1. A competing species model. A stylized model of competing species with population densities $x(t)$ and $y(t)$ is given by
\[
\begin{align*}
\frac{dx}{dt} &= x(1 - x - y), \\
\frac{dy}{dt} &= y \left( \frac{1}{2} - \frac{y}{4} - \frac{3x}{4} \right).
\end{align*}
\]
First, find all four critical points. Then, by calculating the Jacobian matrix, classify each critical point.
Next, use Matlab/Octave to plot the vector field for the system and superimpose several solutions to the equation. Label axes and indicate units.
Solution: Problem 2:
Set $\frac{dx}{dt} = 0$ we get $x = 0$ or $y = 1 - x$.
• If $x = 0$,
  \[
  \frac{dy}{dt} = y \left( \frac{1}{2} - \frac{y}{4} \right) = 0 \quad \Rightarrow \quad y = 0 \text{ or } y = 2
  \]
• If $y = 1 - x$,
  \[
  \frac{dy}{dt} = (1 - x) \left( \frac{1}{2} - \frac{1 - x}{4} - \frac{3x}{4} \right) = 0 \quad \Rightarrow \quad x = 1 \text{ or } x = \frac{1}{2}
  \]
So the critical points are $(0, 0), (0, 2), (1, 0), (\frac{1}{2}, \frac{1}{2})$.
Let
\[
\begin{align*}
f_1(x, y) &= x(1 - x - y), \\
f_2(x, y) &= y \left( \frac{1}{2} - \frac{y}{4} - \frac{3x}{4} \right).
\end{align*}
\]
The Jacobian matrix is
\[
J = \begin{pmatrix}
f_{1x} & f_{1y} \\ f_{2x} & f_{2y}
\end{pmatrix} = \begin{pmatrix}
1 - 2x - y & -\frac{x}{2} \\ -\frac{3x}{4} & 1 - \frac{3x}{4} - \frac{3}{2} y
\end{pmatrix}.
\]
At critical points,
• $J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & 1/2 \end{pmatrix}$ has eigenvalues $\lambda_1 = 1, \lambda_2 = 1/2$, so $(0, 0)$ is an unstable source.
• $J(0, 2) = \begin{pmatrix} -1 & 0 \\ -3/2 & -1/2 \end{pmatrix}$ has eigenvalues $\lambda_1 = -1, \lambda_2 = -1/2$, so $(0, 2)$ is an asymptotically stable sink.
• $J(1, 0) = \begin{pmatrix} -1 & -1 \\ 0 & -1/4 \end{pmatrix}$ has eigenvalues $\lambda_1 = -1, \lambda_2 = -1/4$, so $(1, 0)$ is an asymptotically stable sink.
• $J(1/2, 1/2) = \begin{pmatrix} -1/2 & -1/2 \\ -3/8 & -1/8 \end{pmatrix}$ has eigenvalues $\lambda_1 = \frac{-5 + \sqrt{57}}{16} > 0, \lambda_2 = \frac{-5 - \sqrt{57}}{16} < 0$, so $(1/2, 1/2)$ is an unstable saddle point.
2. Simplest predator-prey model.

Note: in this problem, all the constants and variables are positive.

Consider a prey species (rabbits) with population size \( x(t) \) and a predator species (foxes) with population size \( y(t) \). Suppose that in the absence of the predator, the prey population would experience exponential growth with rate parameter \( a \). In the absence of prey, the predator dies out (exponential decay with parameter \( d \)). Further suppose that the rate of predators catching prey is proportional to \( x(t)y(t) \), and this leads to a loss of prey (parameter \( \beta \)) and an increase in predators (parameter \( \gamma \)). These assumptions lead to probably the simplest form of a predator-prey system:

\[
\begin{align*}
\frac{dx}{dt} &= ax - \beta xy, \\
\frac{dy}{dt} &= -dy + \gamma xy.
\end{align*}
\]

a. Find the critical points of the system and describe them in biological terms.

b. Calculate the Jacobian matrix and linearize around each critical point. Classify the critical points and sketch the vector field by hand.

c. Suppose we modify the system to include harvesting of each species (e.g. the prey are sardines and the predators are tuna, both tasty fish) with harvesting (fishing) efforts \( E_x \) and \( E_y \):

\[
\begin{align*}
\frac{dx}{dt} &= ax - \beta xy - E_xx, \\
\frac{dy}{dt} &= -cy + \gamma xy - E_yy.
\end{align*}
\]

Describe how the equilibria of the system change when (i) only the prey is harvested; (ii) only the predator is harvested; (iii) both are harvested.

Solution: Problem 3:

Set \( \frac{dx}{dt} = 0 \) we get \( x = 0 \) or \( y = a/\beta \).

- If \( x = 0 \),
  \[
  \frac{dy}{dt} = -dy = 0 \quad \Rightarrow \quad y = 0
  \]
• If \( y = a/\beta \),

\[
\frac{dy}{dt} = d \frac{a}{\beta} \left( -1 + \frac{\gamma}{d} x \right) = 0 \quad \Rightarrow \quad x = \frac{d}{\gamma}
\]

So the critical points are \((0,0)\), which means both species extinct, and \((\frac{d}{\gamma}, \frac{a}{\beta})\), which means a steady population.

The Jacobian matrix is

\[
J = \begin{pmatrix}
    a - \beta y & -\beta x \\
    \gamma y & -d + \gamma x
\end{pmatrix}
\]

and

\[
J(0,0) = \begin{pmatrix}
    a & 0 \\
    0 & -d
\end{pmatrix}, \quad J \left( \frac{d}{\gamma}, \frac{a}{\beta} \right) = \begin{pmatrix}
    0 & -\beta d \\
    -\frac{\alpha}{\beta} & 0
\end{pmatrix}.
\]

• At \((0,0)\), let \( x = \delta \hat{x}, y = \delta \hat{y} \) (\( \delta \ll 1 \)). The linearized system is

\[
\frac{d}{dt} \begin{pmatrix}
    \hat{x} \\
    \hat{y}
\end{pmatrix} = \begin{pmatrix}
    a & 0 \\
    0 & -d
\end{pmatrix} \begin{pmatrix}
    \hat{x} \\
    \hat{y}
\end{pmatrix}.
\]

\( J(0,0) \) has eigenvalues \( \lambda_1 = a, \lambda_2 = -d \) and eigenvectors \( v_1 = (1,0)^T, v_2 = (0,1)^T \). This is a saddle point.

• At \((\frac{d}{\gamma}, \frac{a}{\beta})\), let \( x = \frac{d}{\gamma} + \delta \hat{x}, y = \frac{a}{\beta} + \delta \hat{y} \) (\( \delta \ll 1 \)). The linearized system is

\[
\frac{d}{dt} \begin{pmatrix}
    \hat{x} \\
    \hat{y}
\end{pmatrix} = \begin{pmatrix}
    0 & -\beta d \\
    -\frac{\alpha}{\beta} & 0
\end{pmatrix} \begin{pmatrix}
    \hat{x} \\
    \hat{y}
\end{pmatrix}.
\]

\( J(\frac{d}{\gamma}, \frac{a}{\beta}) \) has eigenvalues \( \lambda = \pm i \sqrt{ad} \) and plug in \((\hat{x}, \hat{y})^T = (1,0)^T \) we get

\[
\frac{d}{dt} \begin{pmatrix}
    \hat{x} \\
    \hat{y}
\end{pmatrix} = \begin{pmatrix}
    0 & -\beta d \\
    -\frac{\alpha}{\beta} & 0
\end{pmatrix} \begin{pmatrix}
    \hat{x} \\
    \hat{y}
\end{pmatrix}.
\]

So this is a centre (counterclockwise).

(c)

(i) When we apply this change, we now have two critical points: \((x,y) = (0,0)\) and \((c/\gamma, (\alpha - E_x)/\beta)\). Therefore, the population of the predator will decrease.

(ii) When we apply this change, we now have two critical points: \((x,y) = (0,0)\) and \((c + E_y)/\gamma, \alpha/\beta)\).
Therefore, the population of the prey will increase.

(iii) When we apply this change, we now have two critical points: \((x, y) = (0, 0)\) and \(((c + E_0)\gamma, (\alpha - E_x)/\beta)\). Therefore, the population of the predator will decrease and the prey will increase.

3. Improved predator prey model

Let’s make the model of the preceding question more realistic. First, let’s replace the exponential growth of the prey with a logistic type growth, so \(x'(t) = r(1 - \frac{x}{K})x\) in the absence of predators. We see that all solutions with initial conditions \(x(0) > 0\) tend to the equilibrium \(x = K\). We call \(K\) the carrying capacity of the prey habitat. Now let \(y\) be the population density of the predators and suppose that the predator population declines exponentially in the absence of prey, like \(y'(t) = -dy\).

The previous question’s model can be criticized because there is no limit to the rate of increase of the predator population or the rate of decline of the prey population. In reality, there is an upper limit on the rate at which prey can be caught and eaten by a predator. For this reason, ecological modellers are usually happier to use a “Holling Type II” function for the per-capita predator consumption rate of prey. This function has the form \(p(x) = \frac{mx}{a + x}\), reflecting the following features:

1. \(p(0) = 0\) – if no prey is present, then no predation occurs.
2. \(p(x)\) is an increasing function of \(x\) – increasing prey population leads to an increase in prey consumption by predators.
3. \(p(x) \to m\) as \(x \to \infty\) – there is a maximum possible rate of prey consumption by predators even if prey are very abundant.

Putting this all together, we can write the whole improved model as:

\[ x' = r \left(1 - \frac{x}{K}\right)x - m \frac{xy}{a + x}, \quad (1) \]
\[ y' = -dy + cm \frac{xy}{a + x}. \quad (2) \]

Here \(c\) is a conversion factor between consumption of prey and ensuing increase in predators.

There are six parameters here. We will fix five numerical values and explore how changes in only one parameter, the habitat carrying capacity \(K\), affects the dynamics of the predator-prey system. Fix \(r = m = 10, \quad a = 1, \quad d = 1, \quad c = \frac{1}{4}\).

Solution: Problem 4:

(a) Find all equilibrium points of the system. Note that the position of two of the three equilibrium points will depend on \(K\) and that we are only interested in equilibria in the non-negative (first) quadrant of the \(x - y\) plane since negative populations don’t make sense. State the condition on \(K\) for there to be three interesting equilibria in this quadrant.

Solution:

Set \(y = 0\) we get \(y = 0\) or \(x = \frac{2}{3}\).

- If \(y = 0\), by \(x' = 0\) we have \(x = 0\) or \(K\).
- If \(x = \frac{2}{3}\), by \(x' = 0\) we have \(y = \frac{5}{3}(1 - \frac{2}{3K}) = \frac{5}{3} - \frac{10}{9K}\).

So the equilibrium points are \((0, 0)\), \((K, 0)\) and \((\frac{2}{3}, \frac{5}{3} - \frac{10}{9K})\). These are three distinct points in the first quadrant if and only if \(K > \frac{2}{3}\).

(b) Find the Jacobian of the system and use this to analyze the local behaviour of the system near each equilibrium. You do not need to calculate this for any equilibrium point outside the non-negative quadrant. You should find that there are transitions in local behaviour of at least one equilibria at the following values: \(K = 2/3, K = K^* \simeq 1.266, K = 7/3\). Summarize your findings in a table like this one.

<table>
<thead>
<tr>
<th>Local behaviour near equilibria</th>
<th>((x_1, y_1))</th>
<th>((x_2, y_2))</th>
<th>((x_3, y_3))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) (0 &lt; K &lt; \frac{7}{3})</td>
<td>e.g. saddle point</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(ii) (\frac{2}{3} &lt; K &lt; K^* \simeq 1.266)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(iii) (K^* &lt; K &lt; \frac{7}{3})</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(iv) (K &gt; \frac{7}{3})</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fill in the locations of the equilibria \((x_i, y_i)\) and indicate their stability for each value of \(K\).

Solution:
The Jacobian is

\[
J = \begin{pmatrix}
-\frac{20}{K} x + 10 \frac{-10 y}{(1+x)^2} + 10 x \frac{-10 y}{2(1+x)^2} \\
\frac{5y}{2(1+x)^2} & \frac{10y}{2(1+x)^2} - \frac{10y}{3(1+x)^2}
\end{pmatrix},
\]

and

\[
J(0,0) = \begin{pmatrix} 10 & 0 \\ 0 & -1 \end{pmatrix}
\]

\[
J(K,0) = \begin{pmatrix} -10 & \frac{-10K}{1+K} \\ 0 & \frac{10K}{1+K} \end{pmatrix}
\]

\[
J \left( \frac{2}{3}, \frac{5}{3} - \frac{10}{9K} \right) = \begin{pmatrix} 4 & \frac{-28}{3K} \\ \frac{3}{2} & -4 \end{pmatrix}
\]

The eigenvalues for these matrices are as follow:

- At \((0, 0)\), \(\lambda_1 = 10\) and \(\lambda_2 = -1\).
- At \((K, 0)\), \(\lambda_1 = -10\) and \(\lambda_2 = \frac{3K-2}{2(1+K)}\).
- At \(\left( \frac{2}{3}, \frac{5}{3} - \frac{10}{9K} \right)\), this point is in the first quadrant only if \(K > \frac{2}{3}\). The characteristic equation is

\[
\lambda^2 - \left( 4 - \frac{28}{3K} \right) \lambda + 6 - \frac{4}{K} = 0.
\]

and

\[
\lambda_1 + \lambda_2 = 4 - \frac{28}{3K}, \quad \lambda_1 \lambda_2 = 6 - \frac{4}{K} > 0.
\]

Notice that \(\Delta > 0 \Rightarrow K < K^*,\) so

1) When \(K < K^*,\) the eigenvalues are negative and distinct.
2) When \(K^* < K < \frac{7}{3},\) the eigenvalues are complex with negative real parts.
3) When \(K > \frac{7}{3},\) the eigenvalues are complex with positive real parts.

To summarize,

<table>
<thead>
<tr>
<th>Local behaviour near equilibria</th>
<th>((0, 0))</th>
<th>((K, 0))</th>
<th>(\left( \frac{2}{3}, \frac{5}{3} - \frac{10}{9K} \right))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) (0 &lt; K &lt; \frac{7}{3})</td>
<td>saddle point</td>
<td>sink</td>
<td>saddle point</td>
</tr>
<tr>
<td>(ii) (\frac{2}{3} &lt; K &lt; K^* \approx 1.266)</td>
<td>saddle point</td>
<td>saddle point</td>
<td>sink</td>
</tr>
<tr>
<td>(iii) (K^* &lt; K &lt; \frac{7}{3})</td>
<td>saddle point</td>
<td>saddle point</td>
<td>stable spiral point</td>
</tr>
<tr>
<td>(iv) (K &gt; \frac{7}{3})</td>
<td>saddle point</td>
<td>saddle point</td>
<td>unstable spiral point</td>
</tr>
</tbody>
</table>

(c) Use Matlab/Octave to plot vector fields with a few solution curves for representative values of \(K\). Turn in one plot representing each case from (i)-(iv) in the table of part (c). Mark the equilibrium points on each plot. Label axes and indicate units.

Solution:
See Figure 3.

d) Complete the following table with your informed opinion about the long-term behaviour of the whole system for each range of \(K\).

Solution:

<table>
<thead>
<tr>
<th>Overall behaviour of the system</th>
<th>(0 &lt; K &lt; \frac{7}{3})</th>
<th>(\frac{2}{3} &lt; K &lt; K^* \approx 1.266)</th>
<th>(K^* &lt; K &lt; \frac{7}{3})</th>
<th>(K &gt; \frac{7}{3})</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) all solutions go to ((K, 0)) without oscillating</td>
<td>all solutions go to ((\frac{2}{3}, \frac{5}{3} - \frac{10}{9K})) without oscillating</td>
<td>all solutions go to ((\frac{2}{3}, \frac{5}{3} - \frac{10}{9K})) while oscillating</td>
<td>all solutions oscillate, do not go to any fixed point</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3: Figures for Problem 4(c).

(e) Finally, suppose you are managing a wildlife park. Your visitors come to see lions. The lions subsist on a diet of gazelles and you supply the gazelles with feed. According to the mathematical model, what will happen if you feed the gazelles too much? How might this impact your visitor experience? Explain how this could be called the “paradox of habitat enrichment”.

Solution:
Feeding gazelles increases the carrying capacity $K$. As seen above, if $K > \frac{7}{4}$, the population (for both lion and gazelle) will eventually oscillate. In fact, the bigger the $K$, the greater the oscillation. So the visitors, depending on their time of visit, may see a lot of lions or merely a few. The paradox is that as we improve the habitat for the prey species, this can lead to fluctuating populations of prey and predators, even transiently dropping below the stable levels with “worse” habitat.

4. Matlab/Octave code

```matlab
%% Code for Problem 1

[X1, X2] = meshgrid(0:.1:2,0:.1:2);
F1=@(x1,x2) x1-x1.^2-x1.*x2;
F2=@(x1,x2) .5*x2-.25*x2.^2-.75*x1.*x2;

% make matrices U1 and U2 containing the vector components
U1 = F1(X1,X2);
U2 = F2(X1,X2);
```
% rescale arrow length
L=0.05;
len=length(U1);
for (i=1:len)
    for (j=1:len)
        nr=sqrt(U1(i,j)^2+U2(i,j)^2);
        U1(i,j)=L*U1(i,j)/nr;
        U2(i,j)=L*U2(i,j)/nr;
    end
end

% plot the vector field
quiver(X1,X2,U1,U2,0)
hold on;

% set the time range to run on
tr=[0 20];
f=@(t,x) [F1(x(1),x(2)); F2(x(1),x(2))];
for i=0.1:0.3:2
    ip=[2;i]; % set initial point along line x1=2
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
    ip=[0.05;i]; % now set initial point along line x1=0.05, etc...
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
    ip=[i;2];
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
end;

axis([-1 2 -1 2])
box on;

% set the value of K
K=0.5;
[X1, X2] = meshgrid(0:.1:3,0:.1:3);
F1=@(x1,x2) 10*(1-1/K*x1).*x1-10*x1.*x2./(1+x1);
F2=@(x1,x2) -x2+2.5*x1.*x2./(1+x1);

% make matrices U1 and U2 containing the vector components
U1 = F1(X1,X2);
U2 = F2(X1,X2);

% rescale arrow length
L=0.05;
len=length(U1);
for (i=1:len)
    for (j=1:len)
        nr=sqrt(U1(i,j)^2+U2(i,j)^2);
        U1(i,j)=L*U1(i,j)/nr;
        U2(i,j)=L*U2(i,j)/nr;
    end
end

% plot the vector field
quiver(X1,X2,U1,U2,0)
hold on;
% set and the time range to run on
tr=[0 10];

f=@(t,x) [F1(x(1),x(2)); F2(x(1),x(2))];
for i=0.1:0.6:2
    ip=[2.5;i]; %set initial point along line x1=2.5
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
    ip=[0.05;i]; %now set initial point along line x1=0.05, etc...
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
    ip=[i;0.05];
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
    ip=[i;2];
    [~, xout]=ode45(f,tr,ip);
    plot(xout(:,1),xout(:,2),'r')
end;

% mark the equilibrium points
plot([0 K 2/3],[0 0 5/3-10/9/K],'Marker','o','MarkerEdgeColor','k',...
     'Linewidth',2,'Linestyle','none');
axis([-1.1 2.5 -.1 2.1]);
box on;