# Grade 11/12 Math Circles
February 28, March 6, 2024
Population Modeling

Population Dynamics

Population dynamics refers to how populations change over time and space. This could mean a population spreading out to new areas or disappearing from places it used to be found. Even if a population stays in the same areas, its size might go up or down, stabilize, or follow a regular pattern of change.

Population ecologists use different mathematical methods to study how populations change over time in terms of their sizes. Some of these methods show how populations grow without limits, while others consider limits imposed by factors like limited resources. By using these mathematical models, scientists can accurately describe how populations change and even predict what might happen in the future!
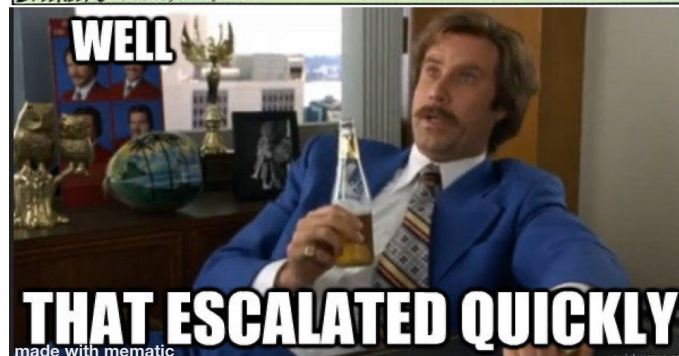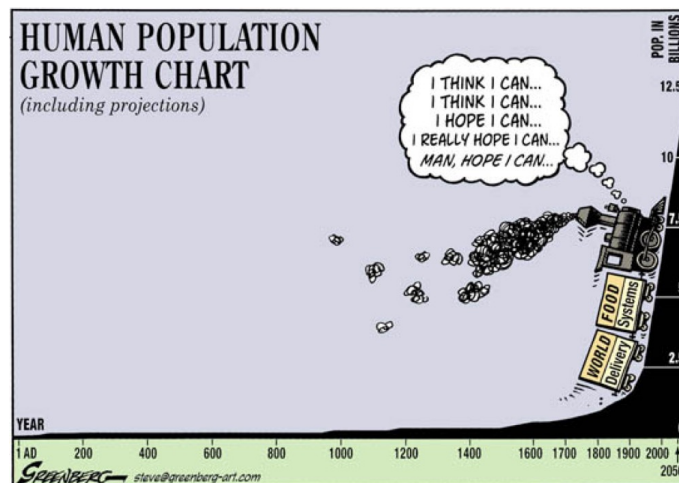
Geometric Growth

To start, let's think about what a "population growth rate" really means.

$$\text{growth rate} = \frac{\text{change in population}}{\text{change in time}} = \frac{\text{births} - \text{deaths}}{\text{change in time}} = \text{birth rate} - \text{death rate}$$

Now let's introduce some variables:

- $N(t) =$ the number of individuals at time t,

- $\Delta t =$ change in time,

- $\Delta N = N(t + \Delta t) - N(t) =$ change in population size,

- birth rate $B = bN$, per capita birth rate b multiplied by the population size N,

- death rate $D = dN$, per capita death rate d multiplied by the population size N.

So we end up with

$$\text{growth rate} = \frac{\Delta N}{\Delta t} = \frac{N(t + \Delta t) - N(t)}{\Delta t} = bN - dN = (b - d)N \equiv r_d N, \tag{1}$$

in which $r_d \equiv b - d$ is the net per capita growth rate. Most organisms live in a seasonal environment, so we usually consider changes in population every year ($\Delta t = 1$ year). Eq. (1) becomes

$$N(t + 1) - N(t) = r_d N(t),$$

or

$$N(t + 1) = N(t) + r_d N(t) = (1 + r_d)N(t).$$

> **Stop and Think**
>
> If the initial population $N(0) = N_0$ (called "N-naught"), what is the population size after $1/2/3$ years? Can you come up with a formula that tells the population size after n years?

In general, we obtain the formula for the population size in Year t with an initial size N_0

$$N(t) = (1 + r_d)^t N_0. \tag{2}$$

We notice that

- If $r_d > 0$ (i.e. birth rate is larger than death rate), the population is growing;

- If $r_d = 0$, the population stays the same;

- If $-1 \le r_d < 0$, the population is shrinking (dies out when $r_d = -1$).

Stop and Think

r_d is guaranteed to be no less than -1, why?

Example 1

Suppose there were 100 rabbits in a region back in 2020. If on average the population grows by 60% every year, how many rabbits would there be in 2023?

Solution:

According to the problem, we can set 2020 as our initial time point, $t = 0$. So $N(0) = 100$. We also know that $r_d = 0.6$. By Eq. (2), we have

$$N(3) = (1 + r_d)^3 N_0 = (1 + 0.6)^3 (100) \approx 410 \text{ rabbits.}$$

Exercise 1

In fact, rabbits might produce new babies every month. If instead, the population grows by $60\%/12 = 5\%$ every month, how many rabbits would there be in 2023?

Exponential Growth

Average vs. Instantaneous Rate of Change

The birth/death/growth rates mentioned above represent "average rates". For instance, if there are 120 births in a year, it doesn't necessarily mean they occur uniformly throughout the year. It's possible that 80 births happen in the first half-year and 40 in the second half. When looking at births per quarter, there could be 20 in the first, 60 in the second, 30 in the third, and 10 in the fourth. Such analysis can extend to births per month or even per day, offering a finer understanding of population dynamics.

Now instead of $\Delta t = 1$ year or 1 month, let's assume $\Delta t = 1$ hour, 1 minute, or even 1 second! By setting this Δt smaller and smaller, eventually, we end up with

$$\lim_{\Delta t \to 0} \frac{N(t + \Delta t) - N(t)}{\Delta t} = \lim_{\Delta t \to 0} \frac{\Delta N}{\Delta t} = \frac{dN}{dt}.$$

If you have not yet seen this in your high school math textbook, the notation $\frac{dN}{dt}$ is called the "derivative", which tells you the slope of the tangent line to the graph of the function at a specific point. We take the limit of Eq. (1) and obtain the following (differential) equation:

$$\lim_{\Delta t \to 0} \frac{N(t + \Delta t) - N(t)}{\Delta t} = \frac{dN}{dt} = rN, \tag{3}$$

where r is the "instantaneous" per capita growth rate. Note that we use r to distinguish it from the discrete-time growth rate r_d. This might seem a bit intimidating, but it just means that the derivative of a function is a function of itself!

- If $\frac{dN}{dt} = 0$, it means that the derivative is always 0, so $N(t)$ is a horizontal line.

- If $\frac{dN}{dt} = r > 0$, it means that the derivative is always some fixed positive value, so $N(t)$ linearly increases.

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- If $\dfrac{dN}{dt} = rt$, $r > 0$, it means that the derivative is a function of time t. When t gets larger, the derivative gets larger, and $N(t)$ increases faster.

- If $\dfrac{dN}{dt} = rN$, $r > 0$, it means that the derivative is a function of the function itself. When $N(t)$ gets larger, the derivative gets larger, $N(t)$ increases faster, and the derivative increases even faster!

This model is more realistic for a population that changes over a continuous time scale. Solving Eq. (3) is beyond the scope of these lectures. For now, we are simply provided that the solution is

$$N(t) = N_0 e^{rt}, \tag{4}$$

given the initial population $N(0) = N_0$. Here, e is the base of natural logarithms ($e \approx 2.71828$).

Stop and Think

Although solving Eq. (3) is challenging for us, we can actually check if $N(t) = N_0 e^{rt}$ is indeed a solution to Eq. (3).

If you have not learned how to calculate derivatives, try with the following rules (we use $f'(x)$ to denote the derivative of $f(x)$):

(1) The derivative of $f(x) = kx$ is $f'(x) = k$.

(2) The derivative of $f(x) = e^x$ is $f'(x) = e^x$.

(3) The derivative of $cf(x)$ is $cf'(x)$.

(4) The derivative of $f(g(x))$ is $f'(g)g'(x)$ ($f'(g)$ means treating $g = g(x)$ as a variable and calculating the derivative of f with respect to g).

> **Example 2**
>
> Suppose there were 100 rabbits in a region back in 2020. If $r = 0.6$ individuals/individual/year was the per capita growth rate and we assumed that the population grew continuously, how many rabbits would there be in 2023?
>
> *Solution:*
>
> Similar to Example 1, we set 2020 as our initial time point, so $N(0) = 100$. Therefore, by Eq. (4), we have
> $$N(3) = N_0 e^{3r} = 100 e^{3(0.6)} = 100 e^{1.8} \approx 604 \text{ rabbits.}$$

Logistic Growth

In a geometric growth model or an exponential growth model, it is assumed that both the birth rate and death rate remain constant. However, if $b > d$ is always true, then the population will grow indefinitely, which is clearly unrealistic. As the population grows, there will be a shortage of food and habitat; there will be greater risks of predation and disease outbreaks. Therefore, when the population grows, the population should grow at a lower rate, or even shrink. The logistic growth model is density-dependent, which means that the growth rate is affected by the population size.

Discrete-time Model

Let's first look at the discrete-time model, the population growth rate is given by

$$\frac{N(t + \Delta t) - N(t)}{\Delta t} = r_d N(t) \left(1 - \frac{N(t)}{K} \right). \tag{5}$$

Here, we introduce a new term, carrying capacity K, which is defined as the largest population that can be supported indefinitely, given the resources available in the environment. The term $(1 - N(t)/K)$ represents density dependence.

> **Stop and Think**
>
> Comparing Eq. (5) with Eq. (1), we can consider $r_d(1 - N(t)/K)$ as the growth rate in the logistic model. What does this growth rate tell us?

From Eq. (5), we can observe the followings:

- When $N(t)$ is much less than K, $N(t)/K \approx 0$ and $1 - N(t)/K \approx 1$, Eq. (5) essentially becomes Eq. (1). In other words, when the population size is much smaller than the carrying capacity, resources are abundant, and the population will experience geometric growth.

- When $N(t)$ increases, $1 - N(t)/K$ decreases. So a larger population results in a lower growth rate.

- When $N(t) > K$, $N(t)/K > 1$ and $1 - N(t)/K < 0$. When the population grows beyond the carrying capacity, the growth rate becomes negative, indicating that the population will shrink.

If we let $\Delta t = 1$ in Eq. (5), we obtain a function that describes the population size at the next time point $t + 1$:

$$N(t + 1) = N(t) + r_d N(t) \left(1 - \frac{N(t)}{K}\right). \tag{6}$$

A very interesting fact about Eq. (6) (sometimes referred to as "logistic map") is that the population growth trajectories are different with different values of r_d.

Let's use Excel to plot population growth trajectories with $N_0 = 10$, $K = 100$, and we vary $r_d = 0.8, 1.5, 2.2, 2.5, 2.7, 2\sqrt{2}$.
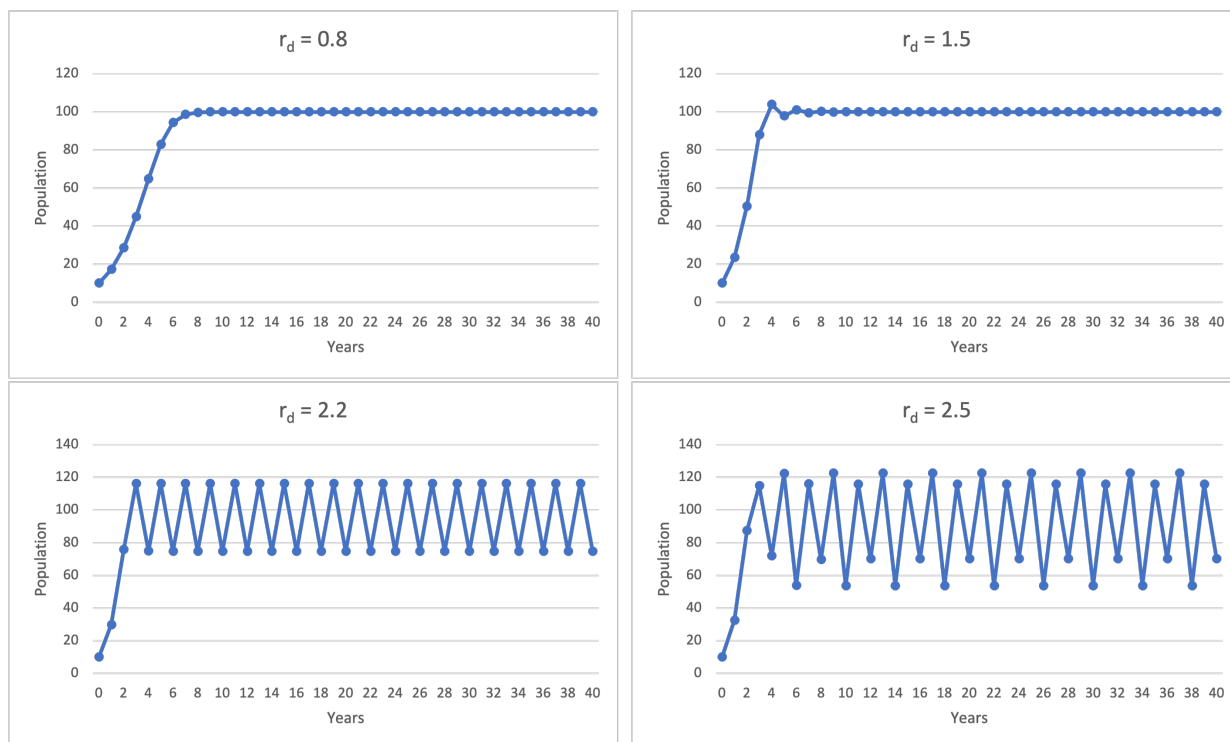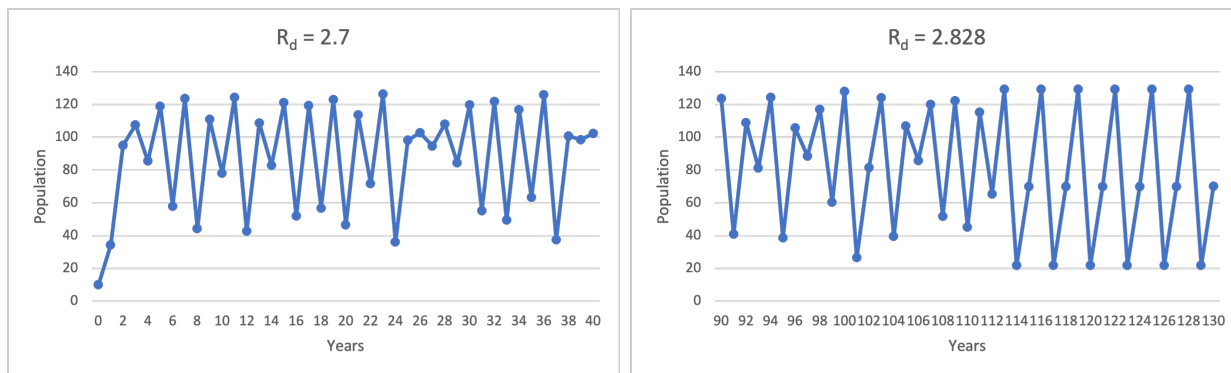
- When $r_d = 0.8$, the population asymptotically approaches the carrying capacity.
- When $r_d = 1.5$, the population overshoots the carrying capacity and exhibits damped oscillations.
- When $r_d = 2.2$, the population eventually oscillates between 2 values.
- When $r_d = 2.5$, the population eventually oscillates among 4 values.
- When $r_d = 2.7$, the population trajectory does not have a specific pattern. (Chaos!)
- When $r_d = 2\sqrt{2} \approx 2.828$, the population eventually oscillates among 3 values. (Hah?)

Chaos is very sensitive to initial conditions. Slightly changing the initial population size N_0 would result in very distinct results. Let's plot the population trajectories with $N_0 = 10, 11$, $K = 100$, and $r_d = 2.7$.
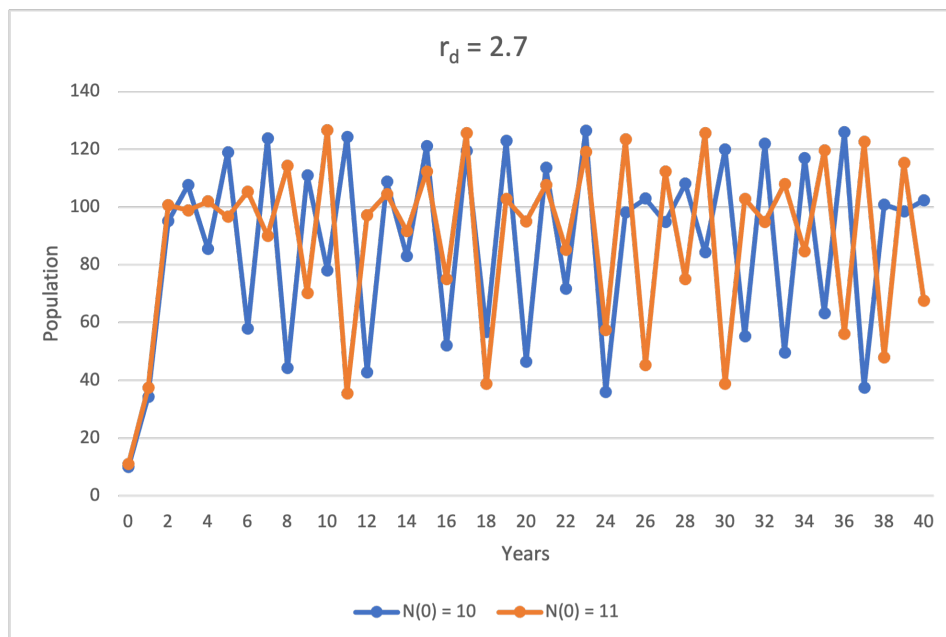
Cobwebbing

Let's modify Eq. (6)

$$
\begin{aligned}
N(t+1) &= N(t) + r_d N(t)\left(1 - \frac{N(t)}{K}\right) \\
&= N(t)\left[1 + r_d\left(1 - \frac{N(t)}{K}\right)\right] \\
&= N(t)\left[(1 + r_d) - \frac{N(t)}{K/r_d}\right] \\
&= (1 + r_d)N(t)\left[1 - \frac{N(t)}{K\left(\frac{1}{r_d} + 1\right)}\right] \equiv pN(t)\left(1 - \frac{N(t)}{q}\right) \quad (7)
\end{aligned}
$$

if we let $p = 1 + r_d$ and $q = K(1/r_d + 1)$. One way to investigate the dynamics of Eq. (7) graphically is to use "cobwebbing", through:

(1) Rewrite Eq. (7) as $N(t+1) = f(N(t))$, so the function $f(N) = pN(1 - N/q)$.

(2) Pick an initial value N_0, draw a vertical line to $f(N)$ curve to find $f(N_0)$.

(3) Draw a horizontal line to $N(t+1) = N(t)$ diagonal to find $N(t_1) = f(N_0)$.

(4) Draw a vertical line to $f(N)$ curve to find $f(N_1)$.

(5) Draw a horizontal line to $N(t+1) = N(t)$ diagonal to find $N(t_2) = f(N_1)$.

(6) Repeat (4) and (5).

Here is an example where we set $p = 1 + r_d = 2$, $q = K(1/r_d + 1) = 1$, and $N_0 = 0.1$. Note that

- the horizontal axis is $N(t)$,

- the vertical axis is $N(t+1)$,

- the red line is $N(t+1) = N(t)$, and

- the blue curve is $N(t+1) = f(N) = 2N(t)(1 - N(t))$.
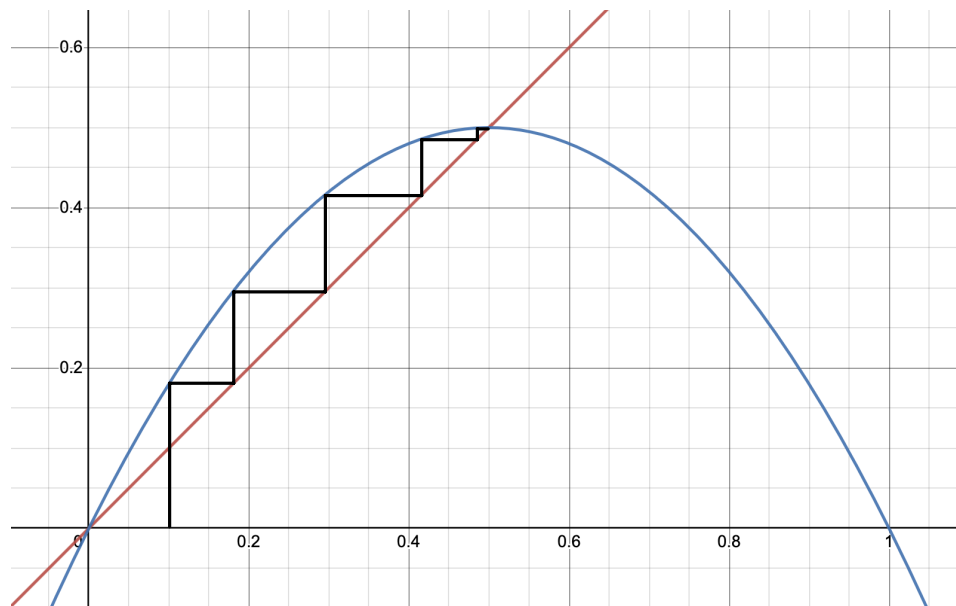
We found that eventually, the trajectory ends up at the point where two curves intersect, $N(t+1) = N(t) = f(N(t))$. Such a point $\bar{N} = f(\bar{N})$ is called the "fixed point". Now let's draw the trajectory where we start with a different initial value $N_0 = 0.05$:
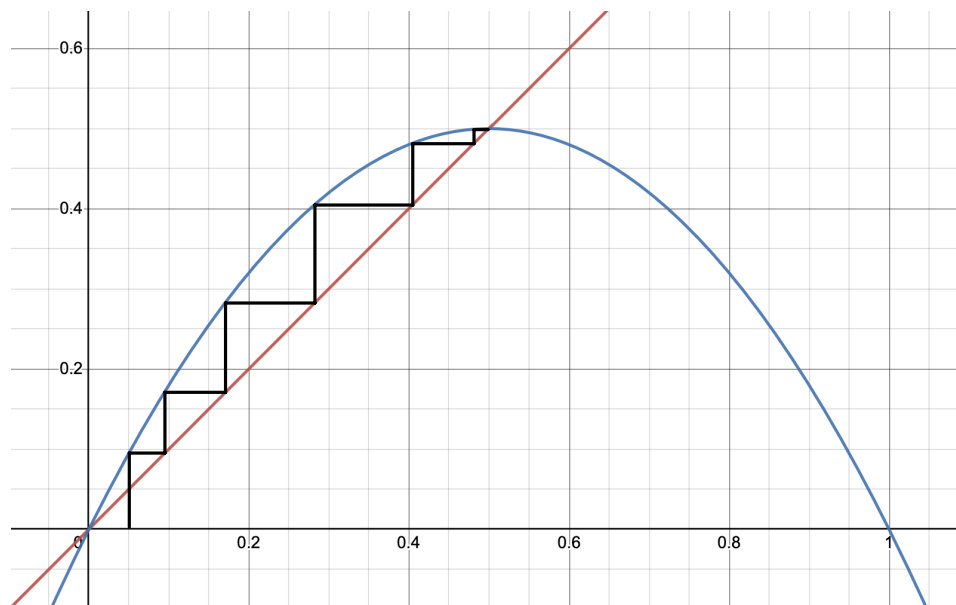
We should convince ourselves that for any initial condition, the trajectory approaches the fixed point $\bar{N}$.

> **Exercise 2**
>
> Using the diagrams on the Appendix page, draw the cobweb diagrams for $N(t+1) = pN(t)(1 - N(t))$ with the following values of p and $N_0 = 0.1$. Find where each trajectory ends up. Discuss what trajectory each cobweb diagram stands for.
>
> (a) $p = 2.4$
>
> (b) $p = 3.2$
>
> (c) $p = 4.0$

Continuous-time Model

Similarly, we can take the limit of Eq. (5) and get a differential equation for the continuous-time model:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{8}$$

whose solution is

$$N(t) = \frac{K}{1 + Ce^{-rt}}, \tag{9}$$

with $C = \dfrac{K}{N_0} - 1$ if the initial population $N(0) = N_0$. Unlike the discrete-time model, if $N_0 < K$, no matter what growth rate r is, the population will grow and approach the carrying capacity eventually. Here, we plot the population trajectories with $N_0 = 5$, $K = 10000$, and $r = 0.8/1.5/2.2/2.5/2.9$.

$N_0 = 5$, $K = 10000$

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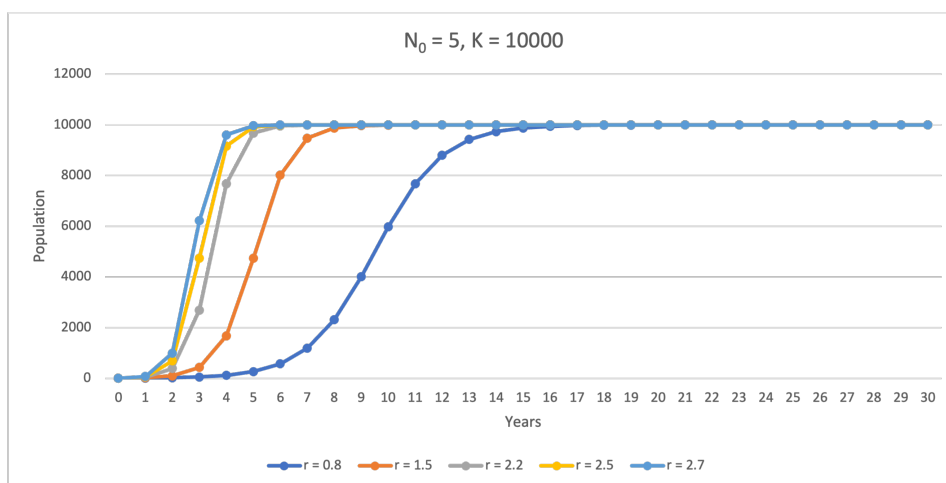
Exercise 3

Scientists found that there is usually a minimal threshold value for the species to survive. Such a phenomenon, called "Allee Effect", changes Eq. (8) to

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

Analyze the equation by considering

(a) what will happen to $N(t)$ if $A < N_0 < K$?

(b) what will happen to $N(t)$ if $0 < N_0 < A$?

Life Tables

So far, we limited our prediction of populations by assuming that all individuals in a population are identical. However, many plants and animals have different life stages in their populations. For example, for animals, the stages could include egg, juvenile, and adult. Life stages could also purely depend on age (e.g. one year old, two years old, etc.). By using a life table, we are able to consider different rates of reproduction (producing babies), growth, and death. For example, a typical life table could look like:

	Egg	Juvenile	Adult
Egg	0	50	300
Juvenile	0.02	0.25	0
Adult	0	0.08	0.5

where stages in each row are the "to" stages and stages in each column are the "from" stages. For example, 50 in the first row and second column represents the rate of change from juveniles to eggs next year. From now on, we refer to the entry at row i and column j as a_{ij}. For example, $a_{12} = 50$.

Stop and Think

What does the number in each box mean? Why are there some zeros? Can those zeros be positive numbers?

- The first row represents the reproduction rates. $a_{11} = 0$ since eggs cannot produce babies. $a_{12} = 50$ means that each juvenile can produce 50 new babies on average each year; $a_{13} = 300$ means that each adult can produce 300 new babies on average each year.

- The diagonal represents the proportions surviving and remaining in the same stage. $a_{11} = 0$ since eggs will either grow into juveniles or die after a year. $a_{22} = 0.25$ means that 25% of the juveniles will survive and remain as juveniles next year; $a_{33} = 0.5$ means that 50% of adults will survive and remain as adults next year.

- The sub-diagonal ($a_{21} = 0.02$ and $a_{32} = 0.08$) represents the proportions surviving and advancing to the next stage. In other words, 2% of eggs will survive and become juveniles, and 8% of juveniles will survive and become adults. Adult is the final stage, so they either survive and remain as adults, or die.

- Eggs cannot directly grow to adults, so $a_{31} = 0$. Adults cannot go back to the juvenile stage, so $a_{23} = 0$.

Stop and Think

From the above table, what are the death rates for each stage?

Exercise 4

Now let's look at a life table that purely depends on age. Assume we know that the average life span of an animal is 4 years.

Age	0	1	2	3	4
0	0	0	5	10	50
1	0.01	0	0	0	0
2	0	0.25	0	0	0
3	0	0	0.25	0	0
4	0	0	0	0.4	0

(a) At what age does this species start to give birth to babies?

(b) Explain why the entries below the sub-diagonal (bottom left) are all zeros.

(c) Explain why the diagonal is all zeros.

Matrices

Before moving on to the applications of life tables, let's introduce (or review) the idea of matrices. Simply speaking, a matrix is a rectangular table of numbers arranged in rows and columns, such as

$$A = \begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix}, B = \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix}, C = \begin{bmatrix} 1 & 2 \end{bmatrix}, D = \begin{bmatrix} 1 \\ 2 \end{bmatrix}.$$

We call a matrix with m rows and n columns as an $m \times n$ (m-by-n) matrix. For example, A and B are both 2×2, C is 1×2, and D is 2×1. We define the following operations (that are necessary for this topic):

- For matrices of the same size (same number of rows AND same number of columns), the sum of matrices is the sum of entries of each matrix. For example,

$$A + B = \begin{bmatrix} 1+5 & 2+6 \\ 3+7 & 4+8 \end{bmatrix} = \begin{bmatrix} 6 & 8 \\ 10 & 12 \end{bmatrix}.$$

We cannot add A and C, nor can we add A and D!

- Multiplying a matrix with a scalar (a number) is multiplying every entry of the matrix with that scalar. For example,

$$2A = \begin{bmatrix} 2 \times 1 & 2 \times 2 \\ 2 \times 3 & 2 \times 4 \end{bmatrix} = \begin{bmatrix} 2 & 4 \\ 6 & 8 \end{bmatrix}, 2C = \begin{bmatrix} 2 \times 1 & 2 \times 2 \end{bmatrix} = \begin{bmatrix} 2 & 4 \end{bmatrix}.$$

- Multiplication of two matrices is defined if and only if the number of columns of the left matrix is the same as the number of rows of the right matrix. For example,

  – we can do both AB and BA;

  – we can do AD but not DA;

  – we can do CA but not AC.

If matrix M is $p \times q$ and matrix N is $q \times r$, then the matrix multiplication MN is $p \times r$. If we let m_{ij} be the entry in the i-th row and j-th column of M, n_{ij} be the entry in the i-th row and j-th column of N, $[MN]_{ij}$ be the entry in the i-th row and j-th column of MN, then

$$[MN]_{ij} = m_{i1}n_{1j} + m_{i2}n_{2j} + \cdots + m_{iq}n_{qj}.$$

Matrix multiplication also satisfies the associativity rule $(MN)K = M(NK)$.

Exercise 5

For the above matrices A, B, C, and D, calculate

(a) AB

(b) BA

(c) AD

(d) CA

Projecting a Population Matrix through Time

Suppose we have a life table written in a matrix

$$
A = \begin{bmatrix} 0 & 50 & 300 \\ 0.02 & 0.25 & 0 \\ 0 & 0.08 & 0.5 \end{bmatrix},
$$

and the initial population of each stage is also stored in a matrix

$$
N(0) = N_0 = \begin{bmatrix} 1000 \\ 50 \\ 10 \end{bmatrix}.
$$

Let's calculate $AN(0)$:

$$
AN(0) = AN_0 = \begin{bmatrix} 0 & 50 & 300 \\ 0.02 & 0.25 & 0 \\ 0 & 0.08 & 0.5 \end{bmatrix} \begin{bmatrix} 1000 \\ 50 \\ 10 \end{bmatrix} = \begin{bmatrix} 0 \times 1000 + 50 \times 50 + 300 \times 10 \\ 0.02 \times 1000 + 0.25 \times 50 + 0 \times 10 \\ 0 \times 1000 + 0.08 \times 50 + 0.5 \times 10 \end{bmatrix} = \begin{bmatrix} 5500 \\ 32.5 \\ 9 \end{bmatrix}.
$$

What does the result mean?

- $0 \times 1000 + 50 \times 50 + 300 \times 10$ is the number of new eggs produced by all juveniles and adults in the first year.

- $0.02 \times 1000 + 0.25 \times 50 + 0 \times 10$ is the number of eggs that survive and grow into juveniles plus the number of juveniles that survive and remain as juveniles in the first year.

- $0 \times 1000 + 0.08 \times 50 + 0.5 \times 10$ is the number of juveniles that survive and grow into adults plus the number of adults that survive and remain as adults in the first year.

Therefore, $AN(0)$ is the population of each stage after one year, $N(1)$. Similarly,

$$N(2) = AN(1) = A(AN_0) = (AA)N_0 = A^2 N_0$$

is the population after two years. So we obtain

$$N(t+1) = AN(t),$$

and thus

$$N(t) = A^t N_0 = (\underbrace{AA \cdots A}_{t \text{ times}})N_0.$$

Exercise 6

The above matrix

$$A = \begin{bmatrix} 0 & 50 & 300 \\ 0.02 & 0.25 & 0 \\ 0 & 0.08 & 0.5 \end{bmatrix}$$

can be written as the sum of two matrices, $A = R + S$, where R only contains reproduction rates and S only contains survival rates. Write down R and S, use the same initial population matrix N_0, and do the following:
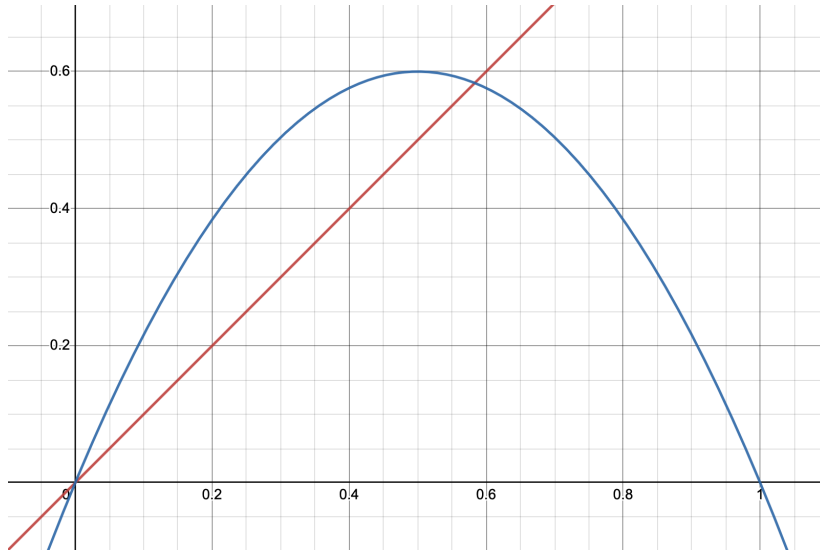
(a) Calculate RN_0 and explain what the result represents.

(b) Calculate SN_0 and explain what the result represents.

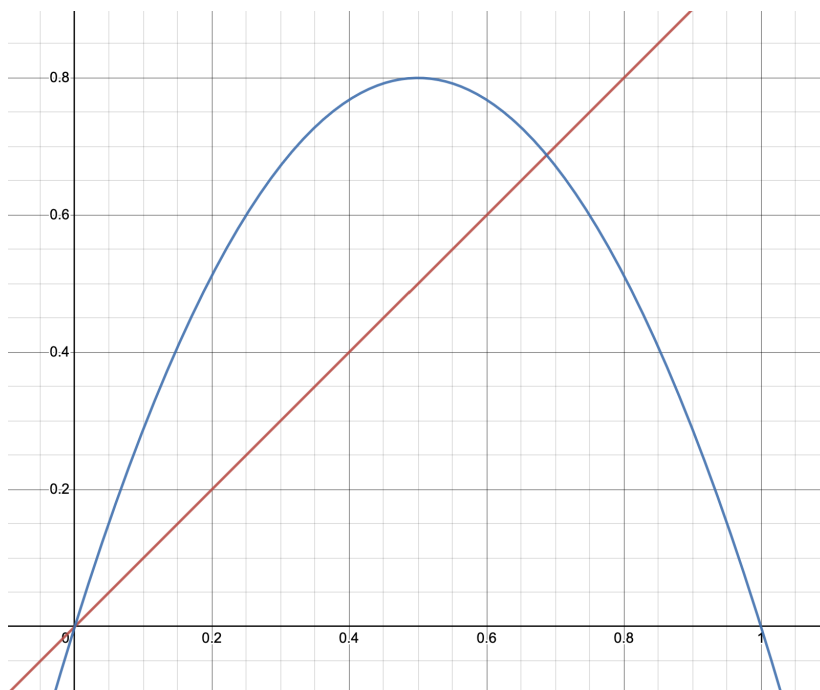(c) Sum up RN_0 and SN_0 and compare with AN_0 we just calculated. What do you find?

Appendix

Using the following diagrams, draw the cobweb diagrams for $N(t+1) = pN(t)(1 - N(t))$ with the following values of p and $N_0 = 0.1$ (10 iterations).

(a) $p = 2.4$

(b) $p = 3.2$

(c) $p = 4.0$