Ratio-Dependent Predator-Prey Models with Nonconstant Predator Harvesting

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The Two Systems

$$\dot{x} = x(1-x) - \frac{axy}{y+x}$$
$$\dot{y} = y\left(-d + \frac{bx}{y+x}\right) - hy$$

$$\dot{x} = x(1-x) - \frac{axy}{y+x}$$
$$\dot{y} = y\left(-d + \frac{bx}{y+x}\right) - \frac{hy}{c+y}$$

Boundedness

- Using a classical differential inequality, we proved that all solutions starting in the first quadrant are uniformly bounded.
- The solutions starting in the first quadrant stay in:

$$\{(x, y) \in \mathbb{R}_+^2 : x + \frac{a}{b}y = \frac{B}{c} + \gamma, \text{ with } \gamma > 0\}$$

Linear Harvesting on the Predator

$$\dot{x} = x(1-x) - \frac{axy}{y+x}$$
$$\dot{y} = y\left(-d + \frac{bx}{y+x}\right) - hy$$

- a=prey capture rate
- b=predator conversion rate
- d=predator death rate
- h=harvesting effort

Equilibria

$$x_1 = 1, \; y_1 = 0,$$

$$x_2 = \phi, \; y_2 = \frac{b - d - h}{d + h}\phi,$$

where $\phi = 1 - a + \frac{ad}{b} + \frac{ah}{b}$.

Stability of Equilibrium Points

$$J(x,y) = \begin{bmatrix} 1 - 2x - \frac{ay^2}{(x+y)^2} & -\frac{ax^2}{(x+y)^2} \\ \frac{by^2}{(x+y)^2} & -d + \frac{bx^2}{(x+y)^2} - h \end{bmatrix}.$$

Jacobian of (x_2, y_2)

$$J(x_2, y_2) = \begin{bmatrix} a - 1 - \frac{a(d+h)^2}{b^2} & -\frac{a(d+h)^2}{b^2} \\ \frac{(b-d-h)^2}{b} & -\frac{(d+h)(b-d-h)}{b} \end{bmatrix}$$

$$a = b\frac{(d+h+1)b-(d+h)^2}{b^2-(d+h)^2}$$

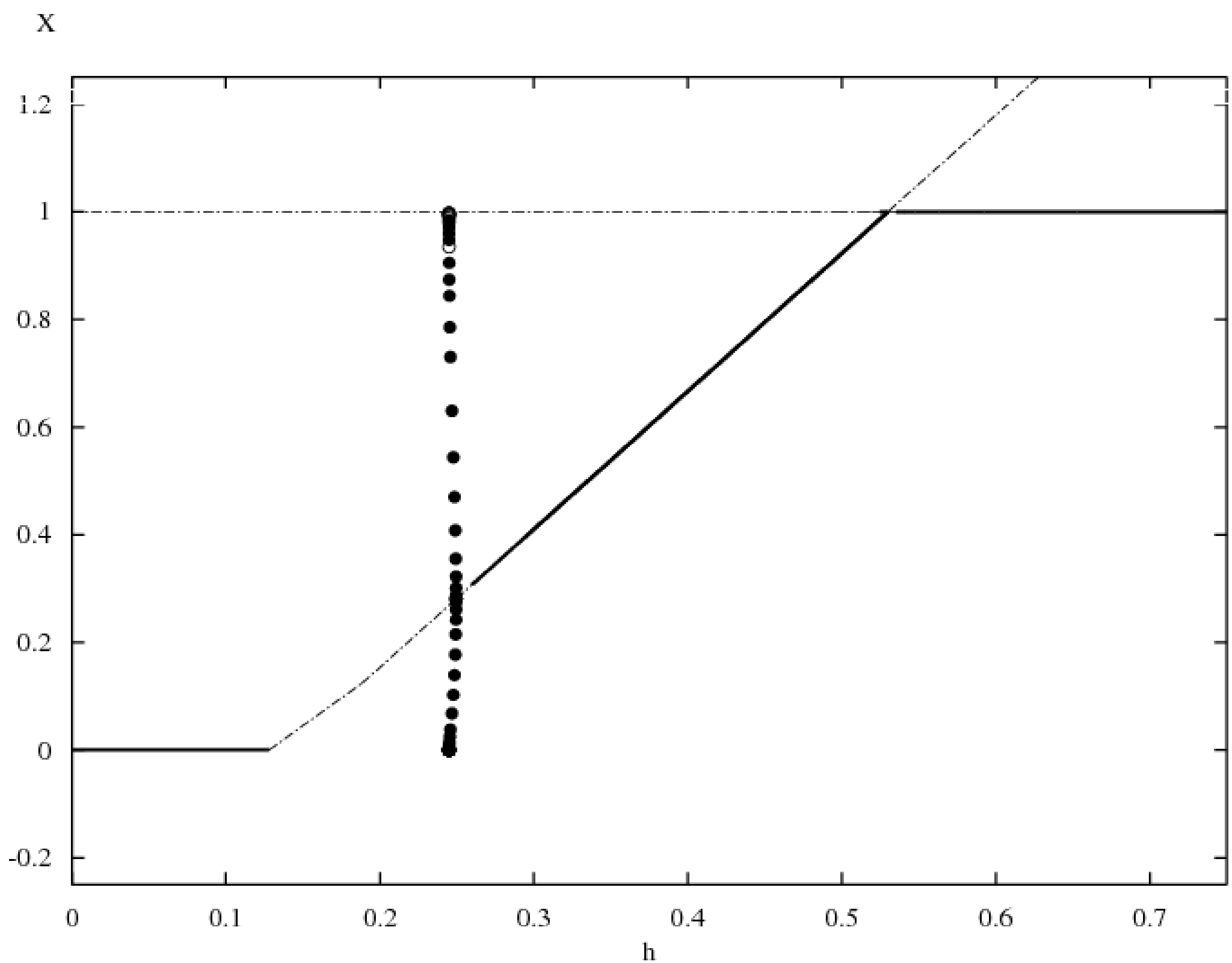
Bifurcations

- Transcritical Bifurcation

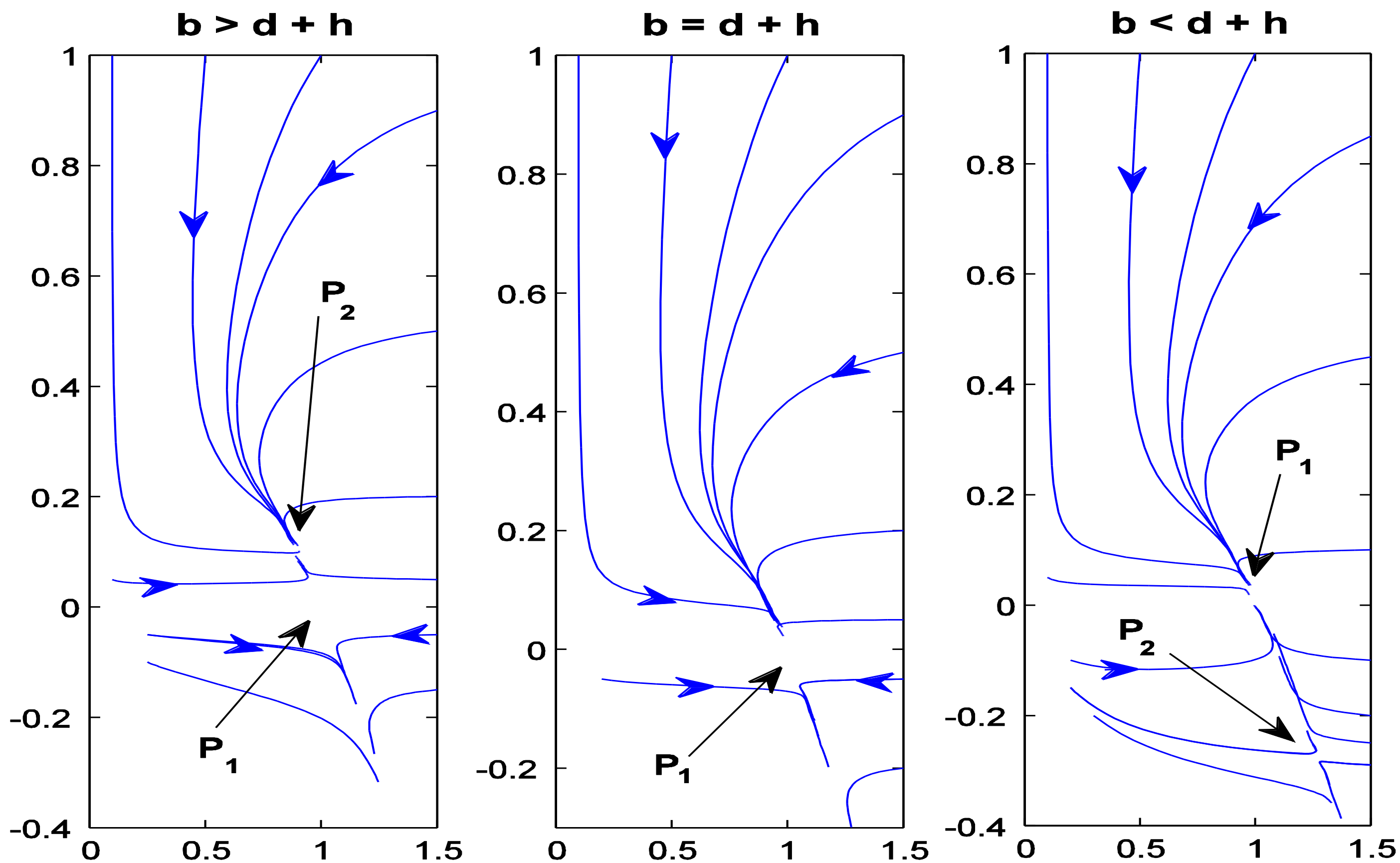
- Hopf Bifurcation

  - Periodic Orbits

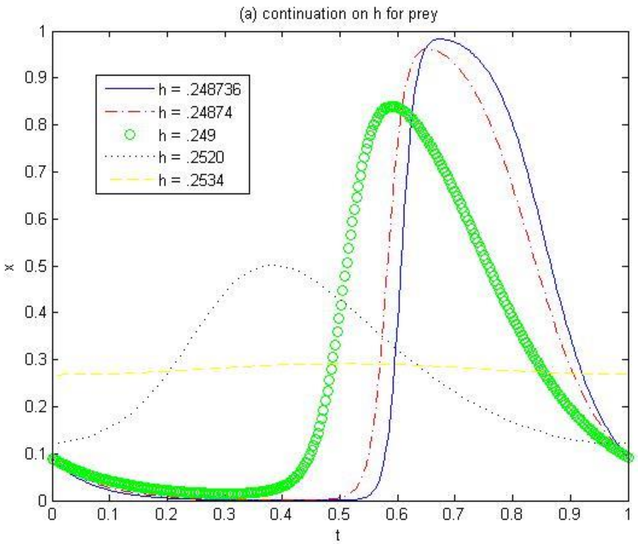
Bifurcation Diagram

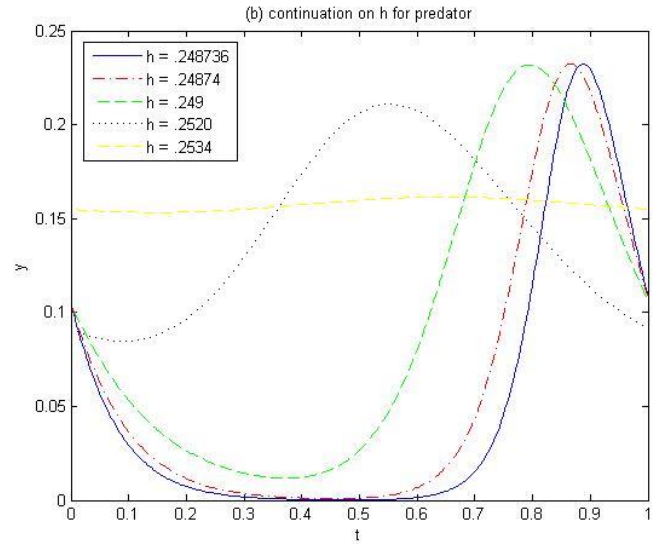


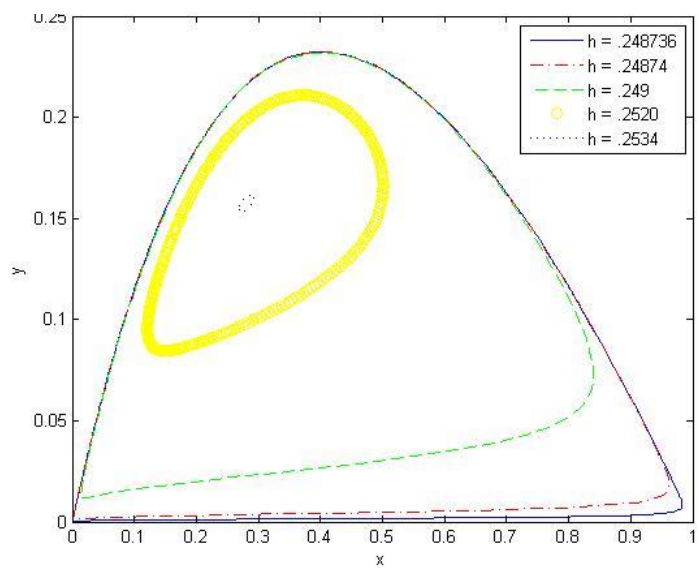
Transcritical Bifurcations



Periodic Orbits







Connecting Orbits

- We found that under certain parameters, many connecting orbits exist.
- If the initial conditions start near one equilibrium, it will move away from the equilibrium and revolve around the periodic orbit.

Rational Harvesting on the Predator

$$
\begin{aligned}
\dot{x} &= x(1-x) - \frac{axy}{y+x} \\
\dot{y} &= y\left(-d + \frac{bx}{y+x}\right) - \frac{hy}{c+y}
\end{aligned}
$$

- a=prey capture rate
- b=predator conversion rate
- c=half-saturation rate
- d=predator death rate
- h=maximum harvesting rate

Equilibrium

```
X=-1/12/b*(-12*b^2*d*a+48*b^3*c^2*a+24*b^2*c*d*a-36*h*a*b^2*c-12*d*c^2*a*b^2-48*b^2*d*c*a^2-24*b^3*c^2+24*b^3*c-8*b^3-60*b^3*c*a+36*b^2*h*a-
72*b^2*h*a^2+12*b*d^2*a^2+8*b^3*c^3-12*b*d^2*c*a^2-36*b*h*a^2*d+8*d^3*a^3+12*a*(-3*b^4-66*h*a^2*b^2*d*c-3*b^4*c^2-12*h*a^3*d^3+6*h^2*b^2*c-
12*h^2*a*b^2*c-3*h^2*b^2*c^2-3*h^2*a^2*d^2+60*h^2*a^2*b*d-12*d^4*a^3*c-24*d^2*a*b^2*c^3-3*d^4*a^2*c^2-3*d^2*b^2*c^4+6*d^3*a*b*c^3+36*d^3*a^2*b*c^2-
18*b^2*d*h*c+66*b^2*d*a*h*c+18*b^2*d*h*c^2+30*h^2*a*b*d*c-36*h*a*b^2*d*c^2-6*h*a^2*d^3*c-6*h*b^2*d*c^3+24*h*a*b*d^2*c^2+96*h*a^2*b*d^2*c-
18*b^2*d^2*a^2-18*b^3*d*a+12*b^3*d*a^2+24*h^2*a^2*b^2+6*h*a*b^3-24*h*a^2*b^3+12*h*a^3*b^3-24*b^4*c*a+6*b^4*c^2*a+30*b^4*c*a^2-3*b^4*c^2*a^2-
12*b^4*c*a^3+36*d*a^2*b^3*c^2+48*d^3*a^3*b*c+6*d*a*b^3*c^3-66*d^2*a^2*b^2*c^2-72*d^2*a^3*b^2*c+48*d*a^3*b^3*c+6*b^4*c+6*b^4*a-
3*b^4*a^2+54*b^2*d*a^2*h+66*b^3*d*a*c+108*b^2*d^2*a^2*c-96*b^3*d*a^2*c-54*b^3*d*a*c^2+36*h*a*b^3*c-24*h*a^2*b^3*c-6*h*a*b^3*c^2+36*h*a^3*b*d^2-
36*h*a^3*b^2*d-6*b*d^3*a-3*b^2*d^2+18*b^2*d^2*a-3*d^4*a^2+12*b*d^3*a^2+6*b^3*d+12*h^3*a*b-3*h^2*b^2-24*h^2*a*b^2+6*h*b^3-30*b*d*a*h^2+6*b^2*d*h-
30*b^2*d*a*h-18*b^3*d*c+18*b^3*d*c^2-6*b^3*d*c^3+66*b^2*d^2*a*c^2+6*d^4*a^2*c-48*b*d^2*a*h*c+12*b^2*d^2*c^3-18*b*d^3*a*c^2-
48*b*d^3*a^2*c+24*b*d^2*a*h+12*b^2*d^2*c+18*b*d^3*a*c-60*b^2*d^2*a*c-18*b^2*d^2*c^2+6*d^3*a^2*h-36*b*d^2*a^2*h-12*h*b^3*c+6*h*b^3*c^2)^(1/2)*b-
24*d*a^2*b^2+60*b^3*c*a^2-24*d^2*a^3*b+24*d*a^3*b^2+12*b^3*a+12*b^3*a^2-8*b^3*a^3)^(1/3)-1/3*(b*d*a-3*h*a*b-2*b^2*c+b^2-d*a*b*c-
b^2*a+4*b^2*c*a+b^2*c^2+d^2*a^2-2*d*a^2*b+b^2*a^2)/b/(-12*b^2*d*a+48*b^3*c^2*a+24*b^2*c*d*a-36*h*a*b^2*c-12*d*c^2*a*b^2-48*b^2*d*c*a^2-
24*b^3*c^2+24*b^3*c-8*b^3-60*b^3*c*a+36*b^2*h*a-72*b^2*h*a^2+12*b*d^2*a^2+8*b^3*c^3-12*b*d^2*c*a^2-36*b*h*a^2*d+8*d^3*a^3+12*a*(-3*b^4-
66*h*a^2*b^2*d*c-3*b^4*c^2-12*h*a^3*d^3+6*h^2*b^2*c-12*h^2*a*b^2*c-3*h^2*b^2*c^2-3*h^2*a^2*d^2+60*h^2*a^2*b*d-12*d^4*a^3*c-24*d^2*a*b^2*c^3-
3*d^4*a^2*c^2-3*d^2*b^2*c^4+6*d^3*a*b*c^3+36*d^3*a^2*b*c^2-18*b^2*d*h*c+66*b^2*d*a*h*c+18*b^2*d*h*c^2+30*h^2*a*b*d*c-36*h*a*b^2*d*c^2-6*h*a^2*d^3*c-
6*h*b^2*d*c^3+24*h*a*b*d^2*c^2+96*h*a^2*b*d^2*c-18*b^2*d^2*a^2-18*b^3*d*a+12*b^3*d*a^2+24*h^2*a^2*b^2+6*h*a*b^3-24*h*a^2*b^3+12*h*a^3*b^3-
24*b^4*c*a+6*b^4*c^2*a+30*b^4*c*a^2-3*b^4*c^2*a^2-12*b^4*c*a^3+36*d*a^2*b^3*c^2+48*d^3*a^3*b*c+6*d*a*b^3*c^3-66*d^2*a^2*b^2*c^2-
72*d^2*a^3*b^2*c+48*d*a^3*b^3*c+6*b^4*c+6*b^4*a-3*b^4*a^2+54*b^2*d*a^2*h+66*b^3*d*a*c+108*b^2*d^2*a^2*c-96*b^3*d*a^2*c-54*b^3*d*a*c^2+36*h*a*b^3*c-
24*h*a^2*b^3*c-6*h*a*b^3*c^2+36*h*a^3*b*d^2-36*h*a^3*b^2*d-6*b*d^3*a-3*b^2*d^2+18*b^2*d^2*a-3*d^4*a^2+12*b*d^3*a^2+6*b^3*d+12*h^3*a*b-3*h^2*b^2-
24*h^2*a*b^2+6*h*b^3-30*b*d*a*h^2+6*b^2*d*h-30*b^2*d*a*h-18*b^3*d*c+18*b^3*d*c^2-6*b^3*d*c^3+66*b^2*d^2*a*c^2+6*d^4*a^2*c-
48*b*d^2*a*h*c+12*b^2*d^2*c^3-18*b*d^3*a*c^2-48*b*d^3*a^2*c+24*b*d^2*a*h+12*b^2*d^2*c+18*b*d^3*a*c-60*b^2*d^2*a*c-18*b^2*d^2*c^2+6*d^3*a^2*h-
36*b*d^2*a^2*h-12*h*b^3*c+6*h*b^3*c^2)^(1/2)*b-24*d*a^2*b^2+60*b^3*c*a^2-24*d^2*a^3*b+24*d*a^3*b^2+12*b^3*a+12*b^3*a^2-8*b^3*a^3)^(1/3)-1/3*(-b*c-
d*a+b*a-2*b)/b+1/2*i*3^(1/2)*(1/6/b*(-12*b^2*d*a+48*b^3*c^2*a+24*b^2*c*d*a-36*h*a*b^2*c-12*d*c^2*a*b^2-48*b^2*d*c*a^2-24*b^3*c^2+24*b^3*c-8*b^3-
60*b^3*c*a+36*b^2*h*a-72*b^2*h*a^2+12*b*d^2*a^2+8*b^3*c^3-12*b*d^2*c*a^2-36*b*h*a^2*d+8*d^3*a^3+12*a*(-3*b^4-66*h*a^2*b^2*d*c-3*b^4*c^2-
12*h*a^3*d^3+6*h^2*b^2*c-12*h^2*a*b^2*c-3*h^2*b^2*c^2-3*h^2*a^2*d^2+60*h^2*a^2*b*d-12*d^4*a^3*c-24*d^2*a*b^2*c^3-3*d^4*a^2*c^2-
3*d^2*b^2*c^4+6*d^3*a*b*c^3+36*d^3*a^2*b*c^2-18*b^2*d*h*c+66*b^2*d*a*h*c+18*b^2*d*h*c^2+30*h^2*a*b*d*c-36*h*a*b^2*d*c^2-6*h*a^2*d^3*c-
6*h*b^2*d*c^3+24*h*a*b*d^2*c^2+96*h*a^2*b*d^2*c-18*b^2*d^2*a^2-18*b^3*d*a+12*b^3*d*a^2+24*h^2*a^2*b^2+6*h*a*b^3-24*h*a^2*b^3+12*h*a^3*b^3-
24*b^4*c*a+6*b^4*c^2*a+30*b^4*c*a^2-3*b^4*c^2*a^2-12*b^4*c*a^3+36*d*a^2*b^3*c^2+48*d^3*a^3*b*c+6*d*a*b^3*c^3-66*d^2*a^2*b^2*c^2-
72*d^2*a^3*b^2*c+48*d*a^3*b^3*c+6*b^4*c+6*b^4*a-3*b^4*a^2+54*b^2*d*a^2*h+66*b^3*d*a*c+108*b^2*d^2*a^2*c-96*b^3*d*a^2*c-54*b^3*d*a*c^2+36*h*a*b^3*c-
24*h*a^2*b^3*c-6*h*a*b^3*c^2+36*h*a^3*b*d^2-36*h*a^3*b^2*d-6*b*d^3*a-3*b^2*d^2+18*b^2*d^2*a-3*d^4*a^2+12*b*d^3*a^2+6*b^3*d+12*h^3*a*b-3*h^2*b^2-
24*h^2*a*b^2+6*h*b^3-30*b*d*a*h^2+6*b^2*d*h-30*b^2*d*a*h-18*b^3*d*c+18*b^3*d*c^2-6*b^3*d*c^3+66*b^2*d^2*a*c^2+6*d^4*a^2*c-
48*b*d^2*a*h*c+12*b^2*d^2*c^3-18*b*d^3*a*c^2-48*b*d^3*a^2*c+24*b*d^2*a*h+12*b^2*d^2*c+18*b*d^3*a*c-60*b^2*d^2*a*c-18*b^2*d^2*c^2+6*d^3*a^2*h-
36*b*d^2*a^2*h-12*h*b^3*c+6*h*b^3*c^2)^(1/2)*b-24*d*a^2*b^2+60*b^3*c*a^2-24*d^2*a^3*b+24*d*a^3*b^2+12*b^3*a+12*b^3*a^2-8*b^3*a^3)^(1/3)-2/3*(b*d*a-
3*h*a*b-2*b^2*c+b^2-d*a*b*c-b^2*a+4*b^2*c*a+b^2*c^2+d^2*a^2-2*d*a^2*b+b^2*a^2)/b/(-12*b^2*d*a+48*b^3*c^2*a+24*b^2*c*d*a-36*h*a*b^2*c-12*d*c^2*a*b^2-
48*b^2*d*c*a^2-24*b^3*c^2+24*b^3*c-8*b^3-60*b^3*c*a+36*b^2*h*a-72*b^2*h*a^2+12*b*d^2*a^2+8*b^3*c^3-12*b*d^2*c*a^2-36*b*h*a^2*d+8*d^3*a^3+12*a*(-
3*b^4-66*h*a^2*b^2*d*c-3*b^4*c^2-12*h*a^3*d^3+6*h^2*b^2*c-12*h^2*a*b^2*c-3*h^2*b^2*c^2-3*h^2*a^2*d^2+60*h^2*a^2*b*d-12*d^4*a^3*c-24*d^2*a*b^2*c^3-
3*d^4*a^2*c^2-3*d^2*b^2*c^4+6*d^3*a*b*c^3+36*d^3*a^2*b*c^2-18*b^2*d*h*c+66*b^2*d*a*h*c+18*b^2*d*h*c^2+30*h^2*a*b*d*c-36*h*a*b^2*d*c^2-6*h*a^2*d^3*c-
6*h*b^2*d*c^3+24*h*a*b*d^2*c^2+96*h*a^2*b*d^2*c-18*b^2*d^2*a^2-18*b^3*d*a+12*b^3*d*a^2+24*h^2*a^2*b^2+6*h*a*b^3-24*h*a^2*b^3+12*h*a^3*b^3-
24*b^4*c*a+6*b^4*c^2*a+30*b^4*c*a^2-3*b^4*c^2*a^2-12*b^4*c*a^3+36*d*a^2*b^3*c^2+48*d^3*a^3*b*c+6*d*a*b^3*c^3-66*d^2*a^2*b^2*c^2-
72*d^2*a^3*b^2*c+48*d*a^3*b^3*c+6*b^4*c+6*b^4*a-3*b^4*a^2+54*b^2*d*a^2*h+66*b^3*d*a*c+108*b^2*d^2*a^2*c-96*b^3*d*a^2*c-54*b^3*d*a*c^2+36*h*a*b^3*c-
24*h*a^2*b^3*c-6*h*a*b^3*c^2+36*h*a^3*b*d^2-36*h*a^3*b^2*d-6*b*d^3*a-3*b^2*d^2+18*b^2*d^2*a-3*d^4*a^2+12*b*d^3*a^2+6*b^3*d+12*h^3*a*b-3*h^2*b^2-
24*h^2*a*b^2+6*h*b^3-30*b*d*a*h^2+6*b^2*d*h-30*b^2*d*a*h-18*b^3*d*c+18*b^3*d*c^2-6*b^3*d*c^3+66*b^2*d^2*a*c^2+6*d^4*a^2*c-
48*b*d^2*a*h*c+12*b^2*d^2*c^3-18*b*d^3*a*c^2-48*b*d^3*a^2*c+24*b*d^2*a*h+12*b^2*d^2*c+18*b*d^3*a*c-60*b^2*d^2*a*c-18*b^2*d^2*c^2+6*d^3*a^2*h-
36*b*d^2*a^2*h-12*h*b^3*c+6*h*b^3*c^2)^(1/2)*b-24*d*a^2*b^2+60*b^3*c*a^2-24*d^2*a^3*b+24*d*a^3*b^2+12*b^3*a+12*b^3*a^2-8*b^3*a^3)^(1/3))
```

Constraints

- b=2h/c, a=2(1−c)/3
- New equation:

$$\dot{x} = x - x^2 - \frac{2(1-c)xy}{3(y+x)}$$

$$\dot{y} = -dy + \frac{2dxy}{y+x} - \frac{2cdy}{2c+y}$$

Equilibrium

$$x_1 = 1,\ y_1 = 0,$$

$$x_2 = \frac{2}{3} + \frac{4}{3}c,\ y_2 = \frac{2}{3} - \frac{8}{3}c$$

Stability of Second Equilibrium

- When $c < \frac{1}{4}$, the equilibrium stays in the first quadrant. When c gets too large, it moves to the fourth quadrant.
- From analysis of the trace and the determinant, the equilibrium is stable for all possible values of c (i.e. $0<c<1$)

Stability of First Equilibrium

- With our constraints, the analysis of the Jacobian is not possible. The equilibrium (1,0) is non-hyperbolic.
- Through numerical analysis, this equilibrium is unstable while the second exists in the first quadrant and stable when the second crosses into the fourth quadrant.

Economic Considerations

- How much does it cost to harvest?
- What is the profit?
- How do we maximize profit and keep the predator alive?

Adding a Profit Equation

$$\rho = (py - c)h = 0$$

- P = price per unit biomass of the predator
- C = harvesting cost per unit effort
- ρ = net profit

Cases for both systems

- There are two cases
  - If $c > py$, then there will be no profit, so the harvesting will shut down and $h = 0$.

  - If $c < py$, then the harvesting will continue

Bionomic Equilibrium for Linear Harvesting

$$(1 - x) - \frac{ay}{y + x} = 0$$

$$-d + \frac{bx}{y + x} - h = 0$$

$$\rho = (py - c)h = 0$$

Bionomic Equilibrium for Linear Harvesting

- $$y_0 = c/p$$
- $$x_0^{\pm} = \frac{-B \pm \sqrt{B^2 - 4C}}{2}$$
  - Where $B = c/p - 1$ and $C = c(a-1)/p$.
- $$h_0^{\pm} = \frac{px_0^{\pm}(b+1) - bc}{px_0^{\pm} + c}$$
  - Where $x_0^{\pm} > \frac{dc}{p(b+1)}$

Bionomic Equilibrium for Rational Harvesting

$$(1-x)-\frac{ay}{y+x}=0$$

$$-d+\frac{bx}{y+x}-\frac{h}{e+y}=0$$

$$\rho=(py-c)h=0$$

Bionomic Equilibrium for Rational Harvesting

- $$y_0 = c/p$$
- $$x_0^{\pm} = \frac{-B \pm \sqrt{B^2 - 4C}}{2}$$
  - Where $B = c/p - 1$ and $C = c(a-1)/p$.
- $$h_0^{\pm} = \frac{pe + c}{px_0^{\pm} + c}[(b-d)x_0^{\pm} - \frac{dc}{p}]$$
  - Where $x_0^{\pm} > \frac{dc}{p(b-d)}$

Traveling Waves

- To account for diffusion of components, we may assume that the predator diffuses more rapidly than the prey; in that case, the first system is generalized to:

$$(u_1)_t = u_1(1-u_1) - \frac{au_1u_1}{u_1+u_2},$$
$$(u_1)_t = (u_2)_{xx} - du_2 + \frac{bu_1u_2}{u_1+y_2} - hu_2$$

- Introducing the wave coordinates,

$$u_1(t,x) = v_1(x+st) = v_1(z), \quad u_2(t,x) = v_2(x+st) = v_2(z)$$

- The PDEs can be written as a set of ODEs:

$$\dot{v_1} = \frac{1}{s}\left[v_1(1-v_1) - \frac{av_1v_1}{v_1+v_2}\right],$$
$$\dot{v_2} = v_3,$$
$$\dot{v_3} = sv_3 + dv_2 - \frac{bu_1v_2}{v_1+v_2} + hv_2$$

Equilibrium

$$v_1 = 1,\ v_2 = 0,\ v_3 = 0$$

$$v_1 = \phi,\ v_2 = \frac{b - d - h}{d + h}\phi,\ v_3 = 0$$

- where $\phi = 1 - a + \frac{ad}{b} + \frac{ah}{b}$

Stability of Equilbria

- Using the Routh–Hurwitz criteria, it can be shown that all of the eigenvalues will never have a negative real part at the same time for either equilibria under any parameters.

- For further study: bifurcations, periodic orbits, etc.

Example

- The fungus *Cordyceps sinensis* survives solely on eating the vegetable caterpillar in Eastern Asia.
- This fungus is harvested for medicinal uses.

Boundedness of Solutions

Theorem 1. *All the solutions of system (1.4) which start in $\mathbb{R}^2_+$ are uniformly bounded.*

Proof. Let $w = x + \frac{a}{b}y$. Then, for any $c > 0$,

$$\dot{w} + cw = x(1 - x + c) - y\left(\frac{ad}{c} + \frac{ah}{b} - \frac{ac}{b}\right) \leq \frac{(c+1)^2}{4} - y\left(\frac{a}{b}(d + h - c)\right).$$

Let $c < d + h$. Then, there exists $B > 0$ such that $\dot{w} + cw \leq B$, or $\dot{w} \leq B - cw$.
Let $\dot{r} = B - cr$, with $r(0) = w(0) = w_0$, whose solution

$$r(t) = \frac{B}{c}\left(1 - e^{-ct}\right) + w_0 e^{-ct}.$$

is bounded for $t \geq 0$. Using a differential inequality [7], we get

$$w(t) \leq r(t) = \frac{B}{c}\left(1 - e^{-ct}\right) + w_0 e^{-ct} \leq \frac{B}{c} \quad \text{as} \quad t \to \infty.$$

Therefore, solutions starting in $\mathbb{R}^2_+$ stay in $S = \{(x, y) \in \mathbb{R}^2_+ : x + \frac{a}{b}y = \frac{B}{c} + \gamma, \text{ for any } \gamma > 0\}$.
□

Remark 2. *A similar result applies to model (1.5), under the condition $d > m$.*