Delay Differential Equations in Population Modeling

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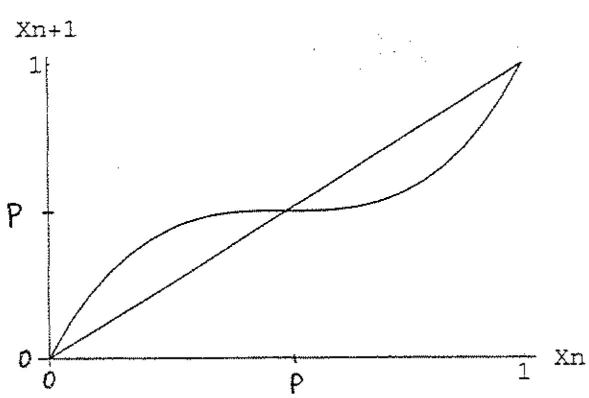
■ Introduction

In this paper we will be concerned with the dynamics of wildlife population. The simplest model representing the change in a population, x, is $\frac{dx}{dt} = a\,x$. This assumes that growth is proportional to the current population size in this model. When a is less than zero the population will decay exponentially, and when a is greater than zero, the population will grow exponentially. However, in the long term, this equation does not give a very realistic model. Every population would either eventually die off or grow without bounds. A more realisitic equation would be $\frac{dx}{dt} = r\,x\,(1 - \frac{x}{K})$, where r and K are constants and K is the carrying capacity of the environment, so that the population decreases if above K and increases if less than K; but, this model assumes that eventually all populations reach a steady state. One problem with these and similar population equations is that they assume that the growth rate is instantaneous. However, there may be factors such as gestation periods or the time for an individual to mature that can affect the population growth, and so, the growth is delayed and not instantaneous. The population growth can be better approximated by using differential equations of the form $\frac{dx}{dt} = f\,(x(t),\ x(t-\tau))$, where $\tau > 0$ is the delay.

In nature there are certain harmless species that often look and/or act similar to another species. This relationship between the mimic and its model is called Batesian Mimicry. Let x be the ratio of models to the total of models and mimics. If x=0 then there are no models present and if x=1 then there are no mimics present. It has been conjectured that there exists some optimal ratio, P, between the two species.



In the simplest case, there exist three fixed points: 0, P, and 1. Thus equation can be modeled with a cubic. Rescaling so that -1, 0, and 1 are the stable points, we get the differential equation

$$\frac{dx}{dt} = -\alpha\, x(t)\,(1 - x^2(t))$$

For initial conditions where $-1<x(t_0)<1$, all solutions of this equation tend toward 0.

-1--→-----------→-----------→--0--←-----------←---------←--1

But as in other population equations, the change may not be instantaneous. There are three ways to add delay to the above differential equation:

$$\frac{dx}{dt} = -\alpha\, x(t-\tau)\,(1 - x^2(t-\tau)) \qquad (1)$$

$$\frac{dx}{dt} = -\alpha\, x(t-\tau)\,(1 - x^2(t)) \qquad (2)$$

$$\frac{dx}{dt} = -\alpha\, x(t)\,(1 - x^2(t-\tau)) \qquad (3)$$

Solutions of these have different forms depending of the value of $\alpha\tau$. The value of τ can be adjusted by rescaling α. Throughout this paper, we take τ to be 1.

■ Linear Delay Differential Equation

The simplest delay differential equation is the linear equation: $x'(t) = -\alpha x(t-\tau)$. Unlike the linear nondelay equation, which decays exponentially to zero for any α, this equation depends on the value of $\alpha\tau$. For small $\alpha\tau$ ($\alpha\tau$ less than $\frac{1}{e}$), $x'(t) = -\alpha x(t-\tau)$ does decay exponentially, but as $\alpha\tau$ grows the solutions change patterns. For $\frac{1}{e} < \alpha\tau < \frac{\pi}{2}$, all solutions decay in an oscillatory manner. For $\alpha\tau = \frac{\pi}{2}$, the solutions are 2π periodic: x(t)=a cos(t) +

b sin(t). For $\alpha\tau > \frac{\pi}{2}$, solutions are periodic with the periods growing with $\alpha\tau$ [8]. We can expect similar differences in nolinear delay equations.

■ Periodic Solutions to $x'(t) = -\alpha x(t-\tau)\,(1 - x^2(t-\tau))$

We will first look at the delay differential equation in which all terms on the right hand side are evaluated at t-τ. Linearizing about the optimal ratio x = 0 gives $x'(t)=-\alpha\, x(t-\tau)$ and locally solutions behave similarly to this linear equation. When $\alpha\tau$ is small enough, less than $\frac{1}{e}$, the delay differential equation will behave similarily to the continuous model and exponentially decay to zero. However, as $\alpha\tau$ gets larger the response time of the equation will lead to overcompensation of the solution resulting in an oscillatory pattern. For $\frac{1}{e} < \alpha\tau < \frac{\pi}{2}$, $\alpha\tau$ is small enough for the solution to decay to the optimal ratio, but $\alpha\tau$ is large enough so that their effect makes the solution decay periodically [5, 8, 10].

Since equation (1) is a delay differential equation, finding an exact solution may not be possible, but by relating it to a system of ordinary non-delay differential equations, we may get a better idea of how our solutions will behave.

Theorem

Consider the system of differential equations

$$\begin{cases} x' = -\alpha y\,(1 - y^2) \\ y' = \alpha x\,(1 - x^2) \end{cases} \qquad (4)$$

If (x(t), y(t)) is a periodic solution of period 4r to (4), then x(t) is a solution to the differential equation $x' = -\alpha f(x(t-r))$ where $f(x) = x(1-x^2)$.

Proof [9]

Let f be odd and locally Lipschitzian.

Suppose that (x(t),y(t)) is a solution to the system of equations such that (x(0),y(0))=(0,-c) where c>0.

Assume that there exists a t>0 such that y(t)=0. Define $r=\inf\{t>0 \ni y(t)=0\}$.

Assume that x(r)=d>0. This will be true close to 0.

The path must cross the line y=-x; thus, there exists a τ in (0,r) such that $x(\tau)=-y(\tau)$.

Define $(x_0(t), y_0(t))=(x(\tau+t), y(\tau+t))$ and $(x_1(t),y_1(t))=(-y(\tau-t), -x(\tau-t))$

$$x_0'(t) = x'(\tau+t) = -a\,y(\tau+t)\,(1-y^2(\tau+t)) = -a\,y_0(t)\,(1-y_0^2(t))$$

$$y_0'(t) = y'(\tau+t) = a\,x(\tau+t)\,(1-x^2(\tau+t)) = a\,x_0(t)\,(1-x_0^2(t))$$

$$x_1'(t) = -y'(\tau-t)\,(-1) = a\,x(\tau-t)\,(1-x^2(\tau-t)) = -a\,y_1(t)\,(1-y_1^2(t))$$

$$y_1'(t) = -x'(\tau-t)\,(-1) = -a\,y(\tau-t)\,(1-y^2(\tau-t)) = a\,x_1(t)\,(1-x_1^2(t))$$

$$(x_0(0), y_0(0))=(x(\tau),y(\tau))$$

$$(x_1(0),y_1(0))=(-y(\tau),-x(\tau))=(x(\tau),y(\tau))$$

Both $(x_0(t), y_0(t))$ and $(x_1(t),y_1(t))$ satisfy the system of equations and have the same initial conditions; therefore, for all t,

$$\begin{cases} x(\tau+t) = -y\,(\tau-t) \\ y(\tau+t) = -x\,(\tau-t) \end{cases} \qquad (5)$$

From (5) we can see that $y(2\tau)=-x(0)=0$, and from the minimality of r, this implies that $r=2\tau$.

$x(r)=x(2\tau)=-y(0)=c$

We can also see that $x(t)>0$ for $0<t\leq r$

Define $(x_2(t), y_2(t))=(y(t+r), -x(t+r))$.

$(x_2(t), y_2(t))$ satisfies (4) and has the same inital condition as $(x(t),y(t))$; therefore, for all t

$$\begin{cases} x(t) = y(t+r) \\ y(t) = -x\,(t+r) \end{cases} \qquad (6)$$

Since $y(t)=-x(t+r)$ and $y(t)<0$ for $0<t<r$, $x(t)>0$ for $r<t<2r$. Thus $x(t)>0$ for $0<t<2r$.

$$-x(t+2r)=y(y+r)=x(t) \quad \Rightarrow \quad x(t+2r)=-x(t) \qquad (7)$$

Define $(x_3(t), y_3(t))=(-x(-t),y(-t))$.

$(x_3(t), y_3(t))$ satisfies the system of equations and has the same initial conditions; therefore, for all t

$$\begin{cases} x(t) = -x\,(-t) \\ y(t) = y(-t) \end{cases} \qquad (8)$$

This implies that x(-t)=-x(t).

$x'(t) = -\alpha y(t)(1 - y^2(t))$

$= -\alpha(-x(t+r))(1-(-x(t+r))^2)$ from (6)

$= -\alpha x(t-r)(1 - x^2(t-r))$ from (7)

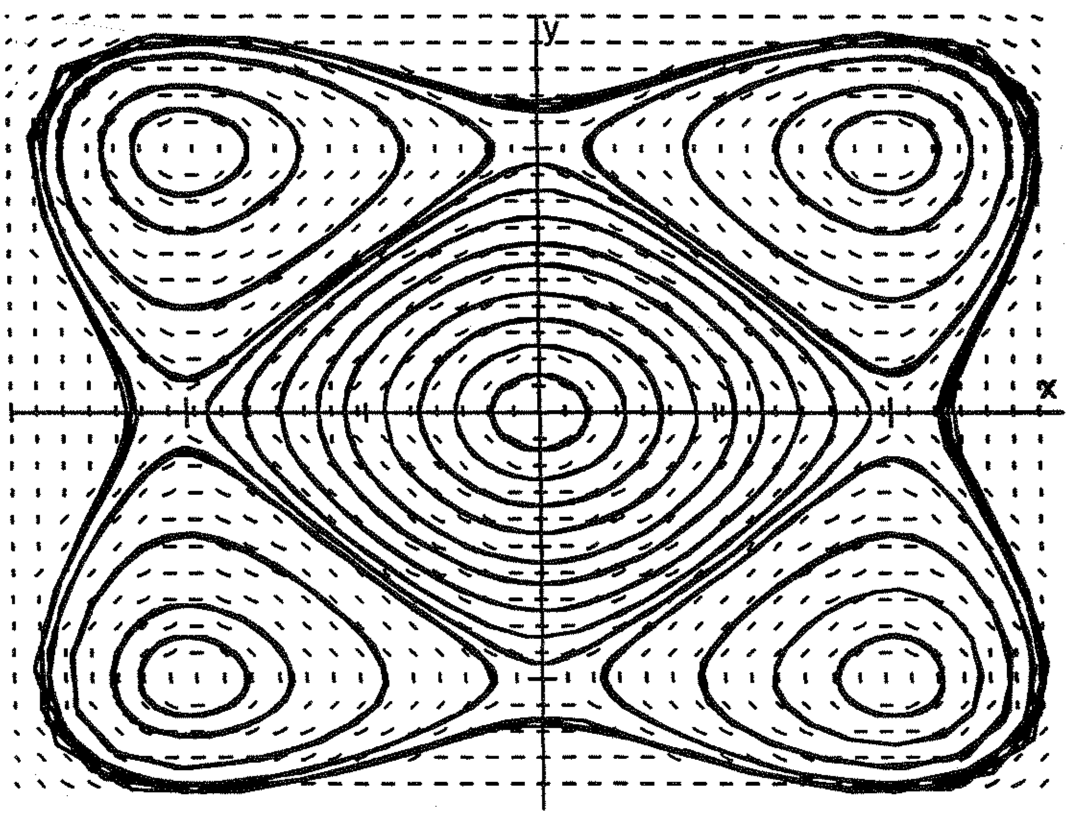
$= -\alpha f(x(t-r))$

where $f(x)=x(1-x^2)$

Therefore, x(t) satisfies $x'(t)=-\alpha f(x(t-r))$■

Not only do solutions to (4) imply solutions to (1) but also these solutions are 4r periodic. This can be seen by the symmetry in the proof.

The phase protrait of system (4) shows five critical points: (0,0), (1,1), (1,-1), (-1,1), (-1,-1).



Near the origin, the system can be approximated by the system of linear equations

$$\begin{cases} x' = -\alpha y \\ y' = \alpha x \end{cases}$$

The solutions are $\frac{2\pi}{\alpha}$ periodic. As solutions get closer to the bounds of the inner region, the period approaches infinity. Therefore, by the Intermediate Value Theorem, there exist periodic solutions of every period between $\frac{2\pi}{\alpha}$ and infintiy.

By the relation between the system of equations and the differential equation $x'(t) = -\alpha f(x(t-r))$ we are guaranteed at least one solution that has period four, as long as $\alpha\tau$ is greater than $\frac{\pi}{2}$. It is also possible to have solutions with a greater period. Using the Adams-Banshforth 3-step methon, numerical approximations to the solutions of (1) show that as $\alpha\tau$

increases there exist solutions of period greater than four. For α between $\frac{\pi}{2}$and about 3, solutions approack a stable orbit of period 4, but from near 3 to about 3.7 ths stable periodic solution has period greater than 4. After $\alpha\tau$=3.7, solutions appear to no longer be periodic; however, they still appear to be oscillatory. Eventually, the solutions tend to become wildly chaotic and leave [-1,1], which makes no sense in this model. Ladde, Lakshmikantham, and Zhang show that for $\alpha\tau > \frac{1}{e}$ every solution oscillates [5].

■ $x'(t) = -\alpha x(t-\tau)(1 - x^2(t))$

Assuming $\alpha < \frac{\pi}{2}$, Kaplan and Yorke show that $x'(t) = -\alpha\, x(t-\tau)\,(1 - x^2(t))$ can be written as

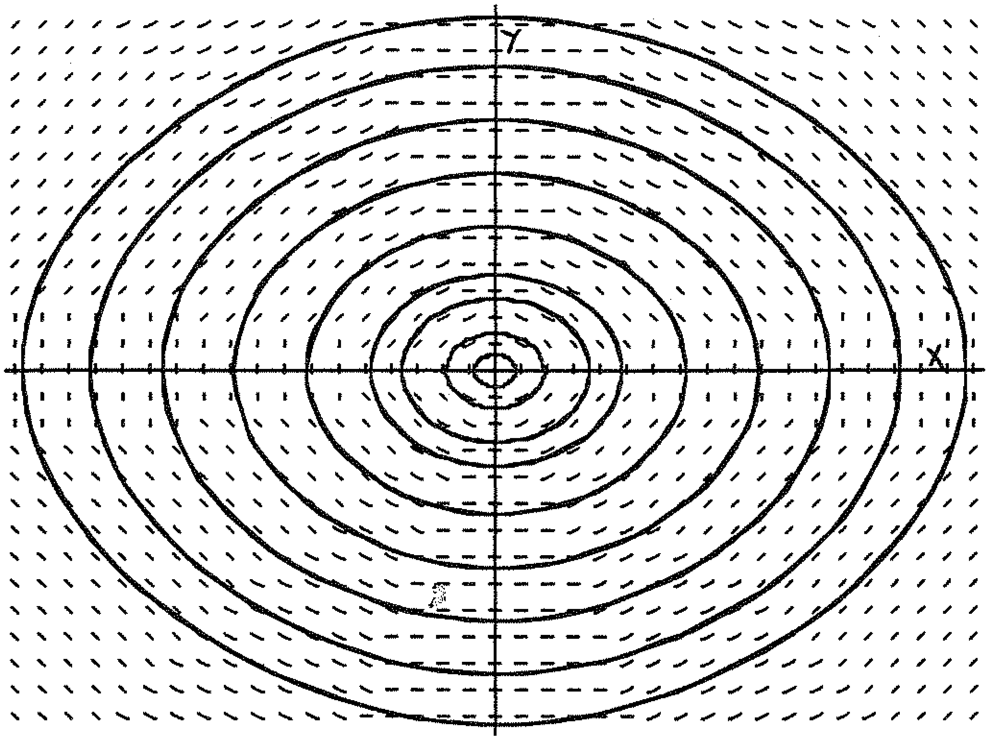
$y'(t) = -\alpha f(y(t-1))$, where

$f(v) = \frac{e^{2v}-1}{e^{2v}+1}$and $y(t) = \frac{1}{2}\ln(\frac{1+x}{1-x})$ [4]. Using the same analysis as we did for $x'(t) = -\alpha\, x(t-\tau)\,(1 - x^2(t-\tau))$, since f is odd, locally Lipschitzian, and can be written as a system of equations, there are

4r periodic solutions [9] of

$$\begin{cases} x' = -\alpha f(y) \\ y' = \alpha f(x) \end{cases} \tag{9}$$

(See the phase portrait of (9) below, which correspond to solutions of the delay equation.)



Because there is only one critical point and periodic solutions of (9) extend to infinity, we may not be guaranteed the possibility of solutions of any particular period. But

for $\alpha\tau > \frac{\pi}{2}$ numerical approximations do show stable orbits of period 4 for the delay equation.

■ $x'(t) = -\alpha\, x(t)\,(1 - x^2(t-\tau))$

The delay equation $x'(t) = -\alpha\, x(t)\,(1 - x^2(t-\tau))$ acts differently from both of the other variations of the Batesian Mimicry equation. With initial conditions $-1<x(t)<1$, $1 - x^2(t)$ is always positive; therefore, x(t) will dominate the differential equation, and solutions to the equation will behave similarily to the linearization, $x'(t) = -\alpha\, x(t)$. All solutions to (3) will decay exponentially to zero.

■ Appendix A

Below is the *Mathematica* code for numerically approximating solutions to the delay differential equations. We used the Adams-Banshforth three step method. The variables a, h, and d represent α, the step size, and the delay respectively. The differential equation used in this case is $x'(t) = -\alpha x(t-\tau)(1-x^2(t-\tau))$ Because of the intrinsic nature of the method at least the first d+3h values must be keyed in; however, we found that often more initial values were necessary.

```
Clear[a, h, d, x, xp, t];
a =;
h =;
d =;
x[0.00] :=;
x[0.01] :=;
x[0.02] :=;
x[0.03] :=;
x[0.04] :=;
x[0.05] :=;
  .
  .
  .
x[1.15] :=;
x[1.16] :=;
x[1.17] :=;
x[1.18] :=;
x[1.19] :=;
x[1.20] :=;
xp[t_] := xp[t] = -a * x[t - d] * (1 - (x[t - d]) ^ 2);
x[t_] := x[t] = x[t - h] + (h / 12) * (23 * xp[t - h] - 16 * xp[t - 2 * h] + 5 * xp[t - 3 * h]);
data = Table[{n, x[n]}, {n, 0., 50.0, .01}];
ListPlot[data, PlotJoined -> True, PlotRange -> All]
```

■ Bibliography

[1] BEGON, M. and MORTIMER, M., Population ecology: A unified study of animals and plants, Sinauer Associates, Inc., Sunderland, Mass., 1981.

[2] BURDEN, R. and FAIRES, J., Numerical Methods, PWS Publishing Company, Boston, 1993.

[3] KAPLAN, J. and YORKE, J., Ordinary differential equations which yield periodic solutions of differential delay equations, *Journal of Mathematical Analysis and Applications* 48, (1974), 317-324.

[4] KAPLAN, J. and YORKE, J., On the stability of a periodic solution of a differential delay equation, *SIAM Journal of Mathematical Analysis* 6, (1975), 268-282.

[5] LADDE, G.S., LAKSHMIKANTHAM, V., and ZHANG, B.G., Oscillation theory of differential equations with deviating arguments, Marcel Dekker, Inc., New York and Basel, 1987.

[6] MAY, R.M., Simple mathematical models with very complicated dynamics, *Nature* 261, (1976), 459-467.

[7] MAY, R.M., Mathematical aspects of the dynamics of animal populations, Studies in Mathematical Biology, Part II: Populations and communities 16, MAA, (1978), 317-366.

[8] MURRAY, J.D., Mathematical Biology, Springer-Verlag, USA, 1993.

[9] NUSSBAUM, R.D. and PEITGEN, H.O., Special and spurious solutions of $x'(t) = -\alpha f(x(t-1))$, *Memoirs of the American Mathematical Society* 51, (1984).

[10] WAN, F. Y. M., Mathematical models and their analysis, Harper and Row, Publishers, Inc., 1989.