Predator-prey delay example

Suppose that you have a general system with one delay of the form:

$$X' = F(X, U)$$

where $U(t) = X(t - \tau)$ and $F : R^{2n} \to R^n$. Fixed points of this satisfy

$$0 = F(X^*, X^*).$$

Such a fixed point is asymptotically stable if it is linearly stable, so lets try this. Form two $n \times n$ matrices

$$A = (a_{ij}) \equiv \frac{\partial F_i}{\partial x_j} \qquad B = (b_{ij}) \equiv \frac{\partial F_i}{\partial u_j}$$

all evaluated at the fixed point. Then, the linearized system satisfies

$$\frac{dY}{dt} = AY(t) + BY(t - \tau).$$

Let $Y(t) = Ve^{\lambda t}$ where V is a constant vector. If the real part of λ is negative, then this solution decays and if it is positive, it grows. Substitution of Y into the previous equation leads to

$$\left(\lambda I - A - Be^{-\lambda\tau}\right) V = 0,$$

a linear equation for V. This has a solution if and only if

$$H(\lambda) \equiv \det\left(\lambda I - A - Be^{-\lambda\tau}\right) = 0.$$

Thus, we must solve this nasty transcendental equation. If there is only one delayed variable, then

$$H(\lambda) = P(\lambda) + Q(\lambda)e^{-\lambda\tau}$$

which is exactly the form of Brauers theorem in the other notes. Note that there are many theorems guaranteeing roots of polynomials have negative real parts. We will discuss these later in class. In the meantime, lets apply this to an example:

$$\frac{dx}{dt} = x(t)(2 - x(t) - y(t - \tau)), \quad \frac{dy}{dt} = y(t)(-1 + x(t))$$

which is a predator-prey model in which the predation is delayed. (x is the prey and y is the predator.) The fixed points satisfy

$$x(2 - x - y) = 0 = y(-1 + x)$$

which has solutions, $(0, 0)$, $(2, 0)$, and $(1, 1)$. We will look at the coexistent state when both populations are nonzero. For this model,

$$[F_1, F_2] = [x_1(2 - x_1 - u_2), x_2(-1 + x_1)]$$

where we identify $x(t) = x_1, y(t) = x_2, x(t-\tau) = u_2, y(t-\tau) = u_2$. Thus, we get

$$A = \begin{bmatrix} 2 - 2x_1 - u_2 & 0 \\ x_2 & (-1 + x_1) \end{bmatrix}$$

and

$$B = \begin{bmatrix} 0 & -x_1 \\ 0 & 0 \end{bmatrix}$$

We evaluate these at $x_1 = x_2 = u_2 = 1$ to get

$$A = \begin{bmatrix} -1 & 0 \\ 1 & 0 \end{bmatrix} \qquad B = \begin{bmatrix} 0 & -1 \\ 0 & 0 \end{bmatrix}$$

The function $W(\lambda)$ is thus

$$H(\lambda) = \det \begin{bmatrix} \lambda + 1 & e^{-\lambda\tau} \\ -1 & \lambda \end{bmatrix} = \lambda^2 + \lambda + e^{-\lambda\tau}$$

In this case, $P(\lambda) = \lambda^2 + \lambda$ and $Q(\lambda) = 1$. Since $P(0) = 0$ and $|Q(i\omega)| > |P(i\omega)|$ for small values of ω, the theorem is violated and we cannot conclude that there is no delay-induced instability. So, this suggests that there might be imaginary roots for some values of τ. Plug $\lambda = i\omega$ into H and we get after rearrangement:

$$e^{-i\omega\tau} = \omega^2 - i\omega.$$

For τ fixed, as ω varies, the LHS traces the unit circle and the RHS traces a parabola $x = y^2$ in the complex plane (x, y). Clearly as ω increases, the parabola and the circle intersect. Indeed, the paravola intersects the unit circle when

$$|\omega^2 - i\omega| = \sqrt{\omega^4 + \omega^2} = 1$$

which has real roots

$$\omega = \pm\sqrt{-1/2 + \sqrt{5}/2} = \pm\omega^*.$$

For a fixed nonzero value of ω^*, we can vary τ so that the intersection on the unit circle occurs for the same values of ω^* for both curves. Thus, we can find a τ so that there are imaginary roots. A bit more effort is required to actually prove that as τ changes past this critical value, an eigenvalue actually crosses the imaginary axis, but, we expect this to generally be the case and so will ignore it. (It doesnt occur for certain exceptional cases.)

I will now give you a numerical analysis of this system using XPP. I will first compute the stability of the fixed point as a function of τ and then simulate the equations past the point of instability. Here is the ODE file

```
# delayed predator prey
# delay(z,tau) returns the value of z at t-tau
x'=x*(2-x-delay(y,tau))
```

```
y'=y*(-1+x)
# delay is zero to start
par tau=0
# I tell XPP that the biggest delay I will want is 10
@ delay=10,total=100
# I give it initial data near the fixed point
init x=1,y=.95
# and change the viewing window
@ ylo=0,yhi=1.5,xhi=100
done
```

Type this in and then run XPP. Do the following

1. Click on [Initialconds Go] to see a solution. Click on [Graphic stuff Add curve] and change the Y-axis to Y and the color to 1 and click OK to see the predator as well.

2. Click on the blue Param button to get the parameter window. Change tau from 0 to 0.5 and click on the little Go button.There is a little more oscillation.

3. Change tau to 1 and repeat. - More damped oscillations

4. Change tau to 1.2 and repeat. The oscillations grow!

5. Somewhere between 1 and 1.2, the fixed point becomes unstable. Lets find out where! Click on [Sing Pts Range] and

   - Range over: tau
   - Steps: 20
   - Start:1
   - End:1.2
   - Stability col: 2

   and click OK. Notice a new window has popped up. It says UNSTABLE and says there are 2 complex roots with positive real parts at the last value of tau computed (1.2). So as the simulation showed, the fixed point is unstable.

6. Click on the blue button that says Data. This has three columns in it. Ignore the labels. The first column is the parameter value (tau), the second if the real part of the maximal eigenvalue. Not that it becomes positive at about 1.15. So that is the critical value for instability!

7. Set tau=1.2 again and click on Go in the parameter window. Now in the main window, click on [Erase] and then [Initialconds Last] and repeat these two commands one more time. The system has settled into a nice periodic solution! Prey rises then predators turn on killing them. The prey fall below 1 so the predators die out. Then the prey return and the cycle begins anew.

8. Click on [File Quit] to exit XPP.

Try this analysis with the SIR model:

$$S(t)' = -I(t)S(t) + (1 - S(t) - I(t-\tau)), \quad I'(t) = I(t)S(t) - I(t)/2$$

with the fixed points $(S, I) = (1/2, 1/3)$. Here is the ODE file

```
s'=-s*i+1-s-delay(i,tau)
i'=s*i-i/2
par tau=0
init s=.5,i=.33
@ total=100,delay=10,xhi=100,ylo=0
done
```

Note that you should let the parameter tau range up to, say 9 or so to find the critical value.