Introduction to Delay Differential Equations with Applications

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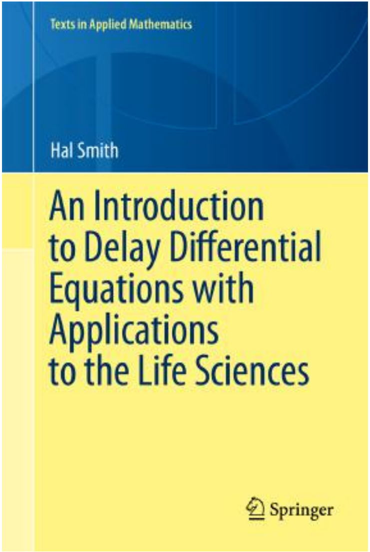
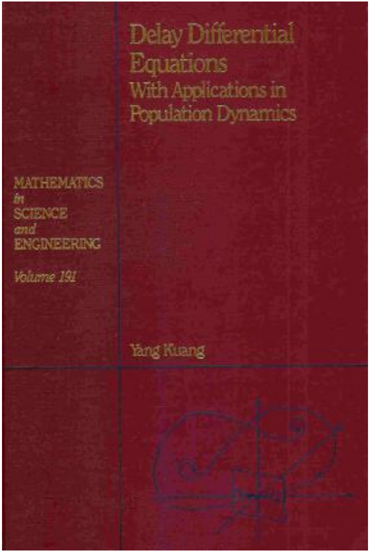
PART 1 - Preliminaries

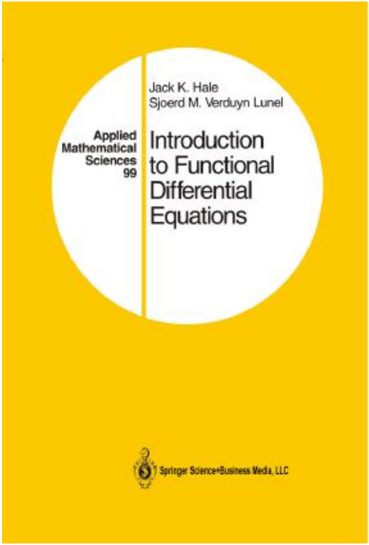
- Examples of DDEs
- Delayed Negative Feedback
- Solving DDEs using a Computer

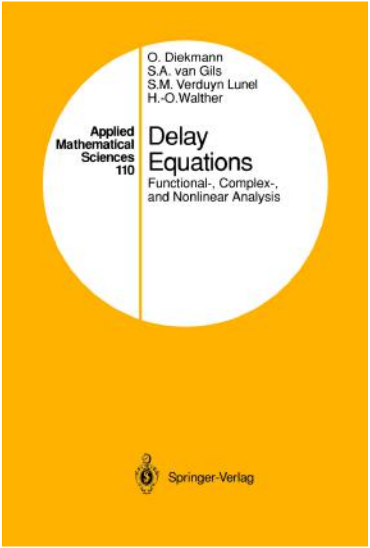
Textbooks in DDEs





Textbooks in DDEs (Graduate Level)





Examples of Delay

Examples of Delay

"How do you send text messages?"

- SIR Epidemic Model with Fixed Period of Temporary Immunity[1]:

$$\begin{aligned} \dot{S}(t) &= -aI(t)S(t) + bI(t-\tau) \\ \dot{I}(t) &= aI(t)S(t) - bI(t) \\ \dot{R}(t) &= bI(t) - bI(t-\tau) \end{aligned}$$

where S, I, and R denote susceptibles, infectives, and recovereds.

- Individuals remain in R class precisely τ units of time.

[1] F. Brauer and C. Castillo-Chavez, *Mathematical Models in Population Biology and Epidemiology*, Springer, New York, 2001.

- The Mackey-Glass Equation for the density of certain blood cells[2]

$$\dot{x}(t) = -ax(t) + \frac{bx(t-\tau)}{x^n(t-\tau) + A^n}$$

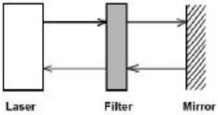
  where $a, b, A, \tau > 0$.

- The delay τ is the time between initiation of cellular production in the bone marrow and release of mature cells into the blood.

[2] L. Glass and M.C. Mackey, *From Clocks to Chaos*, Princeton University Press, Princeton NJ, 1988.

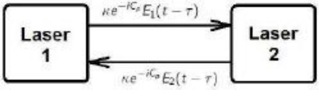
Semiconductor Laser

Lang and Kobayashi (1980), Alsing *et al* (1996)



$$\begin{aligned}\dot{E}(t) &= (1+i\alpha)N(t)E(t) + \kappa e^{-iC_p}E(t-\tau)\\ T\dot{N}(t) &= P - N(t) - (1+2N(t))|E(t)|^2\end{aligned}$$

Erzgraber, Krauskopf and Lenstra (2006)



$$\begin{aligned}\dot{E}_1(t) &= (1+i\alpha)N_1(t)E_1(t) + \kappa e^{-iC_p}E_2(t-\tau) - i\Delta E_1(t)\\ \dot{E}_2(t) &= (1+i\alpha)N_2(t)E_2(t) + \kappa e^{-iC_p}E_1(t-\tau) + i\Delta E_2(t)\\ T\dot{N}_1(t) &= P - N_1(t) - (1+2N_1(t))|E_1(t)|^2\\ T\dot{N}_2(t) &= P - N_2(t) - (1+2N_2(t))|E_2(t)|^2\end{aligned}$$

Warm-Up Example: Delayed Negative Feedback

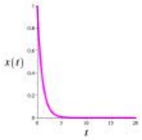
Consider the following IVP

$$\begin{cases} \dot{x}(t) = -x(t), & \text{(ODE)} \\ x(t) = 1 & \text{for } t = 0. \end{cases}$$

Using the ansatz $x(t) = e^{\lambda t}$, we get

$$\lambda + 1 = 0 \qquad (1)$$

and the solution $x(t) = e^{-t}$.



Conclusion

Since the root of (1) has neg. real part, the zero solution of the linear ODE is asymptotically stable.

Consider the following DDE

$$\dot{x}(t) = -x(t-1), \quad \text{(DDE)}.$$

Appropriate IC for the DDE?

$$x(t) = 1 \quad \text{for} \quad t \in [-1, 0]$$

Using the ansatz $x(t) = e^{\lambda t}$, we get

$$\lambda + e^{-\lambda} = 0. \qquad (2)$$

Questions

1. Do all roots of equation (2) have negative real parts?
2. Find the solution to the IVP.

Prove: All roots of $\lambda + e^{-\lambda} = 0$ have negative real parts.

Proof.

- First note that $\lambda + e^{-\lambda} = 0$ doesn't have any real roots.
- Suppose $\lambda = u + iv$ is a root of $\lambda + e^{-\lambda} = 0$ where $u, v \in \mathbb{R}$.
- NTS: $u < 0$
- The root $\lambda = u + iv$ satisfies the transcendental equation, that is,

$$\begin{aligned}
(u+iv) + e^{-(u+iv)} &= 0 \\
(u+iv) + e^{-u}e^{-iv} &= 0 \\
(u+iv) + e^{-u}[\cos(-v) + i\sin(-v)] &= 0 \\
(u+iv) + e^{-u}[\cos(v) - i\sin(v)] &= 0 \\
(e^{-u}\cos v + u) + i(v - e^{-u}\sin v) &= 0 + i0.
\end{aligned}$$

- Thus,

$$\begin{cases} e^{-u}\cos v = -u, \\ e^{-u}\sin v = v. \end{cases}$$

Prove: All roots of $\lambda + e^{-\lambda} = 0$ have negative real parts.

- Recall that a root $\lambda = u + iv$ of $\lambda + e^{-\lambda} = 0$ satisfies

$$-u = e^{-u} \cos v \qquad \text{and} \qquad v = e^{-u} \sin v.$$

- WLOG, suppose $v > 0$, since complex roots come in conjugate pair.
- Going for a contradiction, suppose further that $u \geq 0$.
- Since $u \geq 0$, the first equation tells us that $\cos v \leq 0$. Thus,

$$v \geq \pi/2. \tag{3}$$

- Meanwhile, the second equation gives $|v| = e^{-u}|\sin v|$.
- Note that $|\sin v| \leq 1$. Also, since $u \geq 0$, then $e^{-u} \leq 1$. This implies that

$$|v| \leq 1. \tag{4}$$

- We arrived at a contradiction, since v cannot satisfy both (3) and (4).
- Thus, $u < 0$, and the zero solution of the linear DDE is stable.

Finding the Solution using Method of Steps

Consider the IVP

$$\begin{aligned}\dot{x}(t) &= -x(t-1),\\ x(t) &= 1 \text{ for } t \in [-1, 0].\end{aligned}$$

For $t \in [0, 1]$, we integrate both sides of DDE to obtain

$$x(t) - x(0) = -\int_0^t x(s-1)\, ds.$$

A change of variables yields

$$x(t) = x(0) - \int_{-1}^{t-1} x(s)\, ds.$$

Now using the initial history, we get

$$x(t) = 1 - \int_{-1}^{t-1} 1\, ds = 1 - t.$$

Thus, $x(t) = 1 - t$ on $[0, 1]$.

Method of Steps

We repeat this process now for $t \in [1, 2]$, we get

$$\begin{aligned} x(t) &= x(1) - \int_1^t x(s-1)\ ds &= x(1) - \int_0^{t-1} x(s)\ ds \\ &= 0 - \int_0^{t-1} (1-s)\ ds &= \frac{1}{2}t^2 - 2t + \frac{3}{2}. \end{aligned}$$

Continuing, for $t \in [2, 3]$, we have

$$x(t) = -\frac{1}{6}(t-1)^3 + (t-1)^2 - \frac{3}{2}(t-1) + \frac{1}{6}.$$

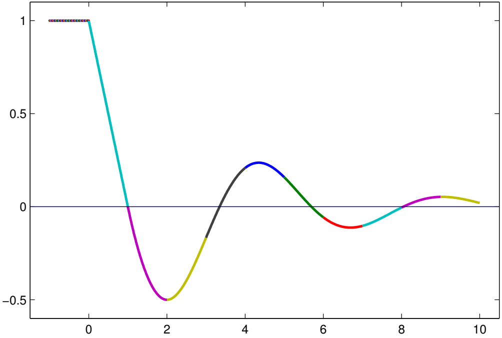
Similarly, for $t \in [3, 4]$, we obtain

$$x(t) = \frac{1}{24}(t-2)^4 - \frac{1}{3}(t-2)^3 + \frac{3}{4}(t-2)^2 - \frac{1}{6}(t-2) - \frac{11}{24}$$

and for $t \in [4, 5]$, we have

$$x(t) = -\frac{1}{120}(t-3)^5 + \frac{1}{12}(t-3)^4 - \frac{1}{4}(t-3)^3 + \frac{1}{12}(t-3)^2 + \frac{11}{24}(t-3) - \frac{19}{120}.$$

Method of Steps



The solution is

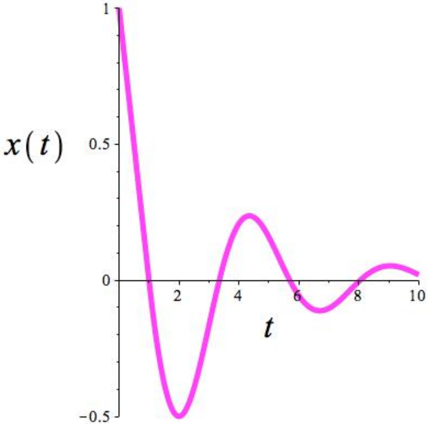
- continuous on $[-1, 10]$,
- smooth except on $[-1, 0]$, and
- The only assumption on the initial history is continuity.

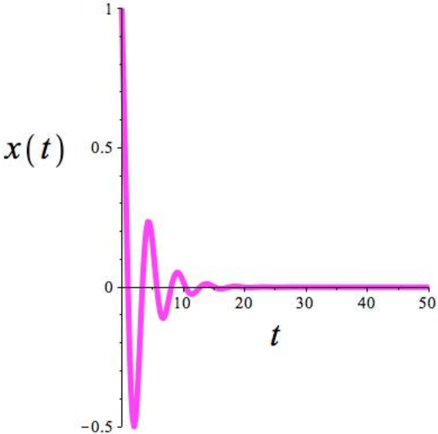
Solving DDEs using a Computer (Maple)

$$ddesys := \left\{ \frac{d}{dt} x(t) + x(t-\tau) = 0, x(0) = 1 \right\} :$$

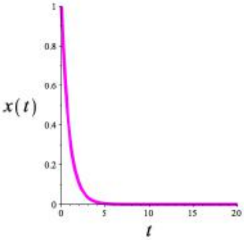
$$dsn := dsolve(eval(ddesys, \{\tau = 1.00\}), numeric) :$$

$$plots[odeplot](dsn, [t, x(t)], 0..50, labels = [t, x(t)]);$$

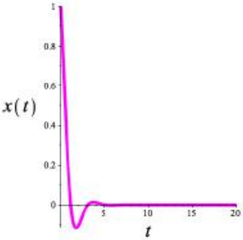




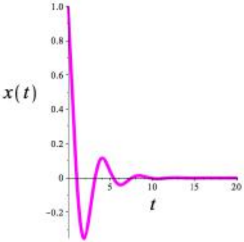
Varying the time delay τ results to oscillations[3]



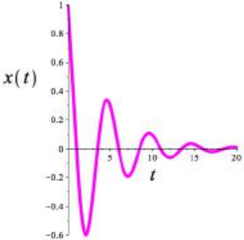
$\tau = 0.10$



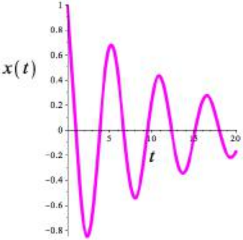
$\tau = 0.60$



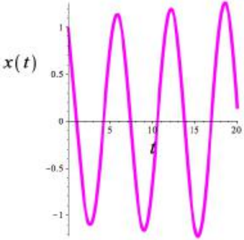
$\tau = 0.85$



$\tau = 1.10$



$\tau = 1.35$

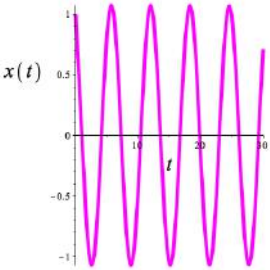


$\tau = 1.60$

[3] DDE $\dot{x}(t) = -x(t-\tau)$ with $x(t) = 1$ for $t \in [-\tau, 0]$

Emergence of Periodic Solutions

- At $\tau = 1.57$, we get the following.



- Suppose $\lambda = iv$, $v > 0$, is a root of

$$\lambda + e^{-\lambda\tau} = 0.$$

So that

$$iv + \cos(v\tau) - i\sin(v\tau) = 0$$

or

$$\begin{aligned} 0 &= \cos(v\tau), \\ v &= \sin(v\tau). \end{aligned}$$

Hence, $v^2 = 1$, i.e. $v = 1$. We get

$$\begin{aligned} \cos(\tau) &= 0, \\ \sin(\tau) &= 1. \end{aligned}$$

Therefore,

$$\tau = \frac{\pi}{2} + 2\pi n, \quad n \in \mathbb{Z}$$

and the critical delay value is $\pi/2$ or approximately 1.57079632679.

Summary

	ODE	DDE
Linear System Initial Condition	$\dot{x}(t) = -x(t)$ $x_0 \in \mathbb{R}$	$\dot{x}(t) = -x(t-\tau)$ $\phi \in C([-\tau, 0], \mathbb{R})$
Equilibrium Solution	$x(t) = 0$	$x(t) = 0$
Characteristic Equation using ansatz $x(t) = e^{\lambda t}$	Polynomial Equation $\lambda + 1 = 0$	Transcendental Equation $\lambda + e^{-\lambda\tau} = 0$
Number of Roots	Finite	Infinite
Stability of Trivial Solution	Asymptotically Stable since $\lambda = -1$	If all roots have negative real part

PART 2 - Linear Systems and Linearization

- Autonomous Linear System
- Characteristic Equations
- Hopf Bifurcation Theorem

Linearized System about an Equilibrium

- Suppose that the following nonlinear system has a fixed point (x^*, y^*).

$$\begin{cases} \dot{x} = f(x,y) \\ \\ \dot{y} = g(x,y) \end{cases}$$

- Let $u = x - x^*$ and $v = y - y^*$. We obtain

$$\dot{u} = \dot{x} = f(x^* + u, y^* + v) = \underbrace{f(x^*, y^*)}_{zero} + \frac{\partial f}{\partial x}(x^*, y^*)u + \frac{\partial f}{\partial y}(x^*, y^*)v + \text{H.O.T.}$$

$$\dot{v} = \dot{y} = g(x^* + u, y^* + v) = \underbrace{g(x^*, y^*)}_{zero} + \frac{\partial g}{\partial x}(x^*, y^*)u + \frac{\partial g}{\partial y}(x^*, y^*)v + \text{H.O.T.}$$

- Neglecting higher order terms, we get the linearized system about (x^*, y^*)

$$\begin{bmatrix} \dot{u} \\ \dot{v} \end{bmatrix} = \underbrace{\begin{bmatrix} \partial f/\partial x & \partial f/\partial y \\ \partial g/\partial x & \partial g/\partial y \end{bmatrix}\Bigg|_{(x^*, y^*)}}_{Jacobian\ \ matrix} \begin{bmatrix} u \\ v \end{bmatrix}.$$

Linearized System about an Equilibrium

Hartman–Grobman Theorem

The behavior of a dynamical system in a domain near a hyperbolic equilibrium point is qualitatively the same as the behavior of its linearization near this equilibrium point, where hyperbolicity means that no eigenvalue of the linearization has real part equal to zero.

ODE vs DDE

	ODE	DDE
1D NLS with equilibrium x^*	$\dot{x}(t) = f(x(t))$	$\dot{x}(t) = f(x(t), x(t-\tau))$ $\dot{x}(t) = f(x(t), y(t))$
Linearized system about x^*	$\dot{x}(t) = a \cdot x(t)$ with $a = \dfrac{\partial f}{\partial x}(x^*)$	$\dot{x}(t) = a \cdot x(t) + b \cdot x(t-\tau)$ $\dot{x}(t) = a \cdot x(t) + b \cdot y(t)$ with $a = \dfrac{\partial f}{\partial x}(x^*, x^*)$, $b = \dfrac{\partial f}{\partial y}(x^*, x^*)$
CE $x(t) = ce^{\lambda t}$	$\lambda - a = 0$	$\lambda - a - be^{-\lambda\tau} = 0$

	ODE	DDE
2D NLS with eq. $X^* = \begin{bmatrix} x_1^* \\ x_2^* \end{bmatrix}$	$\dot{X}(t) = F(X(t))$ $F = \begin{bmatrix} f(x_1, x_2) \\ g(x_1, x_2) \end{bmatrix}$	$\dot{X}(t) = F(X(t), X(t-\tau))$ $\dot{X}(t) = F(X(t), Y(t))$
Characteristic Equation	$\det(\lambda I - A) = 0$ $A = \begin{bmatrix} f_{x_1} & f_{x_2} \\ g_{x_1} & g_{x_2} \end{bmatrix}$ $(x_1, x_2) = (x_1^*, x_2^*)$	$\det(\lambda I - A - Be^{-\lambda\tau}) = 0$ $A = \begin{bmatrix} f_{x_1} & f_{x_2} \\ g_{x_1} & g_{x_2} \end{bmatrix}$, $B = \begin{bmatrix} f_{y_1} & f_{y_2} \\ g_{y_1} & g_{y_2} \end{bmatrix}$ at $(x_1, x_2, y_1, y_2) = (x_1^*, x_2^*, x_1^*, x_2^*)$

Characteristic Equations

DELAY DIFFERENTIAL EQUATIONS

WITH APPLICATIONS IN POPULATION DYNAMICS

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3

Characteristic Equations

3.1. Discrete Delays–Preliminaries

Most studies on delay differential equations start from the local stability analysis of some special solutions. For this purpose, the standard approach is to analyze the stability of the linearized equations about the special solution. If the delay differential equations are autonomous and the special solution is constant, then the linearized equations take the form of linear autonomous delay differential equations. The stability of the trivial solution (i.e., the zero solution) of the linearized equations depends on the locations of the roots of the associated characteristic equation.

When delays are finite, the characteristic equations are functions of delays, and hence the roots of these characteristic equations are also functions of delays. As the lengths of delays change, the stability of the trivial solution may also change. Such phenomena are often referred to as *stability switches*. In the next three sections, we consider the question of stability switches in general linear neutral delay differential equations. The key technique utilized here was developed by Cooke and Grossman (1982) mainly for retarded equations with one discrete delay. Later on, Cooke and van den Driessche (1986) extended this technique to retarded equations with several discrete delays, and Freedman and Kuang (1991) extended it to neutral delay differential equations with one discrete delay. The material of this and the next two sections is adopted from Freedman and Kuang (1991).

Throughout this chapter, the stability of a delay differential equation is referred to as the stability of its trivial solution.

3.2. Discrete Delays—First Order Equations

consider the following first order real scalar linear neutral delay equation

$$\frac{dx(t)}{dt} + \alpha \frac{dx(t-\tau)}{dt} + \beta x(t) + \gamma x(t-\tau) = 0, \tag{2.1}$$

where τ, α, β, γ are real constants. Its characteristic equation is

$$\lambda + \alpha\lambda e^{-\lambda\tau} + \beta + \gamma e^{-\lambda\tau} = 0. \tag{2.2}$$

Theorem 2.1. *In* (2.1), *assume* $|\alpha| \neq 1$; *then the following are true.*

(1) *If* $|\alpha| > 1$, *then* (2.1) *is unstable for all positive delay* τ.

(2) *If* $|\alpha| < 1$, $\gamma^2 < \beta^2$, *or* $\gamma = \beta \neq 0$, *then increasing* τ *does not change the stability of* (2.1).

(3) *If* $|\alpha| < 1$, $\gamma^2 > \beta^2$, *and*

(i) $\beta + \gamma < 0$, *then* (2.1) *is unstable for all positive delay* τ;

(ii) $\beta + \gamma > 0$, *then* (2.1) *is uniformly asymptotically stable when* $\tau < \tau_0$ *and unstable when* $\tau > \tau_0$, *where* $\tau_0 = \theta/\omega$, *and*

$$\omega = \left((\gamma^2 - \beta^2)(1-\alpha^2)^{-1}\right)^{1/2}, \quad \theta = \operatorname{arccot}\left(-\frac{\alpha\omega^2 + \beta\gamma}{\omega(\gamma - \beta\alpha)}\right).$$

- Recall that $\lambda + \alpha\lambda e^{-\lambda\tau} + \beta + \gamma e^{-\lambda\tau} = 0$.

Theorem 2.1. *In* (2.1), *assume* $|\alpha| \neq 1$; *then the following are true.*

(1) *If* $|\alpha| > 1$, *then* (2.1) *is unstable for all positive delay* τ.

(2) *If* $|\alpha| < 1$, $\gamma^2 < \beta^2$, *or* $\gamma = \beta \neq 0$, *then increasing* τ *does not change the stability of* (2.1).

(3) *If* $|\alpha| < 1$, $\gamma^2 > \beta^2$, *and*

(i) $\beta + \gamma < 0$, *then* (2.1) *is unstable for all positive delay* τ;

(ii) $\beta + \gamma > 0$, *then* (2.1) *is uniformly asymptotically stable when* $\tau < \tau_0$ *and unstable when* $\tau > \tau_0$, *where* $\tau_0 = \theta/\omega$, *and*

$$\omega = \left((\gamma^2 - \beta^2)(1 - \alpha^2)^{-1}\right)^{1/2}, \quad \theta = \operatorname{arccot}\left(-\frac{\alpha\omega^2 + \beta\gamma}{\omega(\gamma - \beta\alpha)}\right).$$

- What can we conclude with regards to the CE for the DNFB example

$$\lambda + e^{-\lambda\tau} = 0.$$

using Theorem 2.1?

Exercise

Prove Theorem 2.1 when $\alpha = 0$, i.e. the CE has the form

$$\lambda + \beta + \gamma e^{-\lambda\tau} = 0.$$

1. If $\gamma^2 < \beta^2$ or $\gamma = \beta \neq 0$, then increasing τ does not change the stability of the system.
2. If $\gamma^2 > \beta^2$, and
   - $\beta + \gamma < 0$, then the system is unstable for all $\tau > 0$;
   - $\beta + \gamma > 0$, then the system is asymptotically stable when $\tau < \tau_0$ and unstable when $\tau > \tau_0$, where

   $$\tau_0 = \frac{\operatorname{arccot}(-\beta/\omega)}{\sqrt{\gamma^2 - \beta^2}}.$$

   At $\tau = \tau_0$, the system undergoes a Hopf bifurcation.

Stability analysis of predator-prey population model with time delay and constant rate of harvesting

by Toaha, Syamsuddin, and Malik Abu Hassan

Punjab University Journal of Mathematics **40** (2008): 37–48.

The Model with Time Delay (DDEs)[4]

Consider the following predator-prey model with time delay and constant rate of harvesting

$$\begin{aligned}\dot{x}(t) &= rx(t) - ax(t)x(t-\tau) - bx(t)y(t) - h,\\ \dot{y}(t) &= cx(t)y(t) - dy(t) - k,\end{aligned}$$

where all parameters are assumed to be positive.

[4] Toaha, Syamsuddin, and Malik Abu Hassan. "Stability analysis of predatorprey population model with time delay and constant rate of harvesting." *Punjab University Journal of Mathematics* **40** (2008): 37–48.

Solving for Equilibrium Solutions

- Compute the equilibrium solutions by solving

$$\begin{cases} rx - ax^2 - bxy - h = 0, \\ cxy - dy - k = 0. \end{cases}$$

- Since $h, k > 0$, we can't have $x = 0$ or $y = 0$.
- Look for the intersections of the curves

$$y = \frac{rx - ax^2 - h}{bx} \qquad \text{and} \qquad y = \frac{k}{cx - d}$$

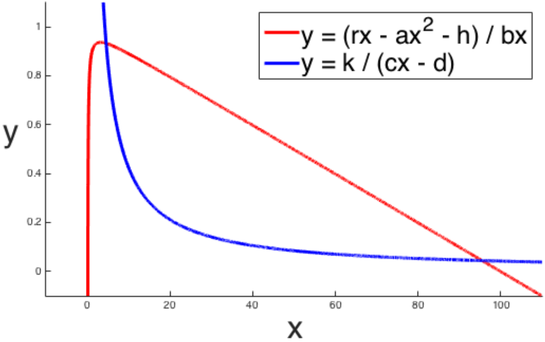
- For a positive equilibrium, we require

$$(r^2 - 4ah) > 0 \qquad \text{and} \qquad (cx - d) > 0.$$

- Use Matlab with the following parameter values:

$$r = 1, \quad a = 0.01, \quad b = 1, \quad c = 0.05, \quad d = 0.3, \quad h = 0.1, \quad k = 0.2,$$

to plot the curves $y = f(x) = \dfrac{rx - ax^2 - h}{bx}$ and $y = g(x) = \dfrac{k}{cx - d}$.



Matlab Codes for Plotting the Curves

```
r = 1; a = 0.01; b = 1; c = 0.05; d = 0.3; h = 0.1; k = 0.2;

x = linspace(0.000001,110,10000);
f = (r*x-(a*x.*x)-h)./(b*x);

xx = linspace(((d/c)+0.001),110,10000);
g = (k)./(c*xx-d);

figure(1); clf; hold on;
plot(x,f,'r','LineWidth',3);
plot(x,g,'b','LineWidth',3);
axis([-10 110 -0.1 1.1]);
xlabel('x','FontSize',30);
ylabel('y   ','FontSize',30,'Rotation',0);
legend('y = (rx - ax^2 - h) / bx','y = k / (cx - d)');
```

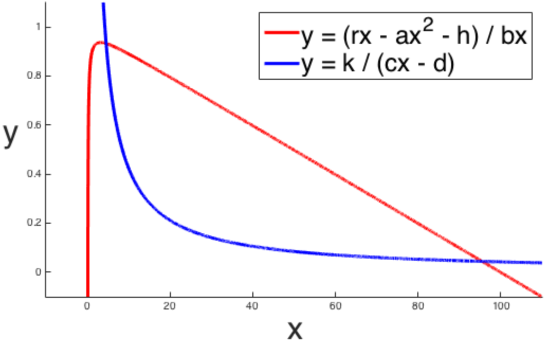
Exercise

- Use Matlab's `fzero` and `feval` with the following parameter values:

$$r = 1, \quad a = 0.01, \quad b = 1, \quad c = 0.05, \quad d = 0.3, \quad h = 0.1, \quad k = 0.2,$$

  to find all the positive equilibria of the model.

- Recall



Solving for Equilibria through Matlab

```
>> r = 1; a = 0.01; b = 1; c = 0.05; d = 0.3; h = 0.1; k = 0.2;
>> f = @(x) (r*x-(a*x.*x)-h)./(b*x);
>> g = @(x) k./(c*x-d);
>> h = @(x) (f(x)-g(x));
>> x1 = fzero(h,10);      y1 = feval(g,x1);
>> x2 = fzero(h,100);     y2 = feval(g,x2);
>> format long
>> [x1 y1; x2 y2]

ans =

  10.518187362771823   0.885310784798016
  95.422031842013041   0.044731705571922
```

Solving for Equilibria through Maple

$r := 1 : a := 0.01 : b := 1 : c := 0.05 : d := 0.3 : h := 0.1 : k := 0.2 :$
$f := r \cdot x - a \cdot x \cdot x - b \cdot x \cdot y - h; g := c \cdot x \cdot y - d \cdot y - k;$

$$-0.01\, x^2 - y\, x + x - 0.1$$

$$0.05\, y\, x - 0.3\, y - 0.2$$

$sol := solve([f = 0, g = 0, x > 0, y > 0], [x, y]);$

$[[x = 10.51818736, y = 0.8853107848], [x = 95.42203184, y = 0.04473170557]]$

Exercise

1. Consider the system

$$\begin{cases} \dot{x} = rx - ax^2 - bxy - h, \\ \dot{y} = cxy - dy - k, \end{cases} \tag{5}$$

where

$$r = 1, \quad a = 0.01, \quad b = 1, \quad c = 0.05, \quad d = 0.3, \quad h = 0.1, \quad k = 0.2,$$

Classify the following equilibria we previous computed

$$\begin{aligned} E_1 &= (10.518187362771823, 0.885310784798016), \\ E_2 &= (95.422031842013041, 0.044731705571922). \end{aligned}$$

2. Consider (5) with the same parameters as above but with $h = 0.01$ and $k = 0.02$. Compute for E_1 and E_2, then determine their local stability.

Exercise 1 - E_1

$r := 1 : a := 0.01 : b := 1 : c := 0.05 : d := 0.3 : h := 0.1 : k := 0.2 :$
$f := r\cdot x - a\cdot x\cdot x - b\cdot x\cdot y - h : g := c\cdot x\cdot y - d\cdot y - k : sol := solve([f=0, g=0, x>0, y>0], [x, y]);$

$$[[x=10.51818736, y=0.8853107848], [x=95.42203184, y=0.04473170557]] \quad \textbf{(1)}$$

$\mathrm{n} := 1 : P := \mathrm{subs}(\mathrm{sol}[n], x); \mathrm{Q} := \mathrm{subs}(sol[n], y);$

$$10.51818736$$

$$0.8853107848 \quad \textbf{(2)}$$

$with(codegen) : with(LinearAlgebra) :$
$F := \textbf{proc}(x, y)\ r\cdot x - a\cdot x\cdot x - b\cdot x\cdot y - h\ \textbf{end proc}:$
$G := \textbf{proc}(x, y)\ c\cdot x\cdot y - d\cdot y - k\ \textbf{end proc}:$
$J := JACOBIAN([F, G]) : print(J(x, y)) :$

$$\begin{bmatrix} -y - 0.02\,x + 1 & -x \\ 0.05\,y & 0.05\,x - 0.3 \end{bmatrix} \quad \textbf{(3)}$$

$M := eval(J(x, y), [x=P, y=Q]) : M1 := \begin{bmatrix} M[1, 1] & M[1, 2] \\ M[2, 1] & M[2, 2] \end{bmatrix} : Eigenvalues(M1);$

$$\begin{bmatrix} 0.06511741800 + 0.6631283315\,\mathrm{I} \\ 0.06511741800 - 0.6631283315\,\mathrm{I} \end{bmatrix} \quad \textbf{(4)}$$

$r := 1 : a := 0.01 : b := 1 : c := 0.05 : d := 0.3 : h := 0.1 : k := 0.2 :$
$f := r\cdot x - a\cdot x\cdot x - b\cdot x\cdot y - h : g := c\cdot x\cdot y - d\cdot y - k : sol := solve([f=0, g=0, x>0, y>0], [x, y]);$

$$[[x=10.51818736, y=0.8853107848], [x=95.42203184, y=0.04473170557]] \quad \textbf{(1)}$$

$\mathrm{n} := 2 : P := \mathrm{subs}(\mathrm{sol}[n], x); \mathrm{Q} := \mathrm{subs}(sol[n], y);$

$$95.42203184$$

$$0.04473170557 \quad \textbf{(2)}$$

$with(codegen) : with(LinearAlgebra) :$
$F := \textbf{proc}(x, y)\ r\cdot x - a\cdot x\cdot x - b\cdot x\cdot y - h\ \textbf{end proc}:$
$G := \textbf{proc}(x, y)\ c\cdot x\cdot y - d\cdot y - k\ \textbf{end proc}:$
$J := JACOBIAN([F, G]) : print(J(x, y)) :$

$$\begin{bmatrix} -y - 0.02\,x + 1 & -x \\ 0.05\,y & 0.05\,x - 0.3 \end{bmatrix} \quad \textbf{(3)}$$

$M := eval(J(x, y), [x=P, y=Q]) : M1 := \begin{bmatrix} M[1,1] & M[1,2] \\ M[2,1] & M[2,2] \end{bmatrix} : Eigenvalues(M1);$

$$\begin{bmatrix} 4.431466714 \\ -0.9135374650 \end{bmatrix} \quad \textbf{(4)}$$

Exercise 2 - E_1

$r := 1 : a := 0.01 : b := 1 : c := 0.05 : d := 0.3 : h := 0.01 : k := 0.02 :$
$f := r \cdot x - a \cdot x \cdot x - b \cdot x \cdot y - h : g := c \cdot x \cdot y - d \cdot y - k : sol := solve([f=0, g=0, x > 0, y > 0], [x, y]);$

$$[[x = 6.428191053, y = 0.9341624419], [x = 99.56243404, y = 0.004275220107]] \quad \textbf{(1)}$$

$\mathrm{n} := 1 : P := \mathrm{subs}(\mathrm{sol}[n], x); \mathrm{Q} := \mathrm{subs}(sol[n], y);$

$$6.428191053$$

$$0.9341624419 \quad \textbf{(2)}$$

$with(codegen) : with(LinearAlgebra) :$
$F := \textbf{proc}(x, y)\ r \cdot x - a \cdot x \cdot x - b \cdot x \cdot y - h\ \textbf{end proc}:$
$G := \textbf{proc}(x, y)\ c \cdot x \cdot y - d \cdot y - k\ \textbf{end proc}:$
$J := JACOBIAN([F, G]) : print(J(x, y)) :$

$$\begin{bmatrix} -y - 0.02\,x + 1 & -x \\ 0.05\,y & 0.05\,x - 0.3 \end{bmatrix} \quad \textbf{(3)}$$

$M := eval(J(x, y), [x = P, y = Q]) : M1 := \begin{bmatrix} M[1, 1] & M[1, 2] \\ M[2, 1] & M[2, 2] \end{bmatrix} : Eigenvalues(M1);$

$$\begin{bmatrix} -0.02065835520 + 0.5463323382\,\mathrm{I} \\ -0.02065835520 - 0.5463323382\,\mathrm{I} \end{bmatrix} \quad \textbf{(4)}$$

$r := 1 : a := 0.01 : b := 1 : c := 0.05 : d := 0.3 : h := 0.01 : k := 0.02 :$
$f := r\cdot x - a\cdot x\cdot x - b\cdot x\cdot y - h : g := c\cdot x\cdot y - d\cdot y - k : sol := solve([f=0, g=0, x > 0, y > 0], [x, y]);$

$$[[x=6.428191053, y=0.9341624419], [x=99.56243404, y=0.004275220107]] \quad (1)$$

$\mathrm{n} := 2 : P := \mathrm{subs}(\mathrm{sol}[n], x); \mathrm{Q} := \mathrm{subs}(sol[n], y);$

$$99.56243404$$

$$0.004275220107 \quad (2)$$

$with(codegen) : with(LinearAlgebra) :$
$F := \textbf{proc}(x, y)\ r\cdot x - a\cdot x\cdot x - b\cdot x\cdot y - h\ \textbf{end proc}:$
$G := \textbf{proc}(x, y)\ c\cdot x\cdot y - d\cdot y - k\ \textbf{end proc}:$
$J := JACOBIAN([F, G]) : print(J(x, y)) :$

$$\begin{bmatrix} -y - 0.02\,x + 1 & -x \\ 0.05\,y & 0.05\,x - 0.3 \end{bmatrix} \quad (3)$$

$M := eval(J(x, y), [x=P, y=Q]) : M1 := \begin{bmatrix} M[1,1] & M[1,2] \\ M[2,1] & M[2,2] \end{bmatrix} : Eigenvalues(M1);$

$$\begin{bmatrix} 4.674368091 \\ -0.9917702905 \end{bmatrix} \quad (4)$$

Linearized System and Characteristic Equation

- Recall the delay model below, with equilibrium $E^* = (x^*, y^*)$,

$$\begin{aligned}\dot{x}(t) &= rx(t) - ax(t)x(t-\tau) - bx(t)y(t) - h,\\ \dot{y}(t) &= cx(t)y(t) - dy(t) - k.\end{aligned}$$

- If we let $X(t) = x(t-\tau)$ and $Y(t) = Y(t-\tau)$, we get

$$\begin{aligned}\dot{x} &= f(x,y,X,Y) = rx - axX - bxy - h,\\ \dot{y} &= g(x,y,X,Y) = cxy - dy - k.\end{aligned}$$

- The linearized system about E^* has corresponding characteristic equation

$$\det(\lambda I - A - Be^{-\lambda\tau}) = 0$$

where

$$\begin{aligned}A &= \begin{bmatrix} f_x & f_y \\ g_x & g_y \end{bmatrix}_{(x,y,X,Y)=(x^*,y^*,x^*,y^*)} = \begin{bmatrix} r - ax^* - by^* & -bx^* \\ cy^* & cx^* - d \end{bmatrix},\\ B &= \begin{bmatrix} f_X & f_Y \\ g_X & g_Y \end{bmatrix}_{(x,y,X,Y)=(x^*,y^*,x^*,y^*)} = \begin{bmatrix} -ax^* & 0 \\ 0 & 0 \end{bmatrix}.\end{aligned}$$

Linearized System and Characteristic Equation

We now write the characteristic equation $\det(\lambda I - A - Be^{-\lambda\tau}) = 0$ with

$$A = \begin{bmatrix} r - ax^* - by^* & -bx^* \\ cy^* & cx^* - d \end{bmatrix} \quad \text{and} \quad B = \begin{bmatrix} -ax^* & 0 \\ 0 & 0 \end{bmatrix}.$$

We get

$$\begin{vmatrix} \lambda - (r - ax^* - by^*) + ax^* e^{-\lambda\tau} & bx^* \\ -cy^* & \lambda - (cx^* - d) \end{vmatrix} = 0.$$

That is,

$$\left[\lambda - (r - ax^* - by^*) + ax^* e^{-\lambda\tau}\right] \left[\lambda - (cx^* - d)\right] + bcx^* y^* = 0$$

or

$$\left(\lambda^2 + a_1\lambda + a_2\right) + \left(a_3\lambda + a_4\right) e^{-\lambda\tau} = 0 \qquad \text{(CE)}$$

where

$$\begin{aligned} a_1 &= -(r - ax^* - by^*) - (cx^* - d), \\ a_2 &= (rx^* - ax^* - by^*)(cx^* - d) + bcx^* y^*, \\ a_3 &= ax^*, \\ a_4 &= -ax^*(cx^* - d). \end{aligned}$$

Local Stability of the Equilibrium E^*

- For the case $\tau = 0$, the characteristic equation
$$\left(\lambda^2 + a_1\lambda + a_2\right) + \left(a_3\lambda + a_4\right) e^{-\lambda\tau} = 0 \tag{CE}$$
reduces to
$$\lambda^2 + (a_1 + a_3)\lambda + (a_2 + a_4) = 0.$$
By RHC, all roots of the above quadratic equation has negative real part iff
$$(a_1 + a_3) > 0 \qquad \text{and} \qquad (a_2 + a_4) > 0.$$
- Suppose $(a_1 + a_3) > 0$ and $(a_2 + a_4) > 0$, and consider now the case $\tau > 0$.

Lemma (Ruan and Wei 2003)

As τ is increased from zero, the sum of the orders of the roots of (CE) in the open right half-plane can change only if a root appears on or crosses the imaginary axis.

- We consider 2 cases: $\lambda = 0$ and $\lambda = i\omega$. The case $\lambda = 0$ is not possible.

Possibility of Purely Imaginary Roots of (CE)

- Recall the characteristic equation

$$\left(\lambda^2 + a_1\lambda + a_2\right) + \left(a_3\lambda + a_4\right) e^{-\lambda\tau} \quad = \quad 0 \qquad \text{(CE)}$$

- If $\lambda = 0$ is a root of (CE), then $(a_2 + a_4) = 0$.

  Since $(a_2 + a_4) > 0$, then $\lambda = 0$ is not a root of (CE).

- Suppose $\lambda = i\omega$ is a simple root of (CE) and WLOG we assume $\omega > 0$. Then,

$$\begin{aligned} (-\omega^2 + ia_1\omega + a_2) + (ia_3\omega + a_4)e^{-i\omega\tau} &= 0, \\ \text{or} \qquad (-\omega^2 + ia_1\omega + a_2) + (ia_3\omega + a_4)(\cos\omega\tau - i\sin\omega\tau) &= 0 + i0. \end{aligned}$$

  Splitting into real and imaginary parts, we get

$$\begin{aligned} (-\omega^2 + a_2) + (a_4\cos\omega\tau + a_3\omega\sin\omega\tau) &= 0, \\ (a_1\omega) + (-a_4\sin\omega\tau + a_3\omega\cos\omega\tau) &= 0. \end{aligned}$$

Possibility of Purely Imaginary Roots of (CE)

That is,

$$\begin{aligned} \omega^2 - a_2 &= a_4 \cos \omega\tau + a_3\omega \sin \omega\tau, \\ a_1\omega &= a_4 \sin \omega\tau - a_3\omega \cos \omega\tau. \end{aligned}$$

Squaring each sides and then adding corresponding sides, we obtain

$$(\omega^2 - a_2)^2 + a_1^2\omega^2 = a_4^2 + a_3^2\omega^2$$

or

$$\omega^4 + \alpha\omega^2 + \beta = 0 \tag{6}$$

where

$$\alpha = a_1^2 - 2a_2 - a_3^2 \quad \text{and} \quad \beta = a_2^2 - a_4^2.$$

If we let $u = \omega^2$, then equation (6) becomes following quadratic equation in u

$$h(u) := u^2 + \alpha u + \beta = 0. \tag{7}$$

If (7) has a positive root $u^* > 0$, then (6) also has a positive root $\omega^* = \sqrt{u^*} > 0$.

When does $u^2 + \alpha u + \beta = 0$ have *simple* positive roots?

- By RHC, if $\alpha > 0$ and $\beta > 0$, then the roots of the quadratic equation have negative real parts, i.e. the quadratic equation doesn't have positive roots.
- The equation $\omega^4 + \alpha\omega^2 + \beta = 0$ doesn't have positive (real) roots.
- As τ is increased from zero, the sum of the orders of the roots of (CE) in the open right half-plane doesn't change.

Theorem 4 (Toaha and Hassan, 2008)

Suppose $(a_1 + a_3) > 0$ and $(a_2 + a_4) > 0$.
If $\alpha > 0$ and $\beta > 0$, then E^* is LAS for all $\tau \geq 0$.

- Exercise: Interpret the given RHC geometrically.

Really, when does $u^2 + \alpha u + \beta = 0$ have positive roots?!

- Exactly one simple positive root when
  - $\alpha < 0$ and $\beta \leq 0$
  - $\alpha = 0$ and $\beta < 0$
  - $\alpha > 0$ and $\beta < 0$
- Exactly two simple positive roots when
  - $\alpha < 0$ and $\beta > 0$ and $\overline{y} < 0$ where $(\overline{x}, \overline{y})$ is the vertex of the parabola.

(These are the inequalities in (3.13) of Toaha and Hassan, 2008.)

Critical Delay Values

- Suppose $\alpha < 0$, $\beta > 0$ and $\overline{y} < 0$.
  Then, the equation $\omega^4 + \alpha\omega^2 + \beta = 0$ has 2 simple positive roots $\omega = \omega_\pm$.
- From

$$\begin{aligned} a_4 \cos\omega\tau &+ a_3\omega \sin\omega\tau &= \omega^2 - a_2, \\ a_4 \sin\omega\tau &- a_3\omega \cos\omega\tau &= a_1\omega. \end{aligned}$$

  we get the critical delay $\tau = \tau_\pm$ corresponding to the positive roots $\omega = \omega_\pm$

$$\tau_k^\pm = \frac{1}{\omega_\pm}\left[\tan^{-1}\left\{\frac{\omega_\pm(a_3\omega_\pm^2 + a_1 a_4 - a_2 a_3)}{(a_4 - a_1 a_3)\omega_\pm^2 - a_2 a_4}\right\} - 2\pi k\right].$$

- **Proof.** Solve

$$\begin{bmatrix} a_3\omega & a_4 \\ a_4 & -a_3\omega \end{bmatrix}\begin{bmatrix} \sin\omega\tau \\ \cos\omega\tau \end{bmatrix} = \begin{bmatrix} \omega^2 - a_2 \\ a_1\omega \end{bmatrix}$$

  for $\sin\omega\tau$ and $\cos\omega\tau$. We get $\tan\omega\tau = \dfrac{\omega(a_3\omega^2 + a_1 a_4 - a_2 a_3)}{(a_4 - a_1 a_3)\omega^2 - a_2 a_4}$.

Transversality Conditions

- Recall that $h(u) = u^2 + \alpha u + \beta$. So $h'(u) = 2u + \alpha = 2\omega^2 + (a_1^2 - 2a_2 - a_3^2)$.

See (3.15) of Toaha and Hassan, 2008

We have

$$\operatorname{sign}\left\{\frac{d(\mathrm{Re}\lambda)}{d\tau}\right\} = \operatorname{sign}\left\{h'(\omega^2)\right\} = \operatorname{sign}\left\{h'(u)\right\}.$$

- In particular,

$$\operatorname{sign}\left\{\frac{d(\mathrm{Re}\lambda)}{d\tau}\right\}\Bigg|_{\substack{\tau=\tau_k^{\pm}\\ \omega=\omega_{\pm}}} = \operatorname{sign}\left\{h'(\omega_{\pm}^2)\right\} = \operatorname{sign}\left\{h'(u_{\pm})\right\} = \pm 1.$$

- That is,

$$\frac{d(\mathrm{Re}\lambda)}{d\tau}\Bigg|_{\tau=\tau_k^+} > 0 \qquad \text{and} \qquad \frac{d(\mathrm{Re}\lambda)}{d\tau}\Bigg|_{\tau=\tau_k^-} < 0.$$

Critical Delay Values (Toaha and Hassan, 2008)

$$\begin{aligned} \tau_0^+ &= 1.37941, \\ \tau_1^+ &= 6.98104, \\ \tau_2^+ &= 12.58266, \\ \tau_3^+ &= 18.68453, \end{aligned} \qquad \text{and} \qquad \begin{aligned} \tau_0^- &= 5.39314, \\ \tau_1^- &= 12.53884, \\ \tau_2^- &= 19.68453, \\ \tau_3^- &= 26.83023. \end{aligned}$$

Dynamics of a Stage Structured Intraguild Predation Model

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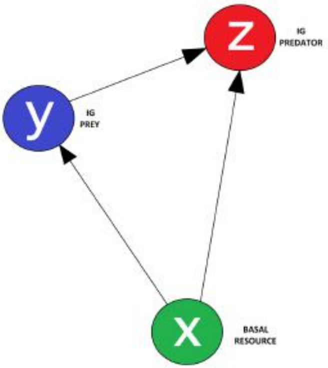


$$\begin{aligned}
\dot{z}(t) &= z(t)\,[-c_0 + c_1 x(t) + c_2 y(t)] \\
\dot{y}(t) &= y(t)\,[-b_0 + b_1 x(t) - b_3 z(t)] \\
\dot{x}(t) &= x(t)\,[\;\, a_0 - a_1 x(t)] - a_2 y(t) - a_3 z(t)]
\end{aligned}$$

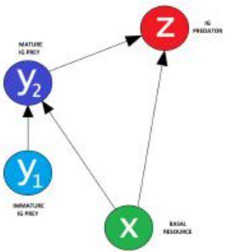
- Omnivory – feeding on more than one trophic level.
- IGP – combination of community modules (predation and competition), and is quite common in nature (Arim and Marquet, 2004).
- Persistence – The IG prey must be superior than the IG predator in competing for the shared basal resource while the IG predator must gain significantly from its consumption of the IG prey (Holt and Polis, 1997).

Stage-Structured IGP Model

Some works on stage-structured models

- Wang, Y., Wu, J., Xiao, Y.: A stage structured predator-prey model with time delays. (2008)
- Yamaguchi, M., Takeuchi, Y., Ma, W.: Dynamical properties of a stage structured three-species model with intraguild predation. (2007)

In our model, we split the IG Prey population $y(t)$ into immature $y_1(t)$ and mature $y_2(t)$ stages with maturation age $\tau \geq 0$



- the immature IG preys have little ability of predation, and
- the immature IG preys are able to avoid predation by the IG predators by taking refuge.

Stage-Structured IGP Model

$$
\begin{aligned}
\dot{x}(t) &= x(t)\left[a_0 - a_1 x(t) - a_2 y_2(t) - a_3 z(t)\right], \\
\dot{y}_1(t) &= -\mu y_1(t) - b_1 e^{-\mu\tau} x(t-\tau) y_2(t-\tau) + b_1 x(t) y_2(t), \\
\dot{y}_2(t) &= -b_0 y_2(t) + b_1 e^{-\mu\tau} x(t-\tau) y_2(t-\tau) - b_3 y_2(t) z(t), \\
\dot{z}(t) &= z(t)\left[-c_0 + c_1 x(t) + c_2 y_2(t)\right],
\end{aligned}
$$

- $\mu > 0$ is the death rate of immature IG preys,
- $b_1 x(t) y_2(t)$ is number of immature IG preys that are born at time t, and
- $b_1 e^{-\mu\tau} x(t-\tau) y_2(t-\tau)$ is the number of immature IG preys that was born at time $(t-\tau)$ which still survives at time t and is transferred from the immature stage to the mature stage at time t.
- The equation for the immature IG prey can be separated from the rest.

Stage-Structured IGP Model

- Renaming $y_2(t)$ to just $y(t)$, we obtain the following system:

$$\begin{aligned} \dot{x}(t) &= x(t)\left[a_0 - a_1 x(t) - a_2 y(t) - a_3 z(t)\right], \\ \dot{y}(t) &= -b_0 y(t) + b_1 e^{-\mu\tau} x(t-\tau) y(t-\tau) - b_3 y(t) z(t), \\ \dot{z}(t) &= z(t)\left[-c_0 + c_1 x(t) + c_2 y(t)\right]. \end{aligned} \tag{8}$$

Goal

Examine the dynamical effects of the maturation age τ.

- System (8) has five possible non-negative equilibrium solutions:

$$\begin{aligned} E_0 &= (0,0,0), \\ E_1 &= (K,0,0), \\ E_2 &= (A,B,0), \\ E_3 &= (C,0,D), \\ E_4 &= (P/S, Q/S, R/S). \end{aligned}$$

Local Stability of Equilibria

- Stability of equilibrium $E_* = (x_*, y_*, z_*)$ is determined by the roots of the characteristic equation

$$\det(\lambda I - M_1 - M_2 e^{-\lambda\tau}) = 0 \tag{9}$$

corresponding to the linearized system about E_* where $[M_1|M_2]$ is given by

$$\left[\begin{array}{ccc|ccc} a_0 - 2a_1 x_* - a_2 y_* - a_3 z_* & -a_2 x_* & -a_3 x_* & 0 & 0 & 0 \\ 0 & -b_0 - b_3 z_* & -b_3 y_* & b_1 e^{-\mu\tau} y_* & b_1 e^{-\mu\tau} x_* & 0 \\ c_1 z_* & c_2 z_* & -c_0 + c_1 x_* + c_2 y_* & 0 & 0 & 0 \end{array}\right].$$

- If all roots of (9) have negative real part, then E_* is LAS.

Strategy

Use Routh-Hurwitz criterion, when $\tau = 0$, to obtain conditions that will guarantee that all roots of (9) have negative real part. Then, check if stability switches occur (or not) as τ is increased from zero.

Equilibrium Solution	Existence Conditions	Stability Conditions
$E_0 = (0,0,0)$	Always exists	Unstable saddle
$E_1 = (K,0,0)$	Always exists	$B < 0$ and $D < 0$
$E_2 = (A,B,0)$	$B > 0$	$R < 0$ and $\frac{a_1}{a_0 b_1} > \tau e^{\mu\tau}$
$E_3 = (C,0,D)$	$D > 0$	$Q < 0$
$E_4 = \left(\frac{P}{S}, \frac{Q}{S}, \frac{R}{S}\right)$	$\frac{P}{S}, \frac{Q}{S}, \frac{R}{S} > 0$	

Note that: $K = \frac{a_0}{a_1}$, $A = \frac{b_0}{b_1 e^{-\mu\tau}}$, $B = \frac{a_0 b_1 e^{-\mu\tau} - a_1 b_0}{a_2 b_1 e^{-\mu\tau}}$, $C = \frac{c_0}{c_1}$, $D = \frac{a_0 c_1 - a_1 c_0}{a_3 c_1}$,
$S = a_1 b_3 c_2 - a_2 b_3 c_1 + a_3 b_1 c_2 e^{-\mu\tau}$, $R = (a_0 c_2 - a_2 c_0) b_1 e^{-\mu\tau} - a_1 b_0 c_2 + a_2 b_0 c_1$,
$Q = -a_0 b_3 c_1 + a_1 b_3 c_0 - a_3 b_0 c_1 + a_3 b_1 c_0 e^{-\mu\tau}$, and $P = a_0 b_3 c_2 - a_2 b_3 c_0 + a_3 b_0 c_2$.

Local Stability of the Positive Equilibrium (Case $\tau = 0$)

- Characteristic equation corresponding to the linearized system around E_4 is

$$\left[\lambda^3 + a(\tau)\lambda^2 + b(\tau)\lambda + c(\tau)\right] + \left[p(\tau)\lambda^2 + q(\tau)\lambda + r(\tau)\right] \; e^{-\lambda\tau} \; = \; 0. \quad (10)$$

- Follow the discussions and notations used in (Beretta and Kuang 2002) in analyzing the roots of such equations with *delay-dependent* coefficients.
- Note that $(a+p), (b+q) > 0$, while $(c+r) > 0$ if $S > 0$.
- Also,$(a+p)(b+q) - (c+r)$ is given by

$$a_1 \left(a_2 b_1 e^{-\mu\tau} \cdot \frac{Q}{S} + a_3 c_1 \cdot \frac{R}{S} \right) \left(\frac{P}{S} \right)^2 + \left(a_2 b_3 c_1 - a_3 b_1 c_2 e^{-\mu\tau} \right) \cdot \frac{P}{S} \cdot \frac{Q}{S} \cdot \frac{R}{S}.$$

- At $\tau = 0$, equation (10) reduces to $\lambda^3 + \rho\lambda^2 + \sigma\lambda + \varphi = 0$ where the coefficients $\rho = (a+p)|_{\tau=0}$, $\sigma = (b+q)|_{\tau=0}$, and $\varphi = (c+r)|_{\tau=0}$.

Theorem

Let $\tau = 0$ in system (8). If $S(0) > 0$ and $(a_2 b_3 c_1 - a_3 b_1 c_2) > 0$, then the positive equilibrium E_4 is LAS. If $S(0) < 0$ or if $(\rho\sigma - \varphi) < 0$, then E_4 is unstable.

Local Stability of the Positive Equilibrium (Case $\tau > 0$)

- Since $S \neq 0$, $(c + r) = S \cdot \frac{P}{S}\frac{Q}{S}\frac{R}{S} \neq 0$. Thus, $\lambda(\tau) = 0$ is not a root of (10).
- If $\lambda(\tau) = i\omega(\tau)$, with $\omega(\tau) > 0$, is a root (10), then

$$(a\omega^2(\tau) - c)^2 + (\omega^2(\tau) - b)^2\omega^2(\tau) \;=\; (p\omega^2(\tau) - r)^2 + q^2\omega^2(\tau). \qquad (11)$$

- Following (Beretta and Kunag 2002), we write (11) into the following form

$$F(\omega, \tau) \;:=\; \omega^6 + \alpha\omega^4 + \beta\omega^2 + \gamma \;=\; 0 \qquad (12)$$

  where $\alpha = a^2 - p^2 - 2b$, $\beta = b^2 - q^2 + 2(pr - ac)$, and $\gamma = c^2 - r^2$.
- If we let $u = \omega^2$, then (12) can be written as

$$H(u, \tau) \;:=\; u^3 + \alpha u^2 + \beta u + \gamma \;=\; 0. \qquad (13)$$

- Note that if (13) has a positive root u_0, then (12) has a positive root $\omega_0 = \sqrt{u_0}$ and consequently, (10) has a pair of purely imaginary roots $\lambda = \pm i\omega_0$.
- If (13) has a positive root, then *stability switches* may occur as τ is varied.

Local Stability of the Positive Equilibrium (Case $\tau > 0$)

- Let $I \subset \mathbf{R}_{+0}$ be the set where $\omega(\tau)$ is a positive root of (12).
- We then define the angle $\theta(\tau) \in [0, 2\pi]$ as solution to the following

$$\begin{cases} \sin\theta(\tau) & = & \dfrac{(p\omega^2(\tau) - r)(\omega^2(\tau) - b)\omega(\tau) + q\omega(\tau)(a\omega^2(\tau) - c)}{p^2\omega^4(\tau) + (q^2 - 2pr)\omega^2(\tau) + r^2}, \\ \\ \cos\theta(\tau) & = & \dfrac{q\omega^2(\tau)(\omega^2(\tau) - b) - (p\omega^2(\tau) - r)(a\omega^2(\tau) - c)}{p^2\omega^4(\tau) + (q^2 - 2pr)\omega^2(\tau) + r^2}. \end{cases}$$

- For $\tau \in I$, we have $\omega(\tau)\tau = \theta(\tau) + 2n\pi$ for $n \in \mathbf{N}_0$.
- For $\tau \in I$ and $n \in \mathbf{N}_0$, we can define the functions

$$S_n(\tau) := \tau - \tau_n(\tau),$$

  where $\tau_n(\tau) = (\theta(\tau) + 2n\pi)/\omega(\tau)$.
- The functions $S_n(\tau)$ are continuous and differentiable.

Local Stability of the Positive Equilibrium (Case $\tau > 0$)

Theorem (Beretta and Kuang (2002))

Assume that $\omega(\tau)$ is a positive root of (12) defined for $\tau \in I \subset \mathbf{R}_{+0}$, and at some $\tau^* \in I$, $S_n(\tau^*) = 0$ for some $n \in \mathbf{N}_0$. Then a conjugate pair of simple purely imaginary roots $\lambda_\pm(\tau^*) = \pm i\omega(\tau^*)$ of (10) exists at $\tau = \tau^*$ which crosses the imaginary axis from left to right (resp. from right to left) if $\delta(\tau^*) > 0$ (resp. $\delta(\tau^*) < 0$), where

$$\delta(\tau^*) = \mathrm{sign}\left\{ \frac{d\mathrm{Re}\lambda}{d\tau}\Big|_{\lambda=i\omega(\tau^*)} \right\} = \mathrm{sign}\left\{F'_\omega(\omega(\tau^*), \tau^*)\right\} \cdot \mathrm{sign}\left\{ \frac{dS_n(\tau)}{d\tau}\Big|_{\tau=\tau^*} \right\}.$$

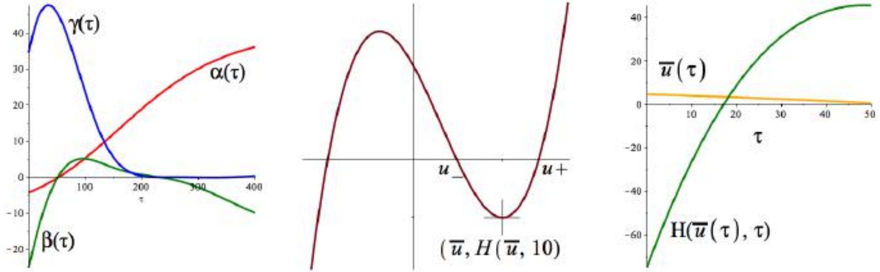
- Since $F'_\omega(\omega(\tau), \tau) = 2\omega(\tau) \cdot H'_u(u(\tau), \tau)|_{u(\tau)=\omega^2(\tau)}$ and $\omega(\tau) > 0$ for $\tau \in I$,

$$\delta(\tau^*) \quad = \quad \mathrm{sign}\left\{H'_u(u(\tau^*), \tau^*)\right\} \; \cdot \; \mathrm{sign}\left\{ \frac{dS_n(\tau)}{d\tau}\Big|_{\tau=\tau^*} \right\}. \qquad (14)$$

- Also, if such τ^* exists and $\delta(\tau^*) \neq 0$, then at $\tau = \tau^*$ the system undergoes a Hopf bifurcation at the positive equilibrium E_4.

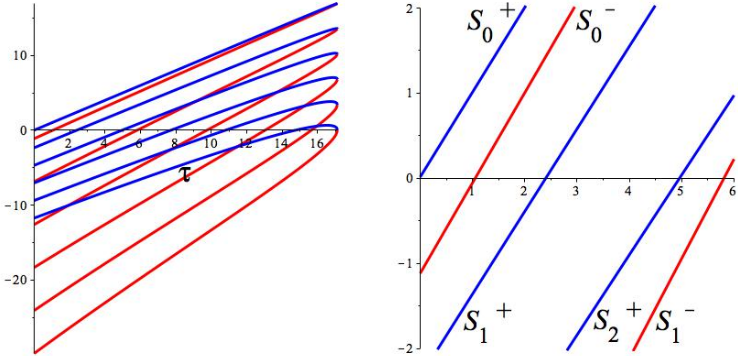
Example

- We use $a_0 = 5.00$, $a_1 = 0.40$, $a_2 = 1.00$, $a_3 = 0.85$, $b_0 = 1.00$, $b_1 = 1.00$, $b_3 = 1.00$, $c_0 = 1.20$, $c_1 = 0.10$, $c_2 = 1.00$, and $\mu = 0.01$.
- At $\tau = 0$, $E_4 = (4.0435, 0.7957, 3.0435)$ is unstable because $(\rho\sigma - \varphi) < 0$. We want to know if stability switches will occur as τ is increased from zero.



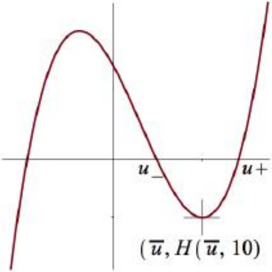
- For τ immediately to the right of zero, $H(u,\tau) = u^3 + \alpha(\tau)u^2 + \beta(\tau)u + \gamma(\tau)$ has coefficients $\alpha(\tau) < 0$, $\beta(\tau) < 0$, and $\gamma(\tau) > 0$.
- Equation (13) has exactly 2 positive simple roots $H(\bar{u},\tau) < 0$.
- We only consider $\tau \in (0, \tau_{end})$ where $\tau_{end} = 17.1276$ is approximately.

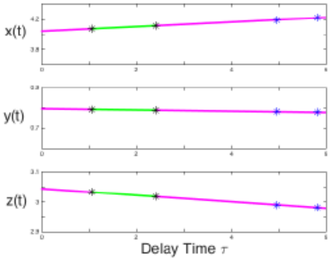
- The characteristic equation has 2 conjugate pairs of simple purely imaginary roots $\lambda(\tau_-^*) = \pm i\omega_-(\tau_-^*)$ and $\lambda(\tau_+^*) = \pm i\omega_+(\tau_+^*)$.
- To find the critical delay values $\tau_\pm^*$ where stability switches may occur we look at the zeros of the functions $S_n^\pm(\tau)$.



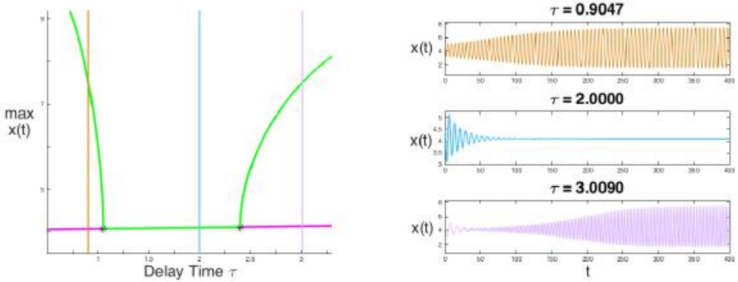
- $S_0^-(\tau)$, $S_1^+(\tau)$, $S_2^+(\tau)$, and $S_1^-(\tau)$ has zero $\tau_0^- = 1.0515$, $\tau_1^+ = 2.4002$, $\tau_2^+ = 4.9575$, and $\tau_1^- = 5.8070$, resp. and $\operatorname{sign}\left\{ \left.\frac{dS_n^\pm(\tau)}{d\tau}\right|_{\tau=\tau_n^\pm} \right\} = +1$.

Example





- Meanwhile, we have that $\operatorname{sign}\{H_u'(u(\tau_n^{\pm}), \tau_n^{\pm})\} = \pm 1$. Therefore, we have $\delta(\tau_n^{\pm}) = \pm 1$.
- At $\tau = \tau_0^- = 1.0515$, we have a switch from unstable to stable, while at $\tau = \tau_1^+ = 2.4002$ we have a switch from stable to unstable.



- Stable branches of periodic solutions (shown in green) emanating from the Hopf bifurcations.
- Time series of $x(t)$ for different delay values illustrating the existence of a stable periodic solution for $\tau < \tau_0^-$ and $\tau > \tau_1^+$, and the local stability of E_4 for $\tau \in (\tau_0^-, \tau_1^+)$.

Summary and Conclusions

- We studied the three-species IGP model with stage structured IG prey population.
- We used the theory developed by Beretta and Kung (2002) to examine the roots of the resulting characteristic equation with delay-dependent coefficients.
- We show the possibility of getting stability switches and illustrate this using numerics.
- One can get periodic coexistence as the positive equilibrium becomes unstable.
- Introducing stage structure in our IGP model enhances persistence of species.

Acknowledgments

Maraming Salamat!

Terima kasih!