1. Population dynamics of rabbits and foxes
(a) A simple Lotka–Volterra Model

We have discussed in detail the Lotka–Volterra model for predator-prey relationships

\[
\frac{dN_{\text{prey}}}{dt} = +R_{\text{prey},o}N_{\text{prey}}(t) - \gamma N_{\text{prey}}(t) N_{\text{pred}}(t)
\]

\[
\frac{dN_{\text{pred}}}{dt} = \epsilon \gamma N_{\text{prey}}(t) N_{\text{pred}}(t) - R_{\text{pred},o} N_{\text{pred}}(t)
\]

but how does it really work in practice? Consider an example of rabbits and foxes. First, we need to consider reasonable parameters — the following are a starting point:

- \( R_{o,\text{prey}} = 0.04 \)
- \( R_{o,\text{pred}} = 0.2 \)
- \( \gamma = 0.0005 \)
- \( \epsilon = 0.1 \)

Assume that the time units are all in days, and that the populations are numbers of individuals per square kilometer.

1. What is the doubling time of rabbits without predation, and the death rate of foxes?
2. Explain whether or not these values are biologically reasonable.
3. Explain the meaning of the terms \( \gamma \) and \( \epsilon \) and consider their values — do these make sense (consider what conditions will lead to a balance of growth/death in each population)?
4. Simulate this system using the same Forward Euler method that we used in the first project; when we have two variables (for example, \( x \) and \( y \)), we simply use the Forward Euler update rule for both of them. That is, at each time step, we set:

\[
x(t + \Delta t) = x(t) + \frac{dx}{dt}(\Delta t)
\]

\[
y(t + \Delta t) = y(t) + \frac{dy}{dt}(\Delta t)
\]

Use initial populations of 200 rabbits and 50 foxes per km\(^2\), and a time step of 0.01 days. Plot the two populations versus time on the same graph, as well as versus each other (on another graph).

5. Determine how the rabbit and fox populations will vary over one year.
6. Discuss the observed behavior of the populations. What is the range in each population? Do you notice anything odd?
7. Repeat your calculations with initial populations of 5000 rabbits and 100 foxes per km\(^2\), and discuss how the behavior of the system changes.
8. Do the same for 4000 rabbits and 80 foxes per km\(^2\). What does this result tell you about the system?
(b) Extending the Lotka–Volterra Model

In class, we have discussed some of the limitations of the Lotka–Volterra model, and how we might begin to address these. Consider two different models, both using the Lotka–Volterra model (with the original set of parameters) as a starting point:

1. A model with unrestricted prey growth replaced by a logistic equation-based model. That is, replacing $\alpha$ with:
   \[ A(U) = \alpha \left( 1 - \frac{U}{K} \right) \]

2. A model with restricted prey growth, as in (1), and with a predator response that saturates at high prey density, using the Holling’s disk equation. That is, replacing $\alpha$ as above, and replacing $\gamma$ with:
   \[ \Gamma(U) = \frac{sU}{1 + shU} \]

Set $K = 10,000$, $s = \gamma$ and $h = 0.2$.

1. Briefly explain what these values mean, in a biological context (Hint: consider how the underlying equations behave at very low or very high populations).
2. For each case, make a plot of the populations versus time and the populations versus each other, in this case for a time span of at least three years.
3. Describe how each trajectory differs from the original Lotka–Volterra model, and from each other, and give a suggested rationale for why these differences arise.
4. For each case, explain whether you expect there to be any stationary points in the system, and whether you expect them to be stable or unstable (or neither). Give an estimate of where these points are located.
2. Coexistence

In some experiments on competition between two species of hydra, it was found that coexistence was only possible if a fraction of the population of each species was removed at regular intervals. A model for the system with this experimental manipulation is given by

\[
\frac{dN_1}{dt} = \frac{r_1 N_1}{K_1}(K_1 - m_1 - N_1 - aN_2),
\]

\[
\frac{dN_2}{dt} = \frac{r_2 N_2}{K_2}(K_2 - m_2 - bN_1 - N_2). \tag{1}
\]

Answer questions from (1) to (6) analytically using a set of parameters: \( r_1, r_2 > 0, K_1 = 100, K_2 = 90, a = 1.2, b = 0.8, m_1 = 2 \) and \( m_2 = 10 \).

(1) Define null clines for each variable \((N_1, N_2)\).
(2) How many stationary points exist?
(3) Draw the set of null clines in 2D space of \(N_1\) and \(N_2\). How many pieces of region do you see in the first quadrant?
(4) Indicate the general direction of motion (1) along the null clines and (2) in the sub-divided regions by null clines using arrows.
(5) Define whether the each stationary point is a stable or unstable stationary point.
(6) Now, show that stable coexistence occurs for this system if \( K_1 = 100, K_2 = 90, a = 1.2, b = 0.8, m_1 = 2 \) and \( m_2 = 10 \) but not for the corresponding system with \( m_1 = m_2 = 0 \).

Assignment Source: AMS333, Professor Thomas McCarthy, Stony Brook University
I. Population Dynamics of Rabbits and Foxes:

A Simple Lotka – Volterra Model:

In this project I will look at the dynamic relationship between rabbit and fox populations. Using the given values, I evaluate the doubling time of the rabbit growth rate, or rather the time needed to double the rabbit population in the absence of predators, to be \( \frac{\ln 2}{0.04} \), or approximately 17.3 days. The doubling time of the fox death rate, or rather the time taken to halve the population of foxes in the absence of prey, is \( \frac{\ln 2}{0.2} \), or approximately 3.5 days. In the absence of one another, rabbits and foxes either reproduce or die off, respectively, exponentially rather than following the Lotka – Volterra model (LV, henceforth).

Neither of these doubling times seem biologically reasonable. Exponential models do not take any real world variables into account, such as the environmental capacities of a system or the ability of predators to seek other types of prey in the absence of, say, rabbits. As far as being numerically reasonable, these values do not make sense either. The gestation period of a female rabbit is approximately 28-30 days, which immediately runs counter to the computed doubling time of roughly half that. The 3.5 day figure of the ‘halving time’ for the fox population does not seem reasonable either. In my opinion, 3.5 days is not long enough for one animal to starve to death let alone half a population. For these reasons, I believe that the respective doubling times do not make biological sense. However, using the LV model, the per capita growth rates of both populations make much more sense because they take the interplay between both species into account.

In the LV model, \( y \) is the predation constant, which describes the level of predatory fitness a species or organism has upon its prey. \( e \) is a constant that represents the relationship between predator growth and predation rate. Deriving the stationary points from the LV model (see reverse) yields a non-trivial point at \( \left( \frac{\beta}{e y}, \frac{a}{y} \right) \) which, using the given values, correspond to a system containing 4000 rabbits and 80 foxes. These populations (in one km\(^2\)), according to the LV model, represent a point of potential coexistence where the growth and death of each species balances the other.

Using values of 200 rabbits and 50 foxes per km\(^2\) as a starting point and a \( \Delta t \) of 0.01 days, the populations seem to have two distinct fluctuations in one year. At around days 117 and 260, the prey population hits a maximum value of approximately 18400; at days 139 and 282 the population hits a minimum value of approximately 190. The predator population hits a maximum of approximately 1130 on days 123 and 266, and an odd minimum result of approximately 0.0008 on days 78 and 220. As we can see, predators are driven (almost) to extinction, according to this model, at certain points in the year when prey populations are low. Conversely, prey density is decimated at high levels of predator population. The interplay of these two interactions are what cause these fluctuations.
Fig 2: Derivation of the non-trivial stationary point:

\[
\frac{dN_{\text{prey}}}{dt} = +R_{\text{prey},o}N_{\text{prey}}(t) - \gamma N_{\text{prey}}(t)N_{\text{pred}}(t)
\]

\[
\frac{dN_{\text{pred}}}{dt} = \epsilon\gamma N_{\text{prey}}(t)N_{\text{pred}}(t) - R_{\text{pred},o}N_{\text{pred}}(t)
\]

\[U = N_{\text{prey}}(t), V = N_{\text{pred}}(t), \alpha = R_{\text{prey},o}, \beta = R_{\text{pred},o}\]

\[
\therefore
\frac{dU}{dt} = \alpha U - \gamma UV \quad \frac{dV}{dt} = \epsilon\gamma UV - \beta V
\]

Scaling the two equations to each other by \(\epsilon\) and adding:

\[
\epsilon aU - \beta V = 0 \iff \begin{cases} (\epsilon) aU - \gamma UV = 0 \\ \epsilon\gamma UV - \beta V = 0 \end{cases}
\]

\[
\epsilon aU - \beta V = 0 \implies \epsilon aU = \beta V \implies V = \frac{\epsilon aU}{\beta}
\]

\[
\frac{dU}{dt} = \alpha U - \gamma U \left( \frac{\epsilon aU}{\beta} \right) = 0 \implies \alpha U \left( 1 - \frac{\epsilon aU}{\beta} \right) \to U = 0 \implies U = \frac{\beta}{\epsilon\gamma}
\]

\[
V = \frac{\epsilon aU}{\beta} \implies V = \frac{\epsilon a\beta}{\beta\epsilon\gamma} \implies V = \frac{a}{\gamma}
\]

There are 2 stationary points, one is non-trivial:

\[(U, V) = \left( \frac{\beta}{\epsilon\gamma}, \frac{a}{\gamma} \right)\]
The above plots show the behavior of the systems, versus time and versus each other, over the course of one year. We can see that at prey and predator populations of 5000 and 100, respectively, the fluctuations become less ‘violent’, and the behavior of the system varies less. At prey and predator populations of 4000 and 80, respectively, we can see that the fluctuations versus time have ceased and the behavior of the system is that of a single stationary point. This corresponds to the above statement about the non-trivial stationary point from the LV model, where it was found that populations of 4000 and 80 would lead to stable coexistence due to the balance of growth and death in both species.

**Extending the Lotka – Volterra Model**

The LV model, by itself, is a poor prediction tool for evaluating predator – prey dynamics. However, with adjustments it can be made more precise. By adding terms or new equations to the model, that represent some biological process, we can use the underlying framework of the equation to make better, more appropriate predictions.
The given values $K = 10,000$, $s = \gamma$, and $h = 0.2$ each represent constants that are required by their individual equations to make the LV model more precise. $K$ represents the carrying capacity of a given ecosystem, while $h$ represents the time occupied for an individual during a kill. The constant $s$ is the same as $\gamma$, the predation constant or level of predatory fitness of one species upon its prey. In the logistic model we can see that at high prey values ($U$) that exceed $K$, there is a negative impact on the prey population such that it declines toward the value of $K$. Likewise in the Hollings disc equation, there is a level of ‘saturation’ that occurs when $U$ is large. The best explanation for this is that when there are many prey in the system (high $U$), such that predator’s occupied time is low per kill, predators respond by leveling out their level of predatory fitness artificially – they don’t need to work as hard anymore – and the new predation function approaches a new, higher, constant value. This has a stabilizing effect on the system, greater than that of just the incorporation of the logistic function.
As we can see from the above plots, the implementation of these terms leads to oscillations that approach some stable value. Contrasting this to the simple LV model, where only if starting with specific population conditions did we experience stability, we can see that these systems are self-regulating. These represent more biologically reasonable results because most biological systems that exist tend towards stability, or if interrupted by some exterior variables – extinction. In the first case, fig 5.1, we can see the implementation of the logistic equation replacement for prey growth. The most striking difference between this and the simple LV model is that the behavior spirals towards a stable point at approximately 4000 rabbits and 50 foxes. In the second case, fig. 5.2, we again see this spiraling behavior. However, the stable point seems to be at a lower prey value of approximately 3300 and a slightly lower predator value of around 48 or so. This is likely a result of the increased value of the new disc-equation predation function from the foxes, resulting from the saturation of prey numbers relative to predator fitness. As for the main difference between the behaviors of these two systems, we can say that the model containing both the logistic and predator response equations approaches stability at an earlier time. This is because of, again, the increased level of predation which leads an already stabilizing system to that end in a more efficient manner. There may also be a stationary point at (0,0) for both models, but this is not biologically reasonable as populations cannot arise from nothing.

II. Coexistence:

Fig. 6: Derivation of stationary points:

\[
\frac{dN_1}{dt} = \frac{R_1 N_1}{K_1} (K_1 - m_1 - N_1 - aN_2) \quad ; \quad \frac{dN_2}{dt} = \frac{R_2 N_2}{K_2} (K_2 - m_2 - bN_1 - N_2)
\]

1) \[
\frac{R_1 N_1}{K_1} (K_1 - m_1 - N_1 - aN_2) = 0 \quad ; \quad 2) \frac{R_2 N_2}{K_2} (K_2 - m_2 - bN_1 - N_2) = 0
\]

1) There are 2 solutions:

\[N_1 = 0 \quad \text{and} \quad (K_1 - m_1 - N_1 - aN_2) = 0 \rightarrow aN_2 = K_1 - m_1 - N_1 \rightarrow N_2 = \frac{K_1 - m_1 - N_1}{a}\]

2) There are 2 solutions:

\[N_2 = 0 \quad \text{and} \quad (K_2 - m_2 - bN_1 - N_2) = 0 \rightarrow N_2 = K_2 - m_2 - bN_1\]

There are FOUR stationary points, one is non-trivial:

\[N_1 = 0, N_2 = 0 \rightarrow (0,0) \]

\[N_1 = 0, N_2 = K_2 - m_2 - bN_1 \quad ; \quad \text{when} \quad N_1 = 0, N_2 = K_2 - m_2 \rightarrow (0, K_2 - m_2)\]

\[N_2 = \frac{K_1 - m_1 - N_1}{a}, N_2 = 0 \quad ; \quad \text{when} \quad N_2 = 0, N_1 = K_1 - m_1 \rightarrow (K_1 - m_1, 0)\]

Non-trivial stationary point:

\[\frac{K_1 - m_1 - N_1}{a} = K_2 - m_2 - bN_1\]

Subtracting \(\frac{K_1 - m_1 - N_1}{a}\) and \(bN_1\) from both sides, and dividing by \(b - \frac{1}{a}\):

\[bN_1 - \frac{N_1}{a} = m_1 - \frac{K_1}{a} + K_2 - m_2 \rightarrow \frac{N_1 (b - \frac{1}{a})}{b - \frac{1}{a}} = \frac{m_1 - \frac{K_1}{a} + K_2 - m_2}{b - \frac{1}{a}} \rightarrow \]

\[N_1 = \frac{a(K_2 - m_2) - K_1 + m_1}{ab - 1} = 50\]

\[N_2 = K_2 - m_2 - b \left( \frac{a(K_2 - m_2) - K_1 + m_1}{ab - 1} \right) = 40 \rightarrow (50, 40) \text{ using given values}\]
**Defining the Nullclines:**

\[
N_2 = \frac{K_1 - m_1 - N_1}{a} \quad \rightarrow \quad N_2 = \frac{100 - 2 - N_1}{1.2} \approx -0.8333(N_1 - 98)
\]

\[
N_2 = K_2 - m_2 - bN_1 \quad \rightarrow \quad N_2 = 90 - 10 - 0.8(N_1) = 80 - 0.8(N_1)
\]

These equations yield the following plot containing four distinct regions bordered by the nullclines:

- **Blue:** N1 Nullcline, **Red:** N2 Nullcline, **●:** Stationary points

As we can see in the above plot, the point (50,40) is the intersection between of these nullclines and is also the non-trivial stationary point defined in the above derivation. Due to the qualitative regimes of behavior about the nullcline, the point is stable and indicates 50 and 40 as the population required to for coexistence between these two species of hydra. The point (0,0) is also stable, but is not reasonable as populations cannot arise from nothing. The other two points, which are not stable, simply correspond to the extinction of one species or the other.
The final plots in this project pertain to a system with different given values, \( m_1 = m_2 = 0 \): 

\[
N_2 = \frac{K_1 - m_1 - N_1}{a} \quad \Rightarrow \quad N_2 = \frac{100 - 0 - N_1}{1.2} \approx -0.8333(N_1 - 100)
\]

\[
N_2 = K_2 - m_2 - bN_1 \quad \Rightarrow \quad N_2 = 90 - 0 - 0.8(N_1) = 90 - 0.8(N_1)
\]

These equations yield the following plot containing 3 distinct regions bordered by the nullclines.

Blue: N1 Nullcline, Red: N2 Nullcline

As we can see, this system has no stable, fixed points that correspond to coexistence between the two species of hydra. There is no intersection of the nullclines, and therefore the behavior can never lead to stable populations of both species. \( N_1 \) will go extinct before \( N_2 \), thereby allowing \( N_2 \) to “win” and recover to a stable population eventually.

Fig. 8: Plot of nullclines for above equations; \( X - axis \ is \ N_1 \ values, Y - axis \ is \ N_2 \ values. \)
III. Appendix of scripts used:

I_a. Population Dynamics of Rabbits and Foxes:

```matlab
clear all
a=0.04; % Ro,prey
c=0.2;  % Ro,pred
b=0.1;  % epsilon
d=0.0005; % gamma

% Set initial conditions
tinit = 0.0;            % start time
tfinal = 365.0;         % stop time
R(1)=200.0;             % initial rabbit population, varies with question
F(1)=50.0;              % initial fox population, varies with question
n = 36500;             % number of time steps
dt = (tfinal-tinit)/n; % time step size
T = [tinit:dt:tfinal]; % create vector of discrete solution times

% Execute forward Euler to solve at each time step
% R(i+1) = R(i) + dt*(a*R(i) - d*R(i)*F(i));
% F(i+1) = F(i) + dt*(d*b*R(i)*F(i) - c*F(i));
for i = 1:n
    R(i+1) = R(i) + dt*R(i)*(a-d*F(i));
    F(i+1) = F(i) + dt*F(i)*(d*b*R(i)-c);
end;

% Plot Results...
S1 = sprintf('Populations at: Fox0=%g, Rabbit0=%g',F(1),R(1));
figure(1)
cf;
plot(R,F);
xlabel('Rabbits');
ylabel('Foxes');
legend(S1,0);
grid;
figure(2)
cf;
plot(T,R,'r-',T,F,'b');
legend('Rabbits','Foxes');
xlabel('time');
ylabel('Fox & Rabbit Population');
```
Population Dynamics of Rabbits and Foxes:

Logistic model incorporation

clear all
a=0.04;  % Ro,prey
c=0.2;   % Ro,pred
b=0.1;  % epsilon
d=0.0005;% gamma
k=10000; % carrying capacity

% Set initial conditions
% start time
% stop time
% initial rabbit population
% initial fox population

% number of time steps
% time step size
% create vector of discrete solution times

% Execute forward Euler to solve at each time step
% R(i+1) = R(i) + dt*(a*R(i) - d*R(i)*F(i));
% F(i+1) = F(i) + dt*(d*b*R(i)*F(i) - c*F(i));

for i = 1:n
    R(i+1) = R(i) + dt*(a*R(i)*(1-R(i)/k)-d*R(i)*F(i));
    F(i+1) = F(i) + dt*F(i)*(d*b*R(i)-c);
end;

%Plot Results...

S1 = sprintf('Populations at: FoxO=%g, Rabbit0=%g',F(1),R(1));

figure(1)
clf;
plot(R,F);
xlabel('Rabbits');
ylabel('Foxes');
legend(S1,0)
grid;

figure(2)
clf;
plot(T,R,'r-',T,F,'-b');
legend('Rabbits','Foxes');
xlabel('time');
ylabel('Fox & Rabbit Population');
I. Population Dynamics of Rabbits and Foxes:

Logistic model and Hollings disc equation incorporation

```plaintext
clear all
a=0.04;  % Ro,prey
c=0.2;   % Ro,pred
b=0.1;   % epsilon
d=0.0005;% gamma
k=10000; % carrying capacity
h=0.2;   % occupied time

% Set initial conditions
tinit = 0.0; % start time
tfinal = 1095.0; % stop time
R(1)=200.0; % initial rabbit population
F(1)=50.0; % initial fox population
n = 109500; % number of time steps
dt = (tfinal-tinit)/n; % time step size
T = [tinit:dt:tfinal]; % create vector of discrete solution times

% Execute forward Euler to solve at each time step
% R(i+1) = R(i) + dt*(a*R(i) - d*R(i)*F(i));
% F(i+1) = F(i) + dt*(d*b*R(i)*F(i) - c*F(i));
for i = 1:n
    R(i+1) = R(i) + dt*(a*R(i)*(1-R(i)/k)-F(i)*(d*R(i)/1+d*h*R(i)));
    F(i+1) = F(i) + dt*(b*F(i)*(d*R(i)/1+d*h*R(i))-c*F(i));
end;

%Plot Results...
S1 = sprintf('Populations at: Fox0=%g, Rabbit0=%g',F(1),R(1));
figure(1)
cf;
plot(R,F);
xlabel('Rabbits');
ylabel('Foxes');
legend(S1,0)
grid;

figure(2)
cf;
plot(T,R,'r-',T,F,'-b');
legend('Rabbits','Foxes');
xlabel('time');
ylabel('Fox & Rabbit Population');
```

II: Coexistence: Mathematica plots:

```
Plot[{-0.8333 (x - 98),80 - 0.8 x},{x,0,105},PlotLegends -> {"N1 Nullcline","N2 Nullcline"}]
Plot[{-0.8333 (x - 100),90 - 0.8 x},{x,0,105},PlotLegends -> {"N1 Nullcline","N2 Nullcline"}]
```