Discrete Population Models for Single Species

Jerry Kiely

School of Mathematical Sciences

Dublin Institute of Technology

Dublin 8

Ireland

d16126734@mydit.ie

October 21, 2019

Contents

List of Figures

List of Tables

Abstract

The author presents a review of *Discrete Population Models for Single Species*. He describes their relevance and applications, gives a graphical approach to solving non-linear models, presents some of the details around *Equilibrium*, *Stability*, and *Chaos*, looks rigorously at the technique of *Linearisation* around equilibrium points, and then reviews *Discrete Models with Delay*.

Chapter 1

Discrete Models

1.1 Introduction

Discrete models, as opposed to continuous models, use difference equations (rather than differential equations) to model biological phenomena, such as populations, when it makes sense to measure the interval of time between events as discrete or fixed. It also makes sense where successive measurements occur at fixed time intervals - such as census data. We are interested in models of the form:

$$x_{t+1} = f(x_t)$$

Where f is a linear or non-linear function of x_t. The sequence $\{x_0, x_1, x_2, \ldots\}$ is called the *orbit*.

As an example, consider a population that changes over time through births and deaths only. Let us denote the population at time t to be x_t, and the population at time $t+1$ to be x_{t+1}. With a birth rate r_b and a death rate r_d, we can describe the rate of change of the population as follows:

$$
\begin{aligned}
x_{t+1} - x_t &= r_b x_t - r_d x_t \\
&= (r_b - r_d)x_t \\
x_{t+1} &= x_t + (r_b - r_d)x_t \\
&= (1 + r_b - r_d)x_t \\
&= r x_t
\end{aligned}
$$

where $r = 1 + r_b - r_d$. From here it is easy to show that:

$$
\begin{aligned}
x_t &= r x_{t-1} \\
&= r(r x_{t-2}) \\
&= r^2 x_{t-2} \\
&= r^2(r x_{t-3}) \\
&= r^3 x_{t-3} \\
&\vdots \\
&= r^t x_0
\end{aligned}
$$

and for this simple model it is clear to see that when $|r| < 1$ then the population decays to zero, and if $|r| > 1$ then the population grows without bound. If $|r| = 1$ then the population exhibits no growth or decay at all, remaining constant at it's initial value.

1.2 Applications

Some examples where discrete models may be used are:

- plant population (annual reproduction)
- insect population (where there is no overlap in generations)
- cell population (within a culture)

1.3 Solutions

Solving a linear discrete model - coming up with a formula that expresses the n-th iterate of our model in terms of the parameters of the model - is easy, and allows us to make long-term predictions about the behaviour of our model. In the non-linear case it is not possible to do this, and hence difficult to make predictions about the long-term model behaviour, population dynamics, etc.

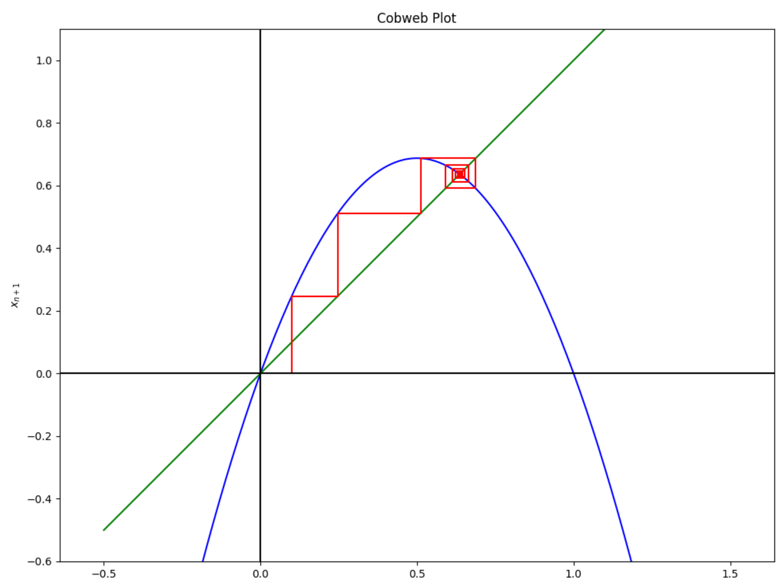

Figure 1.1: Cobweb plot of $x_{t+1} = x_t r(1 - x_t)$

One technique for helping us to understand non-linear discrete models is *cobwebbing*, which is a graphical method for finding equilibrium points. The technique is as follows:

- construct a set of axes with x_t along the horizontal and x_{t+1} along the vertical
- draw the curve of the function $x_{t+1} = f(x_t)$
- draw the line $x_{t+1} = x_t$
- draw a line vertically up from $(x_0, 0)$ on the horizontal till it meets the curve of the function
- this point is (x_0, x_1)
- draw a line horizontally from (x_0, x_1) till it meets the line $x_{t+1} = x_t$
- call this point (x_1, x_1)
- with this point we repeat the above process until we either converge to an equilibrium point or diverge

Equilibrium points are located where the curve and the line intersect - usually denoted x^*.

Chapter 2

Discrete Logistic Growth

2.1 Basics

Consider the Logistic growth model:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where r is the growth rate, and K is the carrying capacity. We can turn this into a discrete model as follows:

$$\begin{aligned}
N_{t+1} - N_t &= rN_t\left(1 - \frac{N_t}{K}\right) \\
N_{t+1} &= N_t + rN_t\left(1 - \frac{N_t}{K}\right) \\
&= N_t\left(1 + r - \frac{rN_t}{K}\right) \\
&= N_t(1+r)\left(1 - \frac{rN_t}{(1+r)K}\right)
\end{aligned}$$

by making a transformation we have:

$$x_{t+1} = f(x_t) = x_t r'(1 - x_t) \quad \text{where} \quad r' = 1 + r \quad \text{and} \quad x_t = \frac{rN_t}{(1+r)K}$$

2.2 Equilibrium

we now investigate the equilibrium states of this model, with $0 \leq r \leq 4$ for simplicity:

$$\begin{aligned} x^* &= x^* r(1 - x^*) \\ r(1 - x^*) &= 1 \\ 1 - x^* &= \frac{1}{r} \\ x^* &= \frac{r-1}{r} \end{aligned}$$

so we have two equilibrium points - $x^* = 0$ and $x^* = (r-1)/r$ with $r > 1$ (as we are not interested in negative populations). In order to understand the behaviour of the equilibrium points we need to look at the first derivative of $f(x)$:

$$\begin{aligned} f(x) &= xr(1 - x) \\ f'(x) &= r(1 - 2x) \end{aligned}$$

2.3 Stability

Examining both these equilibrium points with $|f'(x)| < 1$ denoting stability, and $|f'(x)| > 1$ denoting instability:

$$\begin{aligned} f'(0) &= r \\ f'\left(\frac{r-1}{r}\right) &= 2-r \end{aligned}$$

so $x^* = 0$ is stable for $r < 1$, and unstable for $r > 1$, and $x^* = (r-1)/r$ is stable for $1 < r < 3$, and does not exist for $0 < r < 1$:

	$0 < r < 1$	$1 < r < 3$
$x^* = 0$	stable	unstable
$x^* = \frac{r-1}{r}$	does not exist	stable

Table 2.1: Stability of discrete logistic growth model

2.4 Chaos

$r = 1$ and $r = 3$ are known as *bifurcation points* and represent parameter values where our model's behaviour changes. In order to understand the model's behaviour for $r > 3$ first we observe the following:

$$
\begin{aligned}
x_{t+1} &= f(x_t) \\
&= f(f(x_{t-1})) = f^2(x_{t-1}) \\
&= f^2(f(x_{t-2})) = f^3(x_{t-2}) \\
&\vdots \\
&= f^{t+1}(x_0)
\end{aligned}
$$

and in particular, looking at the second order difference equation:

$$
\begin{aligned}
x_{t+2} &= f^2(x_t) \\
&= f(f(x_t)) \\
&= f(x_t)r(1 - f(x_t)) \\
&= x_t r^2(1 - x_t)(1 - x_t r(1 - x_t))
\end{aligned}
$$

setting $x_{t+2} = x_t = x^*$ we find:

$$
\begin{aligned}
x^* &= x^* r^2(1 - x^*)(1 - x^* r(1 - x^*)) \\
1 &= r^2(1 - x^*)(1 - x^* r(1 - x^*)) \\
1 &= r^2(1 - x^* r + (x^*)^2 r - x^* + (x^*)^2 r - (x^*)^3 r) \\
1 &= r^2 - x^* r^3 + (x^*)^2 r^3 - x^* r^2 + (x^*)^2 r^3 - (x^*)^3 r^3 \\
0 &= 1 - r^2 + x^* r^3 - (x^*)^2 r^3 + x^* r^2 - (x^*)^2 r^3 + (x^*)^3 r^3
\end{aligned}
$$

after some manipulation this reduces to:

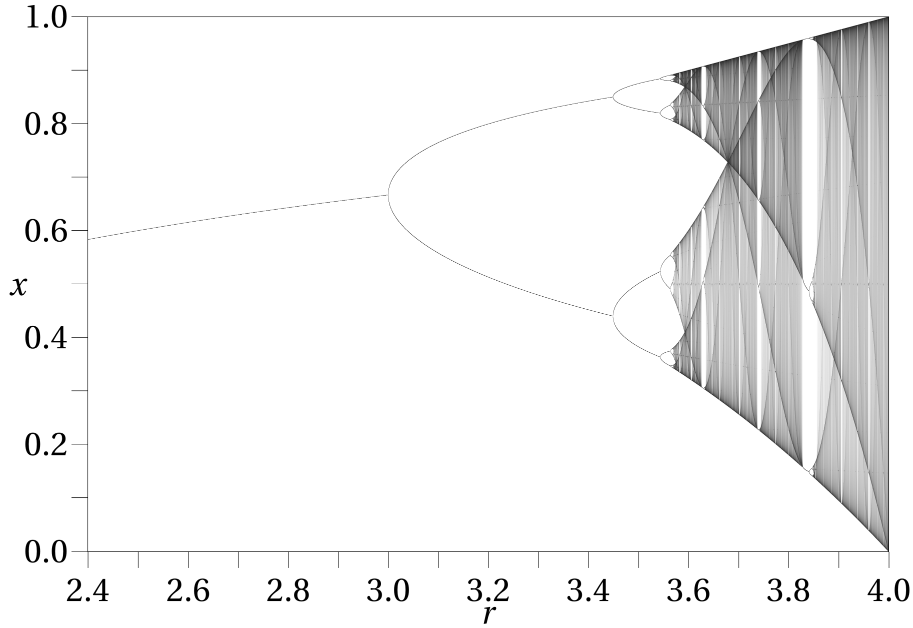

Figure 2.1: Bifurcations

$$(rx^* - (r+1))(r^2(x^*)^2 - r(r+1)x^* + (r+1)) = 0$$

here $rx^* - (r+1) = 0$ gives us one of our original equilibrium points, so instead we look at:

$$r^2(x^*)^2 - r(r+1)x^* + (r+1) = 0$$

this quadratic will give us two real roots if the discriminant is positive:

$$\begin{aligned} r^2(r+1)^2 - 4r^2(r+1) &> 0 \\ r^2 + 2r + 1 - 4r - 4 &> 0 \\ r^2 - 2r - 3 &> 0 \\ (r+1)(r-3) &> 0 \end{aligned}$$

as we have restricted ourselves to $r > 0$, we have $r > 3$, and our solutions are:

$$x^* = \frac{(r+1) \pm \sqrt{(r+1)(r-3)}}{2r}$$

so the next solution is said to have period 2 as there are two possible values. This process continues for increasing r. So p-periodic solutions become $2p$-periodic solutions, and so on.

If an odd periodic solution ($p \geq 3$) exists for some value of r, say r_c, then there is said to be *aperiodic* or *chaotic* solutions for $r > r_c$. Chaotic solutions are solutions that oscillate in random, or unpredictable, ways.

2.5 Analysis

We now investigate the stability of our Logistic growth model analytically through linearisation about an equilibrium point:

$$x_t = x^* + u_t, \qquad |u_t| \ll 1$$

substituting this into our function we get:

$$x^* + u_{t+1} = f(x^* + u_t)$$

Taylor expanding around the equilibrium point we get:

$$x^* + u_{t+1} = f(x^*) + u_t f'(x^*) + \mathcal{O}(u_t^2), \qquad |u_t| \ll 1$$

as x^* is an equilibrium point, $f(x^*) = x^*$, and discarding higher powers of u_t, we get:

$$\begin{aligned} u_{t+1} &= u_t f'(x^*) \\ &= \lambda u_t \\ &= \lambda^{t+1} u_0 \end{aligned}$$

where $\lambda = f'(x^*)$. From this we can draw conclusions about the stability of the equilibrium point. It is clear that:

$$\begin{aligned} |\lambda| < 1 &\implies \lim_{t\to\infty} u_t = 0 \\ |\lambda| > 1 &\implies \lim_{t\to\infty} u_t = \pm\infty \end{aligned}$$

and hence:

$$\begin{aligned} |f'(x^*)| < 1 &\implies x^* \quad \text{is stable} \\ |f'(x^*)| > 1 &\implies x^* \quad \text{is unstable} \end{aligned}$$

Chapter 3

Discrete Models with Delay

3.1 Introduction

So far we have assumed that all members of the population at time t contribute to the population at time $t + 1$, but this is not always the case. For example, depending upon the interval of time, some members of a population may not have yet reached sexual maturity, and hence cannot contribute to the population. As a consequence it makes sense in some cases to introduce a delay term to the model.

$$x_{t+1} = f(x_t, x_{t-\tau})$$

3.2 Analysis

We switch now to a different model - Ricker's model:

$$x_{t+1} = x_t \exp(r(1 - x_t))$$

with $r > 0$ - which has equilibrium points $x^* = 0$ and $x^* = 1$. We make a slight change to this model by introducing a delay term:

$$x_{t+1} = x_t \exp(r(1 - x_{t-1}))$$

again, with $r > 0$. Now we linearise around $x^* = 1$:

$$x_t = 1 + u_t, \qquad |u_t| \ll 1$$

substituting into our equation above we get:

$$\begin{aligned}
1 + u_{t+1} &= (1 + u_t)\exp(r(1 - (1 + u_{t-1}))) \\
&= (1 + u_t)\exp(-ru_{t-1}) \\
&\approx (1 + u_t)(1 - ru_{t-1}) \\
&= 1 - ru_{t-1} + u_t - ru_t u_{t-1} \\
u_{t+1} &= u_t - ru_{t-1}
\end{aligned}$$

the above using the fact that $\exp(x) \approx 1 + x$ for small x.

3.3 Solutions

We have reduced our model to a second order difference equation:

$$u_{t+1} - u_t + ru_{t-1} = 0$$

with characteristic equation:

$$z^2 - z + r = 0$$

with solutions:

$$\begin{aligned} z_{1,2} &= \frac{1}{2}\left[1 \pm \sqrt{1-4r}\right] \qquad 0 < r < \frac{1}{4} \\ z_{1,2} &= \frac{1}{2}\left[1 \pm i\sqrt{4r-1}\right] \qquad \frac{1}{4} < r < 1 \end{aligned}$$

for the case of $0 < r < \frac{1}{4}$ we have:

$$u_t = C_1 z_1^t + C_2 z_2^t$$

and because $0 < z_{1,2} < 1$:

$$\lim_{t\to\infty} u_t = 0$$

and hence:

$$\lim_{t\to\infty} x_t = 1$$

therefore $x^* = 1$ is stable for $0 < r < \frac{1}{4}$. For the case of $\frac{1}{4} < r < 1$ we have:

$$
\begin{aligned}
\rho &= |z_{1,2}| = \sqrt{r} \\
\theta &= \tan^{-1}(\sqrt{4r-1}) \\
z_{1,2} &= \rho e^{\pm i\theta}
\end{aligned}
$$

which leads to:

$$
\begin{aligned}
u_t &= Cz^t + \overline{C}\overline{z}^t \\
&= |A|\, e^{i\gamma}(\rho e^{i\theta})^t + |A|\, e^{-i\gamma}(\rho e^{-i\theta})^t \\
&= 2\,|A|\,\rho^t \left(\frac{e^{i(\theta t+\gamma)} + e^{-i(\theta t+\gamma)}}{2} \right) \\
&= 2\,|A|\,\rho^t \cos(\theta t + \gamma)
\end{aligned}
$$

which is stable as $r < 1$. If we take $r_c = 1$, then at r_c we have:

$$
\begin{aligned}
\theta_c &= \tan^{-1}(\sqrt{4r_c - 1}) \\
&= \tan^{-1}(\sqrt{3}) \\
&= \frac{\pi}{3}
\end{aligned}
$$

from which we get:

$$
u_t = 2\,|A| \cos(\frac{\pi}{3} t + \gamma)
$$

and hence:

$$\begin{aligned}\frac{\pi}{3}t_p &= 2\pi \\ t_p &= 6\end{aligned}$$

and for $r > r_c$ we have $\rho > 1$ which gives us:

$$\lim_{t\to\infty} u_t = \pm\infty$$

and hence:

$$\lim_{t\to\infty} x_t = \pm\infty$$

Chapter 4

Solutions to problems

4.1 $x_{n+1} = \beta x_n + \alpha x_{n-1}$

This is a linear system. The solution is as follows:

$$\begin{aligned} x_{n+1} &= \beta x_n + \alpha x_{n-1} \\ x_{n+1} - \beta x_n - \alpha x_{n-1} &= 0 \end{aligned}$$

with characteristic equation:

$$\lambda^2 - \beta\lambda - \alpha = 0$$

and solutions:

$$\lambda_{1,2} = \frac{\beta \pm \sqrt{\beta^2 + 4\alpha}}{2}$$

our general solution is of the form:

$$x_n = C_1\lambda_1^n + C_2\lambda_2^n$$

which gives us for $n = 0$ and $n = 1$:

$$\begin{aligned} x_0 &= C_1 + C_2 \\ x_1 &= C_1\lambda_1 + C_2\lambda_2 \end{aligned}$$

taking x_1 we get:

$$\begin{aligned} x_1 &= C_1\frac{\beta + \sqrt{\beta^2 + 4\alpha}}{2} + C_2\frac{\beta - \sqrt{\beta^2 + 4\alpha}}{2} \\ &= \frac{\beta}{2}(C_1 + C_2) + \frac{\sqrt{\beta^2 + 4\alpha}}{2}(C_1 - C_2) \\ &= \frac{\beta}{2}x_0 + \frac{\sqrt{\beta^2 + 4\alpha}}{2}(C_1 - C_2) \end{aligned}$$

$$\begin{aligned} C_1 - C_2 &= \frac{2x_1 - \beta x_0}{\sqrt{\beta^2 + 4\alpha}} \\ C_1 + C_2 &= x_0 \end{aligned}$$

solving for C_1 and C_2 we get:

$$\begin{aligned} C_1 &= \frac{x_0(\sqrt{\beta^2 + 4\alpha} - \beta) + 2x_1}{2\sqrt{\beta^2 + 4\alpha}} \\ C_2 &= \frac{x_0(\sqrt{\beta^2 + 4\alpha} + \beta) - 2x_1}{2\sqrt{\beta^2 + 4\alpha}} \end{aligned}$$

so our general solution is:

$$x_n = \left(\frac{x_0(\sqrt{\beta^2+4\alpha}-\beta)+2x_1}{2\sqrt{\beta^2+4\alpha}}\right)\left(\frac{\beta+\sqrt{\beta^2+4\alpha}}{2}\right)^n + \left(\frac{x_0(\sqrt{\beta^2+4\alpha}+\beta)-2x_1}{2\sqrt{\beta^2+4\alpha}}\right)\left(\frac{\beta-\sqrt{\beta^2+4\alpha}}{2}\right)^n$$

4.2 $x_{n+1} = {x_n}/{1+x_n}$

This is a non-linear system.

$$x_{n+1} = \frac{x_n}{1+x_n}$$

finding the equilibrium points:

$$x^* = \frac{x^*}{1+x^*}$$

$$\therefore \quad x^* = 0$$

now we look at the stability:

$$
\begin{aligned}
f(x) &= \frac{x}{1+x} \\
f'(x) &= \frac{1}{(1+x)^2} \\
\\
f'(0) &= 1
\end{aligned}
$$

therefore, strictly speaking, we cannot say that $x^* = 0$ is either stable or unstable. Looking at the system graphically (Figure 4.1) starting in the neighbourhood of 1 and cobwebbing, we see that the system tends towards 0 which would imply $x^* = 0$ is stable.

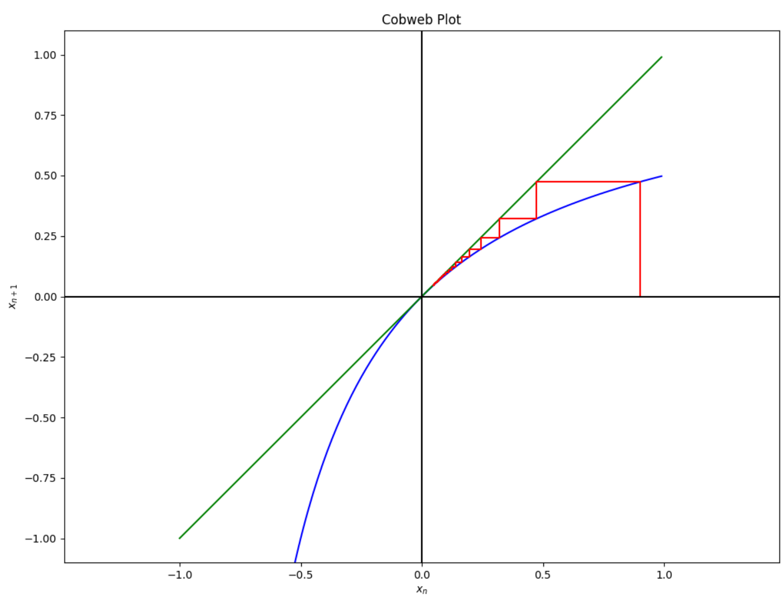

Figure 4.1: Cobweb plot of $x_{n+1} = {}^{x_n}/_{1+x_n}$

4.3 $x_{n+1} = 1/2 + x_n$

This is a non-linear system.

$$x_{n+1} = \frac{1}{2 + x_n}$$

finding the equilibrium points:

$$\begin{aligned} x^* &= \frac{1}{2+x^*} \\ 2x^* + (x^*)^2 &= 1 \\ (x^*)^2 + 2x^* - 1 &= 0 \end{aligned}$$

$$x^* = -1 \pm \sqrt{2}$$

now we look at the stability:

$$\begin{aligned} f(x) &= \frac{1}{2+x} \\ f'(x) &= \frac{-1}{(2+x)^2} \end{aligned}$$

$$\begin{aligned} \left|f'(-1+\sqrt{2})\right| &< 1 \\ \left|f'(-1-\sqrt{2})\right| &> 1 \end{aligned}$$

therefore $x^* = -1 + \sqrt{2}$ is stable, and $x^* = -1 - \sqrt{2}$ is unstable.

4.4 $x_{n+1} = x_n e^{\alpha x_n}$

This is a non-linear system.

$$x_{n+1} = x_n e^{\alpha x_n}$$

finding the equilibrium points:

$$\begin{aligned} x^* &= x^* e^{\alpha x^*} \\ \therefore \quad x^* &= 0 \end{aligned}$$

now we look at the stability:

$$\begin{aligned} f(x) &= x e^{\alpha x} \\ f'(x) &= (1 + \alpha x) e^{\alpha x} \\ f'(0) &= 1 \end{aligned}$$

therefore, strictly speaking, we cannot say that $x^* = 0$ is either stable or unstable. Looking at the system graphically (Figure 4.2) starting in the neighbourhood of 0 and cobwebbing, we see that the system tends towards ∞, i.e. is unbounded, which would imply $x^* = 0$ is unstable.

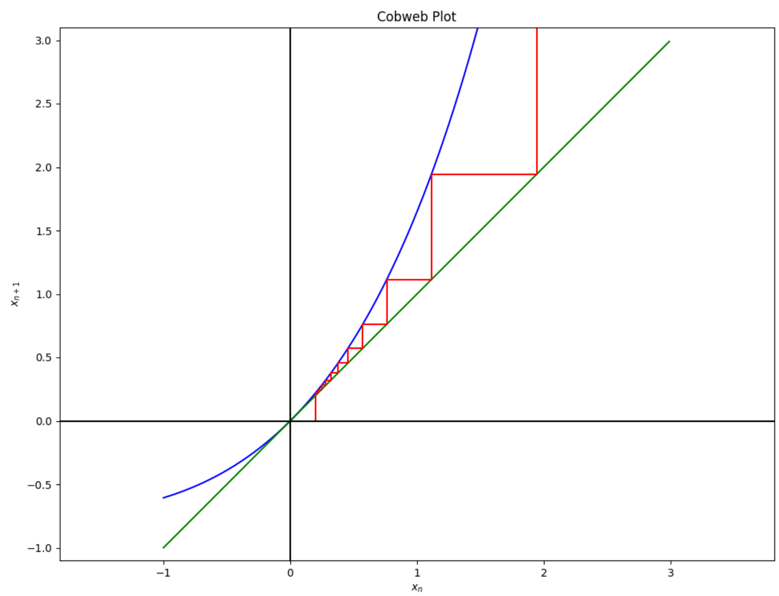

Figure 4.2: Cobweb plot of $x_{n+1} = x_n e^{\alpha x_n}$

4.5 $x_{n+1} = x_n \ln(x_n^2)$

This is a non-linear system.

$$x_{n+1} = x_n \ln(x_n^2)$$

finding the equilibrium points:

$$
\begin{aligned}
x^* &= x^* \ln((x^*)^2) \\
&= 2x^* \ln(x^*)
\end{aligned}
$$

$$
\begin{aligned}
2\ln(x^*) &= 1 \\
\ln(x^*) &= \frac{1}{2} \\
x^* &= \sqrt{e} \\
\therefore \qquad x^* &= 0 \quad \text{or} \quad \sqrt{e}
\end{aligned}
$$

now we look at the stability:

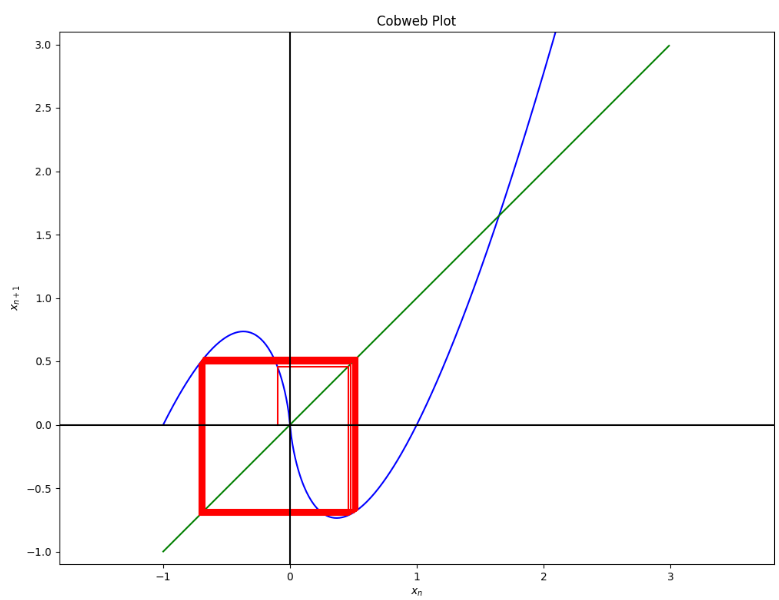

Figure 4.3: Cobweb plot of $x_{n+1} = x_n \ln(x_n^2)$ starting from -0.1

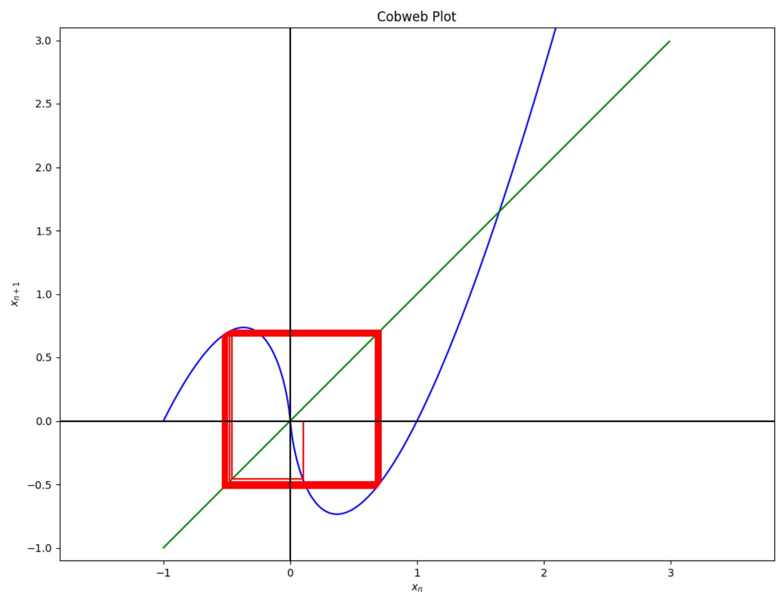

Figure 4.4: Cobweb plot of $x_{n+1} = x_n \ln(x_n^2)$ starting from 0.1

$$f(x) = 2x\ln(x)$$
$$f'(x) = 2(\ln(x) + 1)$$

$$f'(0) = -\infty$$
$$f'(\sqrt{e}) = 3$$

therefore both $x^* = 0$ and $x^* = \sqrt{e}$ are unstable. But looking at the system graphically and cobwebbing starting at -0.1 (Figure 4.3) and then starting at 0.1 (Figure 4.4) - i.e. in the neighbourhood of 0 - we see periodic oscillations that would suggest a periodic solutions to the system.

4.6 $(x_{n+1} - \alpha)^2 = \alpha^2(x_n^2 - 2x_n + 1)$

This is a combination of linear systems.

$$\begin{aligned}
(x_{n+1} - \alpha)^2 &= \alpha^2(x_n^2 - 2x_n + 1) \\
&= \alpha^2(x_n - 1)^2 \\
x_{n+1} - \alpha &= \pm\alpha(x_n - 1) \\
x_{n+1} &= \alpha \pm \alpha(x_n - 1) \\
&= \alpha \pm (\alpha x_n - \alpha)
\end{aligned}$$

this results in two linear systems, the first:

$$\begin{aligned}
x_{n+1} &= \alpha x_n \\
&= \alpha^{n+1} x_0
\end{aligned}$$

and the second:

$$\begin{aligned}
x_{n+1} &= 2\alpha - \alpha x_n \\
&= 2\alpha - \alpha(2\alpha - \alpha x_{n-1}) \\
&= 2\alpha - 2\alpha^2 + \alpha^2 x_{n-1} \\
&= 2\alpha - 2\alpha^2 + \alpha^2(2\alpha - \alpha x_{n-2}) \\
&= 2\alpha - 2\alpha^2 + 2\alpha^3 - \alpha^3 x_{n-2} \\
&\vdots
\end{aligned}$$

$$
\begin{aligned}
&= 2\alpha\Big(\sum_{i=0}^{n}(-\alpha)^i\Big) + (-\alpha)^{n+1}x_0 \\
&= 2\alpha\Big(\frac{1-(-\alpha)^{n+1}}{1+\alpha}\Big) + (-\alpha)^{n+1}x_0 \\
&= \Big(x_0 - \frac{2\alpha}{1+\alpha}\Big)(-\alpha)^{n+1} + \frac{2\alpha}{1+\alpha} \\
&= (-1)^{n+1}\Big(x_0 - \frac{2\alpha}{1+\alpha}\Big)\alpha^{n+1} + \frac{2\alpha}{1+\alpha}
\end{aligned}
$$

both systems converge for $|\alpha| < 1$, the first system converges to 0, the second to $2\alpha/1+\alpha$.

4.7 $x_{n+1} = \sqrt{x_n + 2}$

This is a non-linear system.

$$x_{n+1} = \sqrt{x_n + 2}$$

finding the equilibrium points:

$$
\begin{aligned}
x^* &= \sqrt{x^* + 2} \\
(x^*)^2 &= x^* + 2 \\
(x^*)^2 - x^* - 2 &= 0
\end{aligned}
$$

$$\therefore \quad x^* = -1 \quad \text{or} \quad 2$$

we discard $x^* = -1$ as it is not positive. Now we look at the stability of $x^* = 2$:

$$\begin{aligned} f(x) &= \sqrt{x+2} \\ f'(x) &= \frac{1}{2\sqrt{x+2}} \\ f'(2) &= \frac{1}{4} \end{aligned}$$

therefore the equilibrium point $x^* = 2$ is stable.

Bibliography

[1] F. Brauer and C. Castillo-Chavez. *Mathematical Models in Population Biology and Epidemiology*. Texts in Applied Mathematics. Springer New York, 2012.

[2] J.D. Murray. *Mathematical Biology: I. An Introduction*. Interdisciplinary Applied Mathematics. Springer New York, 2002.