

MA 137 — Calculus 1 for the Life Sciences
Discrete-Time Models
More Population Models
(Section 2.3)

Alberto Corso

⟨alberto.corso@uky.edu⟩

Department of Mathematics
University of Kentucky

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From: Simple Mathematical Models with Very Complicated Dynamics

“First-order difference equations arise in many contexts in the biological, economic and social sciences. Such equations, even though simple and deterministic, can exhibit a surprising array of dynamical behaviour, from stable points, to a bifurcating hierarchy of stable cycles, to apparently random fluctuations. There are consequently many fascinating problems, some concerned with delicate mathematical aspects of the fine structure of the trajectories, and some concerned with practical implications and applications.”

Robert M. May, Nature (1976)

When are discrete time models appropriate?

- when studying seasonally breeding populations with non-overlapping generations where the population size at one generation depends on the population size of the previous generation. (Many insects and plants reproduce at specific time intervals or times of the year.)
- when studying populations censused at intervals. (These are the so-called metered models.)

The exponential (Malthusian) growth model described earlier fits into this category: $N_{t+1} = RN_t$.

We denote the population size at time t by N_t , $t = 0, 1, 2, \dots$. To model how the population size at generation $t + 1$ is related to the population size at generation t , we write $N_{t+1} = f(N_t)$, where the function f (updating function) describes the density dependence of the population dynamics.

A recursion of the form given before is called a first-order recursion because, to obtain the population size at time $t + 1$, only the population size at the previous time step t needs to be known.

A recursion is also called a difference equation or an iterated map.

The name **difference equation** comes from writing the dynamics in the form $N_{t+1} - N_t = g(N_t)$, which allows us to track population size changes from one time step to the next.

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

When we study population models, we are frequently interested in asking questions about the long-term behavior of the population:

Will the population size reach a constant value?

Will it oscillate predictably?

Will it fluctuate widely without any recognizable patterns?

In the three examples that follow

- Beverton-Holt Recruitment Model,
- Discrete Logistic Equation,
- Ricker Logistic Equation,

we will see that discrete-time population models show very rich and complex behavior.

Earlier, we discussed the exponential growth model defined by the recursion $N_{t+1} = RN_t$ with $N_0 =$ population size at time 0.

When $R > 1$, the population size will grow indefinitely, if $N_0 > 0$.

Such growth, called **density-independent growth**, is biologically unrealistic. As the size of the population increases, individuals will start to compete with each other for resources, such as food or nesting sites, thereby reducing population growth.

We call population growth that depends on population density **density-dependent growth**.

The Beverton-Holt Recruitment Model

To find a model that incorporates a reduction in growth when the population size gets large, we start with the ratio of successive population sizes in the exponential growth model and assume $N_0 > 0$:

$$\frac{N_t}{N_{t+1}} = \frac{1}{R}.$$

The ratio N_t/N_{t+1} is a constant. If we graphed this ratio as a function of the current population size N_t , we would obtain a horizontal line in a coordinate system in which N_t is on the horizontal axis and the ratio N_t/N_{t+1} is on the vertical axis.

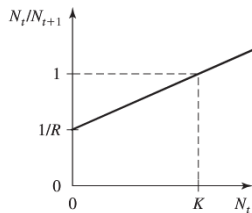
Note that as long as the parent-offspring ratio N_t/N_{t+1} is less than 1, the population size increases, since there are fewer parents than offspring. Once the ratio is equal to 1, the population size stays the same from one time step to the next. When the ratio is greater than 1, the population size decreases.

To model the reduction in growth when the population size gets larger, we drop the assumption that the parent-offspring ratio N_t/N_{t+1} is constant and assume instead that the ratio is an increasing function of the population size N_t . That is, we replace the constant $1/R$ by a function that increases with N_t . The simplest such function is linear.

$$\frac{N_t}{N_{t+1}} = \frac{1}{R} + \frac{1 - \frac{1}{R}}{K} N_t$$

The population density where the parent-offspring ratio is equal to 1 is of particular importance, since it corresponds to the population size, which does not change from one generation to the next.

We call this population size the carrying capacity and denote it by K , where K is a positive constant.



If we solve for N_{t+1} we obtain

$$N_{t+1} = \frac{RN_t}{1 + \frac{R-1}{K}N_t}$$

This recursion is known as the Beverton-Holt recruitment curve.

We have two fixed points when $R > 1$: the fixed point $\hat{N} = 0$, which we call trivial, since it corresponds to the absence of the population, and the fixed point $\hat{N} = K$, which we call nontrivial, since it corresponds to a positive population size.

One can show that, when $K > 0$, $R > 1$, and $N_0 > 0$, we have that

$$\lim_{t \rightarrow \infty} N_t = K.$$

Possible Gen-Ed Project?

The Beverton-Holt stock recruitment model (1957) was used, originally, in fishery models. It is a special case (with $b = 1$) of the following more general model: the Hassell equation.

The Hassell equation (1975) takes into account intraspecific competition, more specifically scramble competition¹, and takes the form

$$N_{t+1} = \frac{R_0 N_t}{(1 + kN_t)^b}.$$

We have under-compensation for $0 < b < 1$;
we have exact compensation for $b = 1$;
we have over-compensation for $1 < b$.

¹In ecology, scramble competition refers to a situation in which a resource is accessible to all competitors.

The Discrete Logistic Equation

The most popular discrete-time single-species model is the discrete logistic equation, whose recursion is given by

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

where R and K are positive constants. R is called the **growth parameter** and K is called the **carrying capacity**.

This model of population growth exhibits very complicated dynamics, described in an influential review paper by **Robert May** (1976).

We first rewrite the model in what is called the **canonical form**

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

where $r = 1 + R$ and $x_t = \frac{R}{K(1 + R)} N_t$.

Advantages

The advantage of this canonical form is threefold:

- (1) The recursion $x_{t+1} = r x_t(1 - x_t)$ is simpler;
- (2) instead of two parameters, R and K , there is just one, r ;
- (3) the quantity $x_t = \frac{R}{K(1 + R)} N_t$ is dimensionless.

What does dimensionless mean? The original variable N_t has units (or dimension) of number of individuals; the parameter K has the same units. Dividing N_t by K , we see that the units cancel and we say that the quantity x_t is dimensionless. The parameter R does not have a dimension, so multiplying N_t/K by $R/(1 + R)$ does not introduce any additional units. A dimensionless variable has the advantage that it has the same numerical value regardless of what the units of measurement are in the original variable.

Reduction to the Canonical Form

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

$$\iff$$

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

$$\iff$$

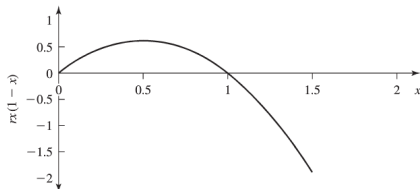
$$\frac{R}{K(1 + R)} N_{t+1} = (1 + R) \frac{R}{K(1 + R)} N_t \left[1 - \frac{R}{K(1 + R)} N_t \right]$$

$$1 < r < 4$$

Notice that we can write $x_{t+1} = r x_t(1 - x_t)$ as $x_{t+1} = f(x_t)$, where the function

$$f(x) = r x(1 - x)$$

is an upside-down parabola, since $r > 1$.



In order to make sure that $f(x_t) \in (0, 1)$ for all t , we also require that $r/4 < 1$, or $r < 4$. In fact, the maximum value of $f(x)$ occurs at $x = 1/2$, and $f(1/2) = r/4$.

Hence we need to impose the assumption that $1 < r < 4$.

Fixed Points of $x_{t+1} = r x_t(1 - x_t)$

We first compute the fixed points of the discrete logistic equation written in standard form.

We need to solve $x = rx(1 - x)$.

Solving immediately yields the solution $\hat{x} = 0$. If $x \neq 0$, we divide both sides by x and find that

$$1 = r(1 - x), \quad \text{or} \quad \hat{x} = 1 - \frac{1}{r}.$$

Provided that $r > 1$, both fixed points are in $[0, 1)$.

The fixed point $\hat{x} = 0$ corresponds to the fixed point $\hat{N} = 0$, which is why we call $\hat{x} = 0$ a trivial equilibrium. When $\hat{x} = 1 - 1/r$ we obtain that $\hat{N} = K$ is the other fixed point.

Long-term Behavior of $x_{t+1} = r x_t(1 - x_t)$

The long-term behavior of the discrete logistic equation is very complicated. We simply list the different cases.

If $1 < r < 3$ and $x_0 \in (0, 1)$, x_t converges to the fixed point $1 - 1/r$.

Increasing r to a value between 3 and 3.449..., we see that x_t settles into a cycle of period 2. That is, for t large enough, x_t oscillates back and forth between a larger and a smaller value.

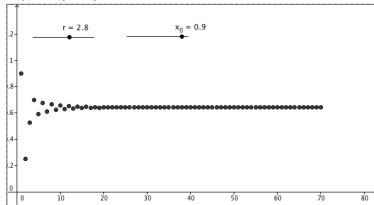
For r between 3.449... and 3.544..., the period doubles: A cycle of period 4 appears for large enough times.

Increasing r continues to double the period: A cycle of period 8 is born when $r = 3.544...$, a cycle of period 16 when $r = 3.564...$, and a cycle of period 32 when $r = 3.567...$

This doubling of the period continues until r reaches a value of about 3.57, when the population pattern becomes **chaotic**.

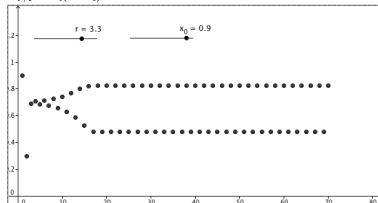
Illustrations Using Applets built with GeoGebra

x_0 = initial population
 $x_{t+1} = rx_t(1 - x_t)$



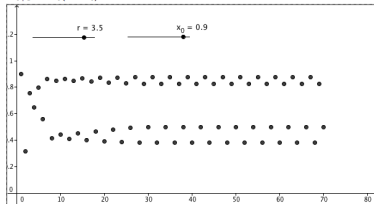
Convergence to the fixed point

x_0 = initial population
 $x_{t+1} = rx_t(1 - x_t)$



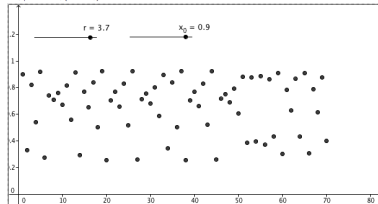
Cycle of period two

x_0 = initial population
 $x_{t+1} = rx_t(1 - x_t)$



Cycle of period four

x_0 = initial population
 $x_{t+1} = rx_t(1 - x_t)$



Chaotic behavior

Ricker Logistic Equation

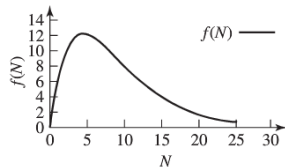
An iterated map that has the same (desirable) properties as the logistic map but does not admit negative population sizes (provided that N_0 is positive) is Ricker's curve. The recursion, called the Ricker logistic equation, is given by

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

where R and K are positive parameters.

As in the discrete logistic model, R is the growth parameter and K is the carrying capacity. The fixed points are $\hat{N} = 0$ and $\hat{N} = K$.

The Ricker logistic equation shows the same complex dynamics as the discrete logistic map [convergence to the fixed point for small positive values of R , periodic behavior with the period doubling as R increases, and chaotic behavior for larger values of R].



Final Comments

- In Section 5.6 we will analyze in greater details and with more tools the stability of the equilibria in the previous models.
- On our class website there are three applets (created with the graphic package GeoGebra) that allow us to visualize the behavior of the previous three models by varying the various parameters. Please use them! These applets require the latest version of Java.
- What we described in Section 2 could be a great source for your Final project (which is due on December 4) both in terms of substantial mathematical component and adequate biological and/or medical content. Please start thinking about a possible project!