MATH 227A: Mathematical Biology
Homework 6

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Problem 1

For the system $x' = y + \mu x$, $y' = -x + \mu y - x^2 y$, show that a Hopf bifurcation occurs. To verify the asymptotic stability at the critical point, use a computer simulation. Also, plot the limit cycle using a computer system for a relevant value of μ.

Consider

$$\begin{cases} x' = y + \mu x, \\ y' = -x + \mu y - x^2 y. \end{cases}$$

The only steady state is the origin $(0, 0)$. The Jacobian at $(0, 0)$ is

$$A(\mu) = \begin{pmatrix} \mu & 1 \\ -1 & \mu \end{pmatrix},$$

with eigenvalues

$$\lambda_{1,2}(\mu) = \mu \pm i.$$

At $\mu = 0$ the eigenvalues are purely imaginary $\pm i$, so the linearization has a purely imaginary pair at $\mu = 0$.

Thus, we see that shows:

- For $\mu < 0$, the origin is (asymptotically) stable since $Re(\lambda) < 0$. We can apply Hartman-Grobman theorem since the real part is non-zero; so, based on the linearization at the origin, we can conclude that the original system also has an **asymptotically stable spiral** for $\mu < 0$.
- At $\mu = 0$, since we cannot apply the Hartman-Grobman theorem for non-hyperbolic steady states, we analyze the stability using numerical simulation. Figure 1 shows the phase plot at the critical value of μ for three different initial conditions. We see that the system has a **stable**

inward spiral here, too. (The code for the numerical solution is included in Listing 1.)

- For $\mu > 0$, the origin becomes unstable as $Re(\lambda) > 0$. Once again, we can apply Hartman-Grobman theorem since the real part is non-zero; we can thus conclude that the original system has an **unstable outward spiral** for $\mu > 0$.

  Thus, according to Hopf theorem, the system undergoes a (supercritical) Hopf bifurcation at $\mu = 0$ for small $\mu > 0$. Specifically, the system sustains limit cycles for $\mu \in (0, \epsilon)$ for small $\epsilon > 0$. The system is shown exhibiting a limit cycle in Figure 1. (The code for the numerical solution is included in Listing 1.)

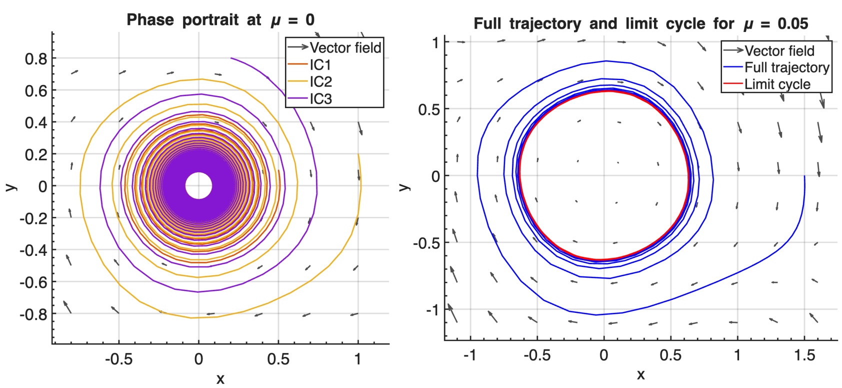

Figure 1: Phase portrait of the system in problem 1. The system has a steady state at the origin. *On the left* are stable inward spiraling trajectories of the system for different initial conditions when $\mu = 0$. *On the right* is the system in the limit cycle regime for small positive μ.

```
% System: x' = y + mu*x;  y' = -x + mu*y - x^2*y

% 1. Simulation at the critical point, mu = 0
mu = 0;
f = @(t,X) [ X(2) + mu*X(1);  -X(1) + mu*X(2) - X(1).^2 .* X(2) ];
% direction field arrows
[xg,yg] = meshgrid(-2:0.3:2, -2:0.3:2);
u = yg + mu*xg;
v = -xg + mu*yg - xg.^2 .* yg;

figure; hold on; title('Phase portrait at \mu = 0');
xlabel('x'); ylabel('y'); axis equal; grid on;
% Draw arrows scaled for clarity
quiver(xg, yg, u, v, 1.5, 'Color', [0.3 0.3 0.3]);

tspan = [0 500];
X0s = [0.5 0.1; 1.0 0.2; 0.2 0.8];
for k=1:size(X0s,1)
```

```
    [t,X] = ode45(f, tspan, X0s(k,:)');
    plot(X(:,1), X(:,2), 'LineWidth', 1.2);
end
legend('Vector field','IC1','IC2','IC3');
prettyfig;

% 2. Simulation for a small positive mu to show the limit cycle.
mu = 0.05;    % small positive value for which a stable limit cycle exists
f = @(t,X) [ X(2) + mu*X(1);  -X(1) + mu*X(2) - X(1).^2 .* X(2) ];
% Vector field
[xg,yg] = meshgrid(-2:0.3:2, -2:0.3:2);
u = yg + mu*xg;
v = -xg + mu*yg - xg.^2 .* yg;

% Simulation
tspan = [0 1000];
X0 = [1.5; 0.0];
[t,X] = ode45(f, tspan, X0);
% Separate trajectory into transient and limit cycle portion
transient = round(length(t)*0.6);

figure; hold on;
quiver(xg, yg, u, v, 1.5, 'Color', [0.3 0.3 0.3]);   % vector field arrows
plot(X(:,1), X(:,2), 'b-', 'LineWidth', 1);          % full trajectory
plot(X(transient:end,1), X(transient:end,2), 'r-', 'LineWidth', 2);  % limit cycle emphasized

title(['Full trajectory and limit cycle for \mu = ', num2str(mu)]);
xlabel('x'); ylabel('y'); axis equal; grid on;
legend('Vector field','Full trajectory','Limit cycle');
prettyfig;
```

Listing 1: Matlab script to numerically solve the system in problem 1 foor stability at critical μ and for limit cycle slightly upward of critical μ.

Problem 2

Suppose that $x' = f(x, y)$, $y' = g(x, y)$ is a 2D ODE and that there is a periodic solution P.

a) Calculate the index of the system using the periodic solution itself as a closed path.

Let P be the periodic orbit. As we traverse one full loop along P, the vector field $(f(x, y), g(x, y))$ is tangent to the orbit and never vanishes. Tracing the direction of this vector around P shows that the vector rotates exactly once counterclockwise before returning to its starting direction. Hence, the index of the system along the closed path P is

$$\text{Index}(P) = 1.$$

b) Suppose that there are two stable spirals inside of the periodic solution. Show that there must also exist at least one saddle in the system.

Suppose there are two stable spirals (sinks) inside the periodic orbit P. The Poincaré Index Theorem states that for any simple closed curve containing isolated equilibria inside,

$$\text{Index}(P) = \sum_{p \text{ inside } P} \text{Index}(p).$$

Each stable spiral has index $+1$, so the total index from the two spirals is

$$1 + 1 = 2.$$

But from part (a) we have $\text{Index}(P) = 1$. Therefore, there must exist at least one additional equilibrium inside P whose index is negative, in order to reduce the total sum back down to 1. The only equilibria in the plane with negative index are saddles (index -1). Thus, there must be at least one saddle inside P.

c) Sketch a possible phase plot of this ODE.

An example phase plot of the system is shown in Figure 2.

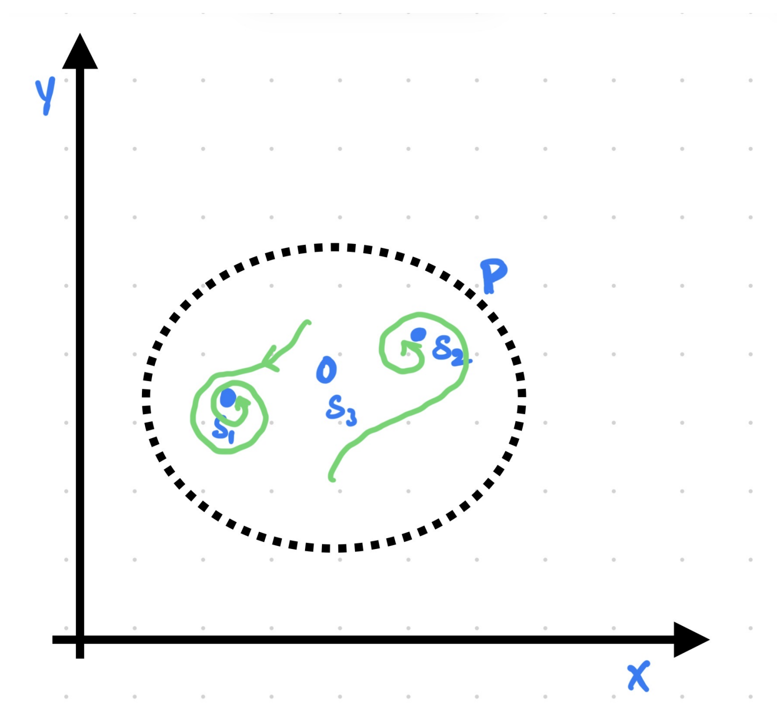

Figure 2: Phase portrait of the system in problem 1. The system has saddle nodes at both (0, 0) and (1, 1).

Problem 3

One of the best known excitable systems is the so-called Fitzhugh-Nagumo model, representing the voltage of a neuron over time. This system can be written as $v' = f(v) - w + I(t)$, $w' = \epsilon(v + d - cw)$, where $I(t)$ is a time-varying function chosen independently. Set $f(v) = v - \frac{v^3}{3}$, $\epsilon = 0.08$, $d = 0.7$, $c = 0.8$.

a) Set first I(t) = 0 for all t. Draw the nullclines of this system on the paper (possibly using Matlab), and plot sample solutions. What behavior do you observe?

Setting $I(t) = 0$ and the rates to zero to get the nullclines, we have the following system,

$$\begin{align*}
v' &= f(v) - w \\
0 &= v - \frac{v^3}{3} - w \tag{1} \\
w' &= \epsilon(v + d - cw) \\
0 &= v + d - cw \\
&= v - 0.7 + 0.8\,w \tag{2}
\end{align*}$$

The nullclines and potential trajectories are shown in Figure 3. The system has exactly one steady state.

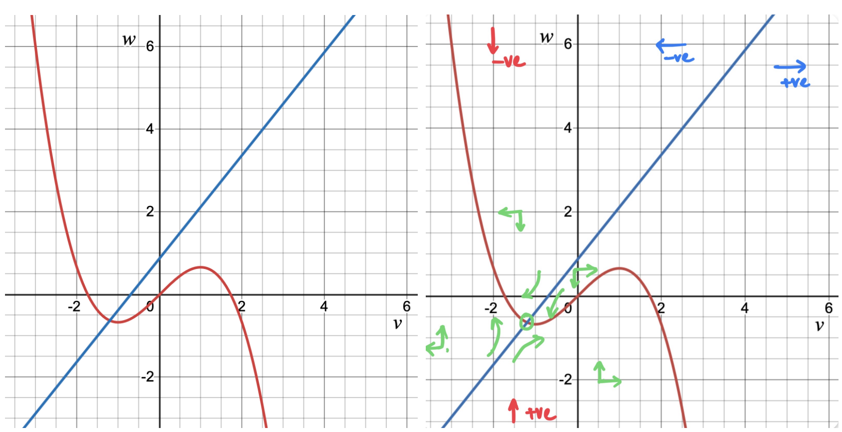

Figure 3: Nullclines of the system in problem 3 for $I(t) = 0$. w-nullcline in blue; v-nullcline in red. *On the right* is a stability analysis of the steady state. The steady state is unstable.

b) Now set $I(t)$ to be a constant larger than zero, e.g. $I = 0.3$ or $I = 0.5$. How do the nullclines change, and what behavior do you observe?

Setting $I(t) = I$, a positive constant, and the rates to zero to get the nullclines, we have the following system,

$$\begin{aligned} v' &= f(v) - w + I \\ 0 &= v - \frac{v^3}{3} - w + I \qquad (3) \\ w' &= \epsilon(v + d - cw) \\ 0 &= v + d - cw \\ &= v + 0.7 - 0.8\,w \qquad (4) \end{aligned}$$

The nullclines and potential trajectories are shown in Figure 4. The system still only has one steady state as I increases; however, the steady states shifts towards middle branch of the cubic curve at $I \approx 0.3$, possibly changing the stability behavior. We now linearize the system to find out if there is a difference in behavior.

At any steady state (v^*, w^*),

$$\begin{aligned} 0 &= f(v^*) - w^* + I, \\ 0 &= \varepsilon(v^* + d - cw^*). \end{aligned}$$

From the second equation (since $\varepsilon \neq 0$) we get

$$w^* = \frac{v^* + d}{c}.$$

Substituting into the first equation yields,

$$f(v^*) + I \;=\; \frac{v^* + d}{c}, \qquad \text{i.e.} \qquad v^* - \frac{(v^*)^3}{3} + I \;=\; \frac{v^* + d}{c}$$

Computing the Jacobian at (v^*, w^*),

$$J(v^*, w^*) \;== \begin{pmatrix} 1 - (v^*)^2 & -1 \\ \varepsilon & -\varepsilon c \end{pmatrix}$$

$$\begin{aligned} \operatorname{tr}(J) &= 1 - (v^*)^2 - \varepsilon c, \\ \det J &= \big(1 - (v^*)^2\big)(-\varepsilon c) - (-1)(\varepsilon) \\ &= \varepsilon\Big(1 - c\big(1 - (v^*)^2\big)\Big) \end{aligned}$$

A Hopf bifurcation occurs when

$$\operatorname{tr} J = 0 \quad \text{and} \quad \det J > 0.$$

Setting $\operatorname{tr} J = 0$ gives

$$1 - (v^*)^2 - \varepsilon c = 0 \qquad \Longrightarrow \qquad (v^*)^2 = 1 - \varepsilon c.$$

Thus the candidate equilibrium v^* at the Hopf must satisfy $v^* = \pm\sqrt{1 - \varepsilon c}$ (provided $1 - \varepsilon c > 0$). To find the corresponding critical input I_{crit} we substitute v^* into the equilibrium condition, and solving for I gives,

$$I \;=\; \frac{v^* + d}{c} - f(v^*) \;=\; \frac{v^* + d}{c} - \Big(v^* - \frac{(v^*)^3}{3}\Big)$$

Using the given values $\varepsilon = 0.08,\ d = 0.7,\ c = 0.8$, we have,

$$1 - \varepsilon c = 1 - 0.08 \cdot 0.8 = 1 - 0.064 = 0.936,$$

$$v^* = \pm\sqrt{0.936} \approx \pm 0.967.$$

Evaluating (I) for the two signs gives two candidate critical inputs:

$$\begin{aligned} I_{\text{crit}}(v^* = +0.967) &\approx 1.418 \\ I_{\text{crit}}(v^* = -0.967) &\approx 0.331 \end{aligned} \tag{5}$$

For $I < I_{\text{crit}}$ the trace is negative at the equilibrium (so the fixed point is stable: node or spiral depending on discriminant), and the determinant is positive for given c and both obtained values of v^*; whereas, for $I > I_{\text{crit}}$ the trace is positive and a small-amplitude limit cycle is expected to appear via a Hopf bifurcation. *The choice of sign matters because the conditions must be satisfied simultaneously; here the negative root $v^* \approx -0.96747$ yields the smaller critical input $I \approx 0.331$ which matches the bifurcation seen near the given parameter regime.*

Based on the linearization and the nullcline analyses, we see that the system shifts from having **stable inward spirals** to **unstable outward spirals** as I increases.

c) Interpret this behavior in terms of relaxation oscillations and timescale decomposition.

We first consider the fast timescale v.

$$v' = f(v) + (I - w) \tag{6}$$

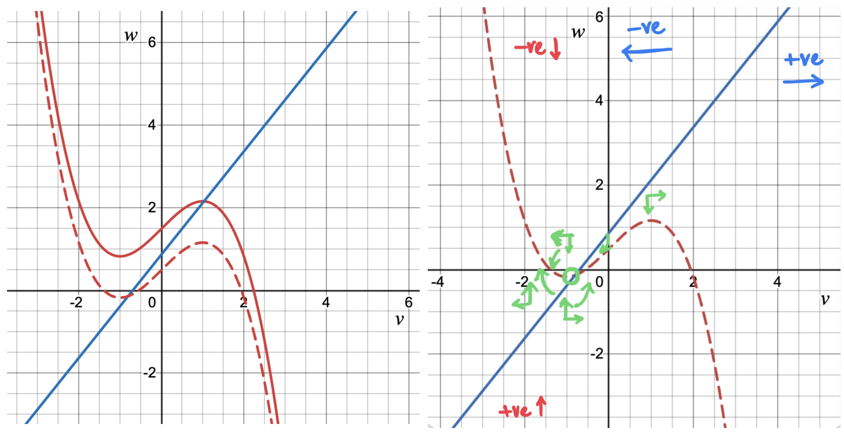

Figure 4: Nullclines of the system in problem 3 for $I(t) = 1$ *(dashed, red)* and $I(t) = 2$ *(solid, red)*. The w nullcline is shown in blue. *On the right* is a stability analysis of the steady state at $I = 1$. The steady state is unstable.

Treating w (due to slower timescale) and I (given) as constants, different cases of the phase plane of the single-variable v system are shown in Figure 6. We see that the system transitions from having one stable steady state for low $I - w$, to three at intermediate $I - w$ — stable at the two ends and unstable on the middle branch of the cubic, finally back to one at high $I - w$.

In the slow timescale, v is effectively at steady state v_{ss}. (We ignore ϵ as we are changing our perspective to the timescale of the slower system.)

$$\begin{aligned} w' &= v + d - cw \\ &= v_{ss} + d - c(f(v_{ss}) + I) \\ &= v_{ss} - c \cdot \left(v_{ss} - \frac{v_{ss}^3}{3} \right) + (d - cI) \\ &= (1 - c)\, v_{ss} + c \cdot \frac{v_{ss}^3}{3} + (d - cI) \end{aligned} \tag{7}$$

So, depending on the relative magnitudes of the cubic and linear $v_s s$ terms, w is either increasing or decreasing. Specifically, w increases when the cubic term dominates—which happens for large v_{ss}, and w decreases when the linear term dominates at low values of v_{ss}.

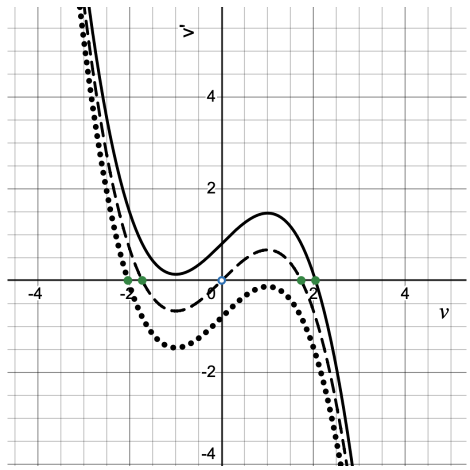

Figure 5: Phase plot of the fast timescale v system for different values of I: $I = 0$ *(dotted)*, $I = 1$ *(dashed)*, $I = 2$ *(solid)*. In the single steady state regime, the only steady state is always stable. In the three steady state regime, the central steady state is unstable while the other two are stable.

Putting the two timescales together, and plotting (6) (solid line) and (7) (dashed line), we get the trajectory shown in Figure 6. Three cases are shown: $I = 0$ and $I = 1$ and $I = 2$. Beginning at the same initial point, the first (last) case always settles to the stable steady state on the lower (upper) branch when $w' = 0$. For the second case, x' is positive initially for large v_{ss} (reference the dashed line representing w' as a function of v_{ss}). Once it reaches the knee of the cubic function, it jumps over to the other stable branch on the phase portrait and w begins to decrease as y has now changed its sign and so has w'. The system is never able to reach $w' = 0$ and remains oscillating.

d) Explain why this system can be considered excitable with respect to the input function I(t).

The Hopf bifurcation argument in part (b) and the timescale decomposition analysis in Figure 6, each summarize why I acts like an excitatory input. In the Hopf bifurcation picture, low values of $I < I_{\text{crit}}$ place the system in stable inward spiral. As I increases beyond I_{crit}, the system briefly exists in a regime of limit cycles and later moves into an outward spiral regime. Thus, there are not oscillations initially but when I becomes large enough, there is a brief regime of oscillations (until I reaches its upper critical value corresponding to positive v^* as shown in (5)).

Likewise in the timescale decomposition analysis, we see that at intermediate values of I (akin to the range of I between its two critical values in the Hopf argument), the system is never able to reach a stable steady state. Geometrically, for I values that position $w' = 0$ in the middle branch of

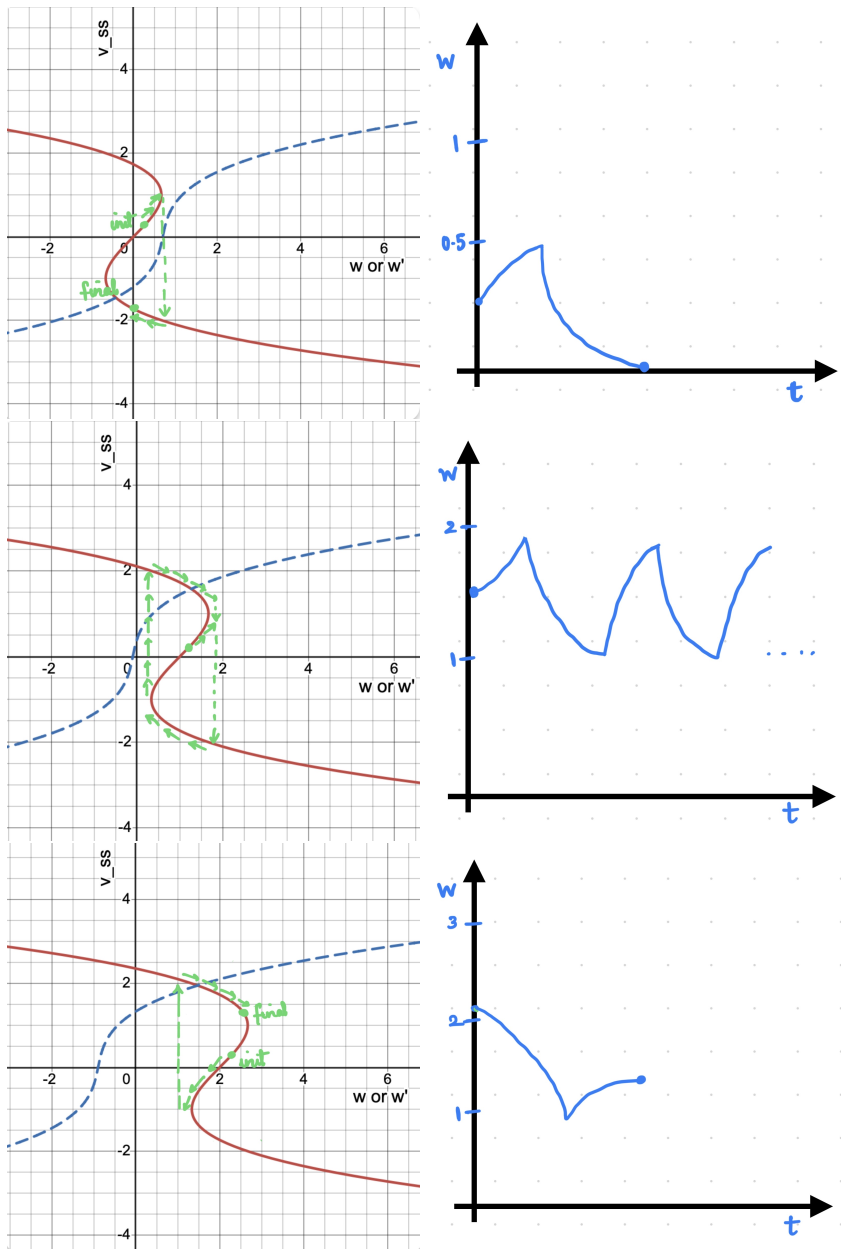

Figure 6: Combined slow and fast timescale phase and time evolution plots for $I = 0$ *(top)*, $I = 1$ *(middle), and* $I = 2$ *(bottom).* On the phase plots, w is shown as a function of y_{ss} in *solid red*, while w' vs. y_{ss} is shown in *dashed blue*. The zero crossing of w' determines if/where the system settles at steady state.

the cubic curve (see Figure 6), the system exhibits oscillations.

Thus, small $I(t)$ can "excite" the system into oscillatory behavior, and retracting the excitation will eventually allow the system to settle into its lower steady state on the lower cubic equation branch. Alternatively, making $I(t)$ a very high value (beyond its upper critical value, i.e., placing $w' = 0$ on the upper branch of the cubic equation) would "switch" the system into an excited steady state associated with a larger v_{ss}.

Problem 4

Given the predator-prey system,

$$\begin{cases} \dot{x} = bx - x^2 - \dfrac{xy}{1+x}, \\ \dot{y} = -ay^2 + \dfrac{xy}{1+x}, \end{cases} \qquad x, y \geq 0,\ a, b > 0.$$

where $x, y \geq 0$ are the populations and $a, b > 0$ are parameters.

a) Sketch the nullclines and discuss the bifurcations that occur as b varies.

The system is

$$\begin{cases} \dot{x} = bx - x^2 - \dfrac{xy}{1+x}, \\ \dot{y} = -ay^2 + \dfrac{xy}{1+x}. \end{cases}$$

Nullclines:

$$\begin{aligned} \text{x-nullcline: } \dot{x} = 0 &\implies bx - x^2 - \frac{xy}{1+x} = 0 \\ &\implies x = 0 \quad \text{or} \quad b - x - \frac{y}{1+x} = 0 \\ &\implies x = 0 \quad \text{or} \quad y = (1+x)(b-x) \end{aligned}$$

$$\begin{aligned} \text{y-nullcline: } \dot{y} = 0 &\implies -ay^2 + \frac{xy}{1+x} = 0 \\ &\implies y = 0 \quad \text{or} \quad -ay + \frac{x}{1+x} = 0 \\ &\implies y = 0 \quad \text{or} \quad y = \frac{x}{a(1+x)} \end{aligned}$$

The nullclines are plotted in Figure 7. The x-nullcline is a downward parabola intersecting the axes at $x = 0$ $(y = b)$ and $x = b$ $(y = 0)$. The y-nullcline is increasing and saturates at $y \to 1/a$ as $x \to \infty$. As b varies, no steady states are formed or destroyed; however, there may exist a Hopf bifurcation as we will analyze further.

b) Show that a positive fixed point $x* \geq 0, y* \geq 0$ exists for all $a, b > 0$. (Don't try to find the fixed point explicitly; use a graphical argument

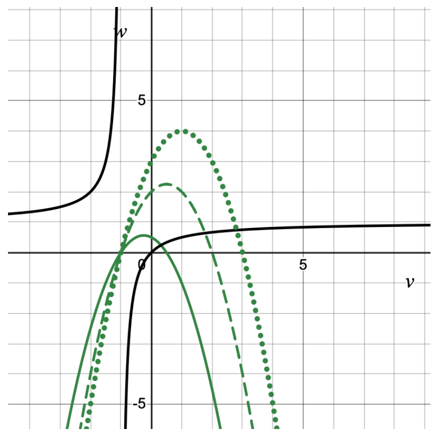

Figure 7: Nullclines of the system in problem 4 for different values of b: $b = 0$ *(solid),* $b = 1$ *(dashed), and* $b = 2$ *(dotted).* x-nullcline in green; y-nullcline in black.

instead.)

A positive fixed point (x^*, y^*) satisfies the steady-state equations

$$bx^* - (x^*)^2 - \frac{x^*y^*}{1+x^*} = 0, \qquad -ay^{*2} + \frac{x^*y^*}{1+x^*} = 0.$$

From the second equation (for $y^* > 0$) we have

$$ay^* = \frac{x^*}{1+x^*} \qquad \Longrightarrow \qquad y^* = \frac{x^*}{a(1+x^*)}.$$

Substituting this expression for y^* into the first equation gives

$$bx^* - (x^*)^2 - \frac{x^*}{1+x^*} \cdot \frac{x^*}{a(1+x^*)} = 0 \qquad \Longrightarrow \qquad bx^* - (x^*)^2 - \frac{(x^*)^2}{a(1+x^*)^2} = 0.$$

Dividing both sides by $x^* > 0$ yields

$$b - x^* - \frac{x^*}{a(1+x^*)^2} = 0.$$

Consider the left-hand side as a function of $x^* \geq 0$:

$$f(x^*) = b - x^* - \frac{x^*}{a(1+x^*)^2}.$$

At $x^* = 0$, $f(0) = b > 0$, and as $x^* \to \infty$, $f(x^*) \to -\infty$. Since f is continuous, the Intermediate Value Theorem guarantees that there exists some $x^* > 0$ such that $f(x^*) = 0$. Substituting back gives $y^* = x^*/(a(1+x^*)) > 0$, showing that a positive fixed point exists for all $a, b > 0$.

c) Show that a Hopf bifurcation occurs at the positive fixed point at a_c

A Hopf bifurcation occurs when the trace of the Jacobian at the positive fixed point vanishes. The Jacobian of the system is

$$J(x,y) = \begin{pmatrix} b - 2x - \dfrac{y}{(1+x)^2} & -\dfrac{x}{1+x} \\ \dfrac{y}{(1+x)^2} & -2ay + \dfrac{x}{1+x} \end{pmatrix}.$$

The trace is

$$\begin{aligned} \mathrm{Tr}(J) &= \left(b - 2x - \frac{y}{(1+x)^2}\right) + \left(-2ay + \frac{x}{1+x}\right) \\ &= b - 2x - \frac{y}{(1+x)^2} - 2ay + \frac{x}{1+x}. \end{aligned}$$

At a Hopf bifurcation, $\mathrm{Tr}(J) = 0$. Using the fixed point condition $y^* = \frac{x^*}{a(1+x^*)}$, we get

$$\begin{aligned} 0 &= b - 2x^* - \frac{x^*}{a_c(1+x^*)^3} - 2\frac{x^*}{1+x^*} + \frac{x^*}{1+x^*} \\ &\implies 2x^* = b - 2 \\ &\implies x^* = \frac{b-2}{2}. \end{aligned}$$

Finally, substituting $x^* = \frac{b-2}{2}$ into the fixed point equation $y^* = (1+x^*)(b-x^*) = \frac{x^*}{a_c(1+x^*)}$, we solve for a_c:

$$a_c = \frac{4(b-2)}{b^2(b+2)}.$$

Hence, a Hopf bifurcation occurs at the positive fixed point when

$$a = a_c = \frac{4(b-2)}{b^2(b+2)}.$$

d) Using a computer, check the validity of the expression in (c) and determine whether the bifurcation is subcritical or supercritical. Plot typical phase portraits above and below the Hopf bifurcation.

The system is numerically simulated below and above a_c, and the trajectories are shown in Figure 8, and the code to generate it is included in Listing 2. We see that the system has an unstable outward spiral for $a < a_c$ and a stable inward spiral for $a > a_c$. So, the system exhibits **supercritical Hopf bifurcation** for $a \in (a_c, a_c + \epsilon)$ for small $\epsilon > 0$.

```
% Parameters
b = 3; % example value, must be >2 for Hopf
a_c = 4*(b-2)/(b^2*(b+2)); % Hopf bifurcation value
fprintf('Hopf bifurcation occurs at a_c = %.4f\n', a_c);

% System
predprey = @(t,Y,a) [b*Y(1) - Y(1)^2 - (Y(1)*Y(2))/(1+Y(1));
                     -a*Y(2)^2 + (Y(1)*Y(2))/(1+Y(1))];
```

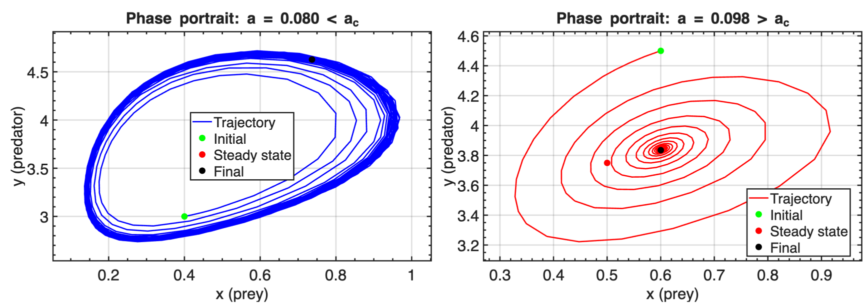

Figure 8: Simulation trajectories of the system on a phase portrait below and above a_c.

```
%% Compute positive fixed point (y* in terms of x*)
x_fixed_fun = @(x,a) b - x - (x./(a*(1+x)^2));
x_guess = 0.5;
xstar = fzero(@(x) x_fixed_fun(x,a_c), x_guess);
ystar = xstar/(a_c*(1+xstar));
fprintf('Positive fixed point at a_c: x* = %.4f, y* = %.4f\n', xstar, ystar);

%% Time integration
tspan = [0 200];

% Below Hopf
a1 = a_c*0.9;
Y0 = [xstar*0.8; ystar*0.8]; % initial condition
[t1,Y1] = ode45(@(t,Y) predprey(t,Y,a1), tspan, Y0);

% Above Hopf
a2 = a_c*1.1;
Y0 = [xstar*1.2; ystar*1.2]; % initial condition
[t2,Y2] = ode45(@(t,Y) predprey(t,Y,a2), tspan, Y0);

%% Figure 1: below Hopf
figure;
plot(Y1(:,1), Y1(:,2), 'b', 'LineWidth', 1.5)
hold on
plot(Y1(1,1), Y1(1,2), 'go', 'MarkerFaceColor','g', 'MarkerSize',8) % initial
plot(xstar, ystar, 'ro', 'MarkerFaceColor','r', 'MarkerSize',8)      % fixed point
plot(Y1(end,1), Y1(end,2), 'ko', 'MarkerFaceColor','k', 'MarkerSize',8) % final
xlabel('x (prey)')
ylabel('y (predator)')
title(sprintf('Phase portrait: a = %.3f < a_c', a1))
legend('Trajectory','Initial','Steady state','Final','Location','best')
grid on
prettyfig;

```

```
%% Figure 2: above Hopf
figure;
plot(Y2(:,1), Y2(:,2), 'r', 'LineWidth', 1.5)
hold on
plot(Y2(1,1), Y2(1,2), 'go', 'MarkerFaceColor','g', '
    MarkerSize',8) % initial
plot(xstar, ystar, 'ro', 'MarkerFaceColor','r', 'MarkerSize'
    ,8)      % fixed point
plot(Y2(end,1), Y2(end,2), 'ko', 'MarkerFaceColor','k', '
    MarkerSize',8) % final
xlabel('x (prey)')
ylabel('y (predator)')
title(sprintf('Phase portrait: a = %.3f > a_c', a2))
legend('Trajectory','Initial','Steady state','Final','Location
    ','best')
grid on
prettyfig;
```

Listing 2: Matlab script to numerically solve the system in problem 4d.