable** if $R > 1$.

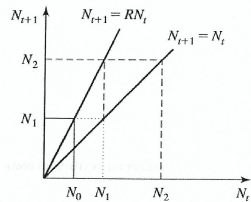
The case $R = 1$ is called **neutral**, since, no matter what the value of N_0 is, $N_t = N_0$ for $t = 1, 2, 3, \dots$

Cobwebbing

We can determine **graphically** whether a fixed point is stable or unstable.

The fixed points of exponential growth recursive sequence are found graphically where the graphs of $N_{t+1} = RN_t$ and $N_{t+1} = N_t$ intersect.

We see that the two graphs intersect where $N_t = 0$ only when $R \neq 1$.

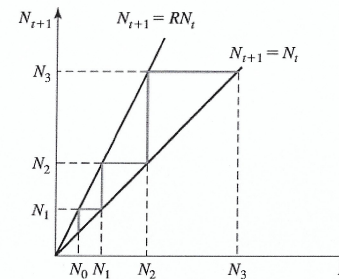


We can use the two graphs on the left to follow successive population sizes. Start at N_0 on the horizontal axis. Since $N_1 = RN_0$, we find N_1 on the vertical axis, as shown by the solid vertical and horizontal line segments. Using the line $N_{t+1} = N_t$, we can locate N_1 on the horizontal axis by the dotted horizontal and vertical line segments.

Using the line $N_{t+1} = RN_t$ again, we can find N_2 on the vertical axis, as shown in the figure by the broken horizontal and vertical line segments. Using the line $N_{t+1} = N_t$ once more, we can locate N_2 on the horizontal axis and then repeat the preceding steps to find N_3 on the vertical axis, and so on.

This procedure is called **cobwebbing**.

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In the **figure on the left**, $R > 1$, and we see that if $N_0 > 0$, then N_t will not converge to the fixed point $\hat{N} = 0$, but instead will move away from 0 (and, in fact, will go to infinity as t tends to infinity).

In the **figure on the right**, $0 < R < 1$, we see that if $N_0 > 0$, then N_t will return to the fixed point $\hat{N} = 0$.

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General Case

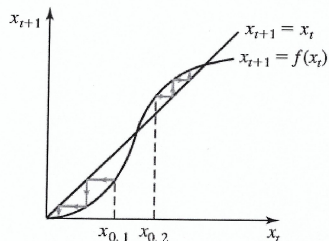
The general form of a first-order recursion is

$$x_{t+1} = f(x_t), \quad t = 0, 1, 2, \dots$$

We assume that the function f is differentiable in its domain.

- To find fixed points **algebraically**, we solve $x = f(x)$.
- To find them **graphically**, we look for points of intersection of the graphs of $x_{t+1} = f(x_t)$ and $x_{t+1} = x_t$.

The graphs in the picture intersect more than once, which means that there are multiple equilibria. We can use the cobwebbing



procedure from the previous subsection to graphically investigate the behavior of the difference equation for different initial values.

Two cases are shown in the picture, one starting at $x_{0,1}$ and the other at $x_{0,2}$. We see that x_t converges to different values, depending on the initial value.

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Stability Criterion

To determine the stability of an equilibrium — that is, whether it is stable or unstable — we will start at a value that is different from the equilibrium and check whether the solution will return to the equilibrium. We allow only initial values that are close to the equilibrium (we call it a **small perturbation**). The reason for looking only at small perturbations is that if there are multiple equilibria and if we start too far away from the equilibrium of interest, we might end up at a different equilibrium, not because the equilibrium of interest is unstable, but simply because we are drawn to another equilibrium.

If we are concerned only with small perturbations, we can approximate the function $f(x)$ by its linearization at the equilibrium \hat{x} . Since the slope of the tangent-line approximation of $f(x)$ at \hat{x} is given by $f'(\hat{x})$, we are led to the following criterion,

Theorem (Stability Criterion)

An equilibrium \hat{x} of $x_{t+1} = f(x_t)$ is locally stable if $|f'(\hat{x})| < 1$.

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Proof:

We look at the linearization of $f(x)$ about the equilibrium \hat{x} and investigated how a small perturbation affects the future of the solution.

We denote a small perturbation at time t by z_t and write

$$x_t = \hat{x} + z_t$$

Then

$$x_{t+1} = f(x_t) = f(\hat{x} + z_t)$$

Now, the linear approximation of $f(\hat{x} + z_t)$ at \hat{x} is $L(\hat{x} + z_t) = f(\hat{x}) + f'(\hat{x})z_t$.

Taking this into account, we can approximate $x_{t+1} [= \hat{x} + z_{t+1}]$ by

$$\hat{x} + z_{t+1} \approx f(\hat{x}) + f'(\hat{x})z_t.$$

Since $f(\hat{x}) = \hat{x}$ (\hat{x} is an equilibrium), we find that

$$z_{t+1} \approx f'(\hat{x})z_t$$

This approximation reminds of the equation $y_{t+1} = Ry_t$ for exponential growth, where we identify y_t with z_t and R with $f'(\hat{x})$. Since the solution of $y_{t+1} = Ry_t$ is $y_t = y_0 R^t$ and $R^t \rightarrow 0$ as $t \rightarrow \infty$ for $|R| < 1$, we obtain the criterion $|f'(\hat{x})| < 1$ for local stability. That is, if $|f'(\hat{x})| < 1$, then the perturbation z_t will converge to $\hat{z} = 0$ or, equivalently, $x_t \rightarrow \hat{x}$ as $t \rightarrow \infty$. 11/16

(Again) Example 1: (Neuhauser, Example # 1, p. 274)

Use the stability criterion to characterize the stability of the equilibria of

$$x_{t+1} = \frac{1}{4} - \frac{5}{4}x_t^2, \quad t = 0, 1, 2, \dots$$

We already found the equilibria (fixed points) of

$$x_{t+1} = \frac{1}{4} - \frac{5}{4}x_t^2 = f(x_t) \quad \text{where} \quad f(x) = \frac{1}{4} - \frac{5}{4}x^2$$

We saw that $\hat{x}_1 = \frac{1}{5} = 0.2$
 $\hat{x}_2 = -1$

Now, let's use the stability criterion:

$$f(x) = \frac{1}{4} - \frac{5}{4}x^2 \quad f'(x) = -\frac{5}{2}x$$

$$f'(-1) = -\frac{5}{2}(-1) = \frac{5}{2} > 1 \quad \therefore \boxed{\hat{x}_2 = -1 \text{ is unstable}}$$

$$f'\left(\frac{1}{5}\right) = -\frac{5}{2}\left(\frac{1}{5}\right) = -\frac{1}{2} \quad \text{and} \quad |f'\left(\frac{1}{5}\right)| = \frac{1}{2} < 1$$

$$\therefore \boxed{\hat{x}_1 = \frac{1}{5} \text{ is locally stable}}$$

What about the cobwebbing, say with starting point $x_0 = -0.9$?

We already computed some values

$$x_0 = -0.9; \quad x_1 = -0.7625; \quad x_2 = -0.4767$$

$$x_3 = -0.0341; \quad x_4 = 0.2485; \quad x_5 = 0.1728$$

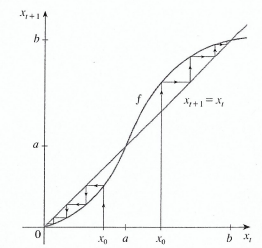
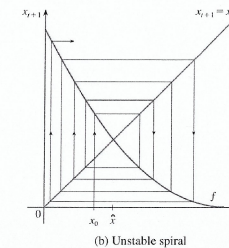
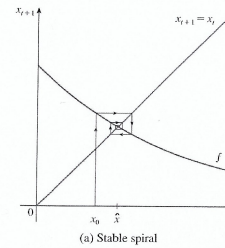
$$x_6 = 0.2127; \quad x_7 = 0.1935; \quad \dots$$

Here is how the picture of the cobwebbing looks like:

Geometric Considerations

We know from the Stability Criterion that when the slope of the tangent line to f at the equilibrium \hat{x} is between -1 and 1 , x_t converges to the equilibrium \hat{x} .

The solution x_t approaches the equilibrium in a **spiral** (thus exhibiting **oscillatory** behavior) when the slope of the tangent line at the equilibrium is negative, whereas it approaches it in **one direction** (thus exhibiting **nonoscillatory** behavior) when the slope of the tangent line at the equilibrium is positive.



Example 2: (Neuhauser, Example # 2, p. 275)

Use the stability criterion to characterize the stability of the equilibria of

$$x_{t+1} = \frac{x_t}{0.1 + x_t}, \quad t = 0, 1, 2, \dots$$

We need to find the fixed points of

$$x_{t+1} = \frac{x_t}{0.1 + x_t} \quad t = 0, 1, 2, \dots \quad f(x) = \frac{x}{0.1 + x}$$

i.e. we need to solve $x = \frac{x}{0.1 + x}$

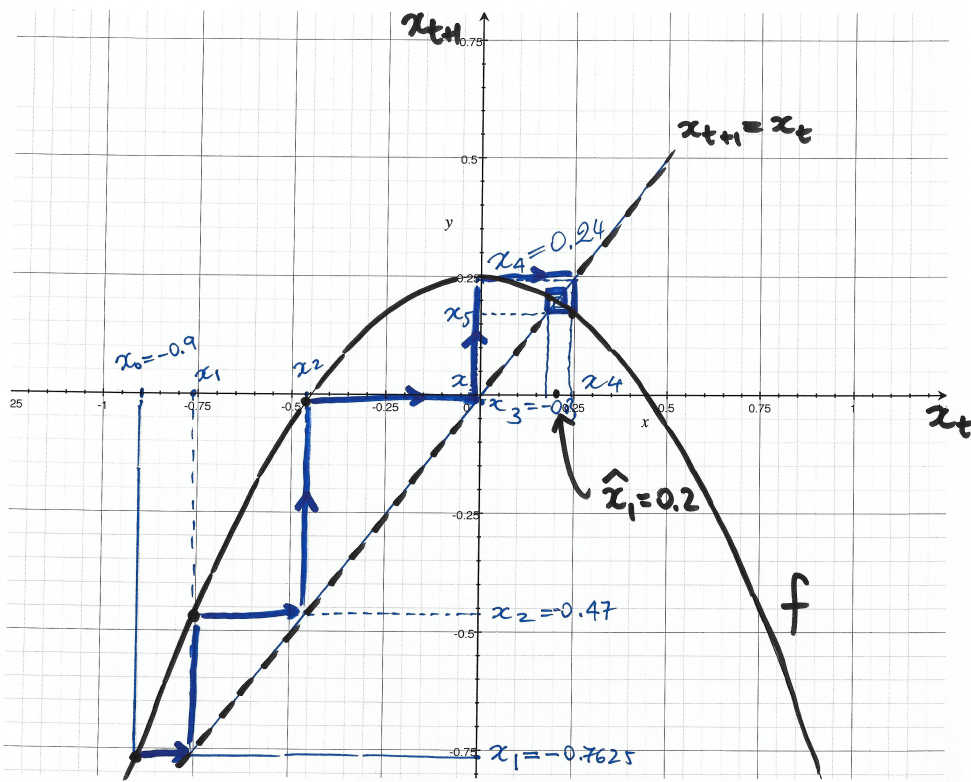
$$\Leftrightarrow x(0.1 + x) = x \Leftrightarrow$$

$$x[0.1 + x - 1] = 0 \Leftrightarrow x[x - 0.9] = 0$$

$$\therefore \boxed{\hat{x}_1 = 0} \text{ and } \boxed{\hat{x}_2 = 0.9}$$

Now to use the stability criterion we need $f'(x)$:

$$f(x) = \frac{x}{0.1 + x} \Rightarrow f'(x) = \frac{1 \cdot (0.1 + x) - x(1)}{(0.1 + x)^2} = \frac{0.1}{(0.1 + x)^2}$$



Hence :

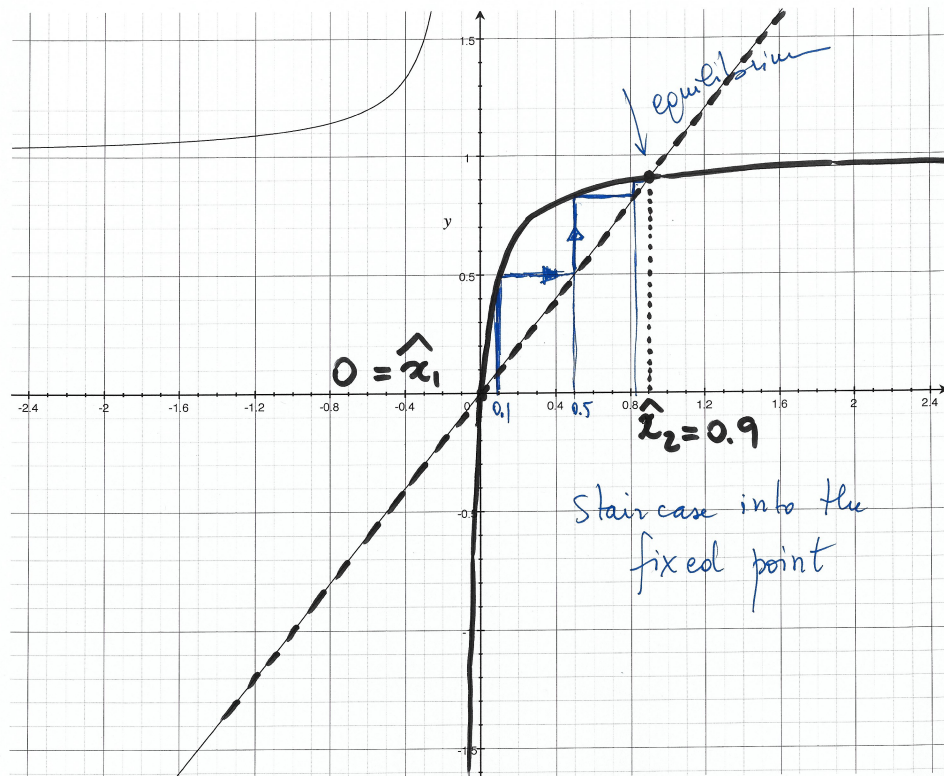
$$\hat{x}_1 = 0 \implies f'(0) = \frac{0.1}{(0.1+0)^2} = \frac{0.1}{0.01} = \underline{\underline{10}}$$

$$\hat{x}_2 = 0.9 \implies f'(0.9) = \frac{0.1}{(0.1+0.9)^2} = \frac{0.1}{1^2} = 0.1$$

$\hat{x}_2 = 0.9$ is locally stable

$\hat{x}_1 = 0$ is unstable

Here is an example of cobwebbing with $x_0 = 0.1$



Example 3: (Neuhauser, Example # 4, p. 276)

Denote by N_t the size of a population at time t , $t = 0, 1, 2, \dots$. Find all equilibria and determine their stability for the **discrete logistic growth sequence**

$$N_{t+1} = N_t \left[1 + R \left(1 - \frac{N_t}{K} \right) \right]$$

where we assume that the parameters R and K are both positive.

$$N_{t+1} = N_t \left(1 + R \left(1 - \frac{N_t}{K} \right) \right) = f(N_t)$$

to find the equilibria we need to solve

$$N = N \left[1 + R \left(1 - \frac{N}{K} \right) \right] \iff \boxed{\hat{N}_1 = 0} \quad \text{OR} \quad \underline{\underline{0}}$$

$$1 = 1 + R \left(1 - \frac{N}{K} \right) \iff 0 = R \left(1 - \frac{N}{K} \right)$$

$$\iff 1 - \frac{N}{K} = 0 \iff \boxed{\hat{N}_2 = K}$$

Now to use the stability criterion we need $f'(N)$ from $f(N) = N \left(1 + R \left(1 - \frac{N}{K} \right) \right)$
 $= N + RN - \frac{R}{K} N^2$

$$\text{Hence } f'(N) = 1 + R - \frac{2R}{K}N$$

$$\text{Now when } \hat{N}_1 = 0 \implies f'(0) = 1 + R - 0 = 1 + R$$

which is strictly > 1

$\therefore \hat{N}_1 = 0$ is unstable

$$\text{Now when } \hat{N}_2 = K \implies f'(K) = 1 + R - \frac{2R}{K} \cdot K$$
$$= 1 + R - 2R$$
$$= \underline{\underline{1 - R}}$$

$$\text{Hence } \hat{N}_2 = K \text{ is locally stable} \iff |1 - R| < 1$$

$$\iff -1 < 1 - R < 1 \iff \boxed{0 < R < 2}$$

Another Idea for a Possible Project?

Biologist T.S. Bellows investigated the ability of several difference equations to describe the population dynamics of insects. He found that the so called *Generalized Beverton-Holt model* provided the best description. If x_n denotes the population density in the n -th generation, then the model is of the form

$$x_{n+1} = \frac{r x_n}{1 + x_n^b}$$

where r is the intrinsic fitness of population and b measures the abruptness of density dependence.

For three insect species, Bellows found the following parameter estimates:

- * Budworm moth: $r = 3.5$ and $b = 2.7$;
- * Colorado potato beetle: $r = 75$ and $b = 4.8$;
- * Meadow plant bug: $r = 2.2$ and $b = 1.4$.

- Use these parameter estimates to determine which population supports a stable equilibrium.
- For the species that do not support a stable equilibrium simulate their dynamics.