

Rochester Institute of Technology

RIT Digital Institutional Repository

Theses

7-2013

Population Modeling with Delay Differential Equations

Shawna Nelson

Follow this and additional works at: <https://repository.rit.edu/theses>

Recommended Citation

Nelson, Shawna, "Population Modeling with Delay Differential Equations" (2013). Thesis. Rochester Institute of Technology. Accessed from

This Thesis is brought to you for free and open access by the RIT Libraries. For more information, please contact repository@rit.edu.

Population Modeling with Delay Differential Equations

By

Shawna Nelson

Submitted in partial fulfillment of the requirements for the degree

Master of Science

at

Rochester Institute of Technology

College of Science

Rochester, NY

July 2013

Rochester Institute of Technology
School of Mathematical Sciences
Applied & Computational Mathematics Program
Master's Thesis

Applicant's Name: SHAWNA NELSON
Please Print

Applicant's Signature: _____ Date: 07/14/13

Thesis Title: Population Modeling with Delay Differential Equations

Proposed Defense Date: 07/30/2013

Advisor's Name: Dr. Tamas Wiandt Signature: _____

Committee Member 1: Dr. David Ross Signature: _____

Committee Member 2: Dr. Ephraim Agyingi Signature: _____

Committee Member 3: _____ Signature: _____

Graduate Programs Director: _____ Date: _____
Dr. Tamas Wiandt

To complete your program, you need to secure all necessary signatures in time for graduation. A one-page summary describing your thesis and an overview of the area of your thesis should be attached. Describe the principal ideas and deliverables of your thesis. Annotated references, books, papers, URLs and previous master's projects or theses should be included.

Abstract

We investigate a delay differential equation system version of a model designed to describe finite time population collapse. The most commonly utilized population models are presented, including their strengths, weaknesses and limitations. We introduce the Basener-Ross model, and implement the Hopf bifurcation test to identify whether there is a Hopf bifurcation in this system. We attempt to improve upon the Basener-Ross model (which uses ordinary differential equations) by introducing delay differential equations to account for the gestational period of humans. We utilize the singularity-removing transformation of the original Basener-Ross system for the delay differential equation system as well. The new system is shown to have a Hopf bifurcation. We also investigate how the bifurcation diagram of the original ODE model changes with the introduction of delays.

I would like to acknowledge and thank my advisor Tamas Wiandt for all his guidance. The time, energy, and insight that he contributed to this paper has been invaluable.

Thanks to my husband Nicholas for being there for me, my beautiful daughters Jessica and Marissa for their patience, my handsome son David for his support and my wonderful Mother for loving me. This would not have been possible without each and every one of you!

Contents

1	Introduction	1
1.1	Basic Population Models	1
1.2	History of Easter Island	3
1.3	The Basener-Ross Model	4
1.4	Hunt's Theory	5
1.5	The Hopf Bifurcation Test	6
1.6	Lyapunov Functions	10
2	A DDE Modification of the Basener-Ross Model	11
2.1	Scaling	12
2.2	The Singularity at the Origin	14
3	Hopf Bifurcation in the DDE Model	15
3.1	General Theory	15
3.2	The Modified System	17
4	Numerical Simulations	20
A	Appendix	26

1 Introduction

1.1 Basic Population Models

Population modeling is a very popular application field of dynamical systems. Throughout its history, several models of population growth were investigated, ranging from discrete to continuous, from ordinary to partial differential equations, and from deterministic to stochastic models.

To give a very short introduction to this topic, we include the two simplest and most popular types of models. The Malthusian growth model, also known as the exponential law, was introduced by Reverend Thomas Robert Malthus. Malthus believed that regardless of the population size, the population would increase at a fixed rate over a certain amount of time. This model was widely used by economists and became known as the first principle of population dynamics. The variable P denotes the size of the population and the parameter r is the growth rate or net reproduction rate, which is the difference between the birth and death rates. The resulting simple differential equation is

$$\dot{P} = rP,$$

which has the solution

$$P(t) = P_0 e^{rt},$$

where P_0 is the initial population size, r is the growth rate, and t is time.

The population increases or decreases over time, depending on the sign of r , at a constant rate proportional to the initial population. Because the Malthusian model has only one variable and one parameter, it is extremely limited and is used primarily for short term predictions. One of the missing factors in the Malthusian model is the carrying capacity, which dictates what population size the environment can support. The absence of this concept led to what was known as the Malthusian catastrophe.

Another shortcoming is that the long term behavior is either unbounded growth

or inevitable extinction. It was obvious that a better model was needed, one that would take into account other variables.

The Logistic Growth Model, (LGM) was created by the Belgian mathematician Pierre Verhulst in 1838. It incorporates the carrying capacity, K , to provide a more realistic model for population growth.

The carrying capacity is the point where the birth and death rates are equal, therefore population stabilizes over time. The rate of population growth, r , decreases as the population, P , rises and reaches 0 when $P = K$. If the population grows larger than K , the growth rate becomes negative and the population declines. Therefore, the modeling assumption for the logistic growth model is that the maximum sustainable population size is K . The growth rate thus could be given by:

$$r = r_0(1 - \frac{P}{K}),$$

where K , the upper limit of the population, is the carrying capacity.

The resulting differential equation is

$$\dot{P} = rP = r_0(1 - \frac{P}{K})P,$$

which has the solution

$$P(t) = \frac{KP_0}{P_0 + (K - P_0)e^{-r_0t}}$$

The logistic curve appears when P_0 is less than K , and the population size increases until it reaches this plateau. When P_0 is greater than K the population size decreases until it again reaches a plateau. The population is constant when $P_0 = 0$ or $P_0 = K$. The last two described are the equilibrium points, the latter is stable.

A shortcoming of the LGM is that the population growth rate, r , controls both the growth and the decline rates. In reality the death rate not necessarily has the same form as the birth rate, so if an animal has a long gestational period but a short life this model will not work. Next, we turn our attention to population collapse.

1.2 History of Easter Island

A famous example of civilization collapse is the history of Easter Island. Te-Pito-te-Henua, meaning "end of the land," was the original name of the island and its inhabitants came to be known as Rapa Nui. This was such a remote island that people still speculate how it became inhabited and by whom. There are suggestions that the first inhabitants were either Peruvian or Polynesian. Those who believe they were Polynesian believe so because the populations on the closest islands were of Polynesian descent, and a visiting Polynesian was able to communicate with the natives. Furthermore it was rumored that a Polynesian chief, his wife and extended family sailed to the island in a double canoe, looking for a new land for his family. However, the striking similarity of the Rapa Nui and Incan stonework imply a Peruvian source for the settlers. It is believed the island was settled anywhere between 300 and 1200 AD.

On Easter Sunday in 1722 Admiral Jacob Roggeveen and his Dutch expedition landed on the island, naming it Easter Island as it is commonly known by today. Upon the arrival of the Dutch it is estimated there were about 2,000–3,000 inhabitants. There is also uncertainty about the peak population but estimates range anywhere from 9,000 to 15,000 and historians seem to agree that the peak occurred about 1500 AD.

The Rapa Nui used up many of the large trees in order to make homes, ships for travel, and for fire to cook and keep warm. It was thought the majority of the large trees were used to transport the giant stone statues called moai. The moai were thought to be representative of spirits of ancestors and an integral part of the Rapa-Nui civilization. Numerous moai were built and transported all over the island. This led to deforestation, which in turn led to wars over resources. Natural disasters also contributed to the quick reduction in population. The lack of food may have even led to cannibalism.

In the 1800s, slave traders repeatedly raided the island, with the largest raid capturing the king and 1,000 other natives. After the slavers were ordered to return the natives (of which only a tenth remained), they were returned, although

infected with smallpox. The epidemic spread through the island leaving only a few hundred survivors.

1.3 The Basener-Ross Model

The paper *Booming and Crashing Populations and Easter Island* by Bill Basener and David Ross uses a variation of the logistic growth model to account for the sudden collapse. Ordinary differential equations (ODEs) are used to model the population behavior. In their model Basener and Ross account for numerous variables and parameters, which are as follows: P is the population, and R is the amount of self-replenishing resources on the island. K is the carrying capacity for the resource and c is the rate at which the resources grow. The harvesting constant is h and $-hP$ describes the effect of harvesting of the resource. aP is the net growth rate of the population. In this system the island is capable of supporting a maximum population of R .

$$\frac{dR}{dt} = cR\left(1 - \frac{R}{K}\right) - hP \quad (1)$$

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{R}\right) \quad (2)$$

The parameters were chosen to be the realistic values of $K = 70,000$, $c = 0.01$, $h = 0.048$, and $a = 0.0045$. One possible behavior of solutions of this model is a rapid increase in population until $P = R$, the maximum population, and then a sudden crash to extinction. The system contains a singularity at $P = R = 0$, so a change of variables is used to eliminate it, and time is scaled so $a = 1$ and there is one less parameter. The transformation is given by $z = P$ and $\xi = P/R$; system (1)-(2) turns into

$$\begin{aligned} z' &= z(1 - \xi) \\ \xi' &= (h - 1)\xi^2 + (1 - c)\xi + \frac{c}{K}z \end{aligned}$$

The bifurcation diagram from [1] tells a story about what happens for different

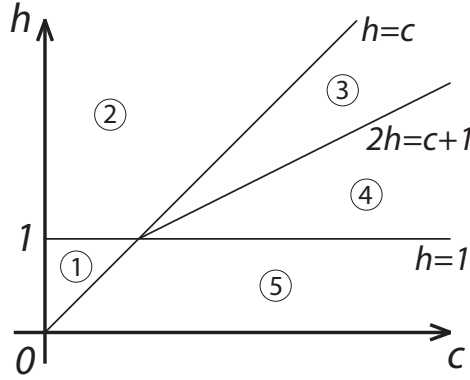


Figure 1: Bifurcation diagram: h - c plane

values of h and c . On Figure 1, the model corresponding to parameter values in region 1 results in systems where the behavior of solutions is asymptotic extinction for all initial values; similarly, region 2 gives finite time extinction, region 3 gives extinction, which happens in finite time for certain initial conditions, region 4 gives a mixed region where extinction and survival are both possible, depending on the initial conditions, and region 5 corresponds to parameter values which give survival for all initial conditions.

A degenerate Hopf bifurcation is present when $c > h$, $h > 1$, and $2h - c - 1$ changes sign. (Between regions 3 and 4 on the bifurcation diagram.)

The Basener-Ross model was inspired by the fate of Easter Island, and it gives the possibility of booming and crashing populations. We mention that in the past few years, an alternative theory was proposed for the history of Easter Island, which actually disputes the reigning scientific theory. We describe this theory in the next section.

1.4 Hunt's Theory

Terry Hunt, an archaeologist at the University of Hawaii and Carl Lipo, an anthropologist at California State University, proposed a new theory about the fate

of Easter Island.

In 2000, Hunt and Lipo took their students to the Northern shore of Easter Island, where they believe the first settlers landed, to excavate. Soil samples from their dig radiocarbon dated to about 1200 AD, leading them to believe that the islanders arrived there much later than previously thought. With this shocking news in hand, the new mystery to unravel was how the civilization collapsed in a matter of about 300 years. This would mean showing how the island was deforested in such a short period of time.

Contrary to popular belief that the Rapa Nui used large trees to transport the moai, which is what many scientists believe led to the deforestation, Hunt believed that the islanders walked the giant stone statues. Hunt's theory was they tied ropes to them and yanked back and forth "walking" them like we would do with a large appliance instead of using massive logs to roll the moai to their final destination. Since hauling the moai was not the way the island was deforested there must have been some other contributing factor.

Among the digs, many rat bones were found; they were thought to have arrived on the island either as a source of food or as stowaways. From the amount of bones found, it was believed that the rat population had risen to millions during the first few years. There was evidence of them feeding on the palm seeds and the trees, which would cut off all new growth, and kill the living trees. Hunt did not believe that humans could deforest an island so quickly by themselves and now he had found his culprit. After numerous years of the seeds being destroyed and the trees being eaten, deforestation was inevitable. In time this would lead to the demise of the islanders.

1.5 The Hopf Bifurcation Test

We revisit the Basener-Ross model and prove the existence of the degenerate Hopf bifurcation when $c > h > 1$, and $2h - c - 1$ changes sign. This proof will give us some insight when we might have a non-degenerate Hopf bifurcation in similar systems. We choose $K = 1$ to simplify the computation; general K values can

be dealt easily with the appropriate modifications. Recall that the transformed system is

$$\begin{aligned}\dot{z} &= z(1 - \xi) \\ \dot{\xi} &= \xi(1 - \xi) + c(z - \xi) + h\xi^2.\end{aligned}$$

We introduce new variables which shift the equilibrium point to the origin. Let $w = \xi - 1$ and $u = z - 1 + h/c$; the system transforms into

$$\begin{aligned}\dot{u} &= -w(u + 1 - h/c) \\ \dot{w} &= -(1 + c - 2h)w + cu - w^2 + hw^2.\end{aligned}$$

The Jacobian of this system at (0,0) is

$$J = \begin{bmatrix} 0 & h/c - 1 \\ c & -1 - c + 2h \end{bmatrix},$$

with eigenvalues

$$\lambda_{1,2} = h - \frac{c+1}{2} \pm \sqrt{\frac{(1-c)^2 + 4h(h-c)}{4}}.$$

To shift the parameters to the origin we introduce

$$\mu = h - \frac{c+1}{2};$$

with this notation, the eigenvalues are

$$\lambda = \mu \pm \sqrt{\mu^2 + \mu + \frac{1-c}{2}}.$$

We can see that when $\mu = 0$, we get a purely imaginary eigenvalue. Our aim is to put the linear part of the system into the following standard form to check for a

Hopf bifurcation:

$$\begin{aligned}\dot{x} &= \mu x + \sqrt{-\mu^2 - \mu + \frac{c-1}{2}} \cdot y \\ \dot{y} &= -\sqrt{-\mu^2 - \mu + \frac{c-1}{2}} \cdot x + \mu y\end{aligned}$$

To find the linear transformation needed to put the original system into the standard form, we find the eigenvectors of

$$A = J = \begin{bmatrix} 0 & \frac{\mu}{c} + \frac{1}{2c} - \frac{1}{2} \\ c & 2\mu \end{bmatrix}.$$

One of the (complex) eigenvectors is

$$\mathbf{v}_1 = \begin{bmatrix} -\frac{\mu}{c} - \frac{\sqrt{\mu^2 + \mu + \frac{1-c}{2}}}{c} \\ 1 \end{bmatrix};$$

now let $\begin{bmatrix} x \\ y \end{bmatrix} = L^{-1} \begin{bmatrix} u \\ w \end{bmatrix}$, where

$$L = \begin{bmatrix} -\frac{1}{c}\sqrt{\frac{c-1}{2} - \mu^2 - \mu} & -\frac{\mu}{c} \\ 0 & 1 \end{bmatrix}.$$

Recall that

$$\begin{aligned}\dot{u} &= (h/c - 1)w - uw \\ \dot{w} &= cu - (1 + c - 2h)w - w^2 + hw^2.\end{aligned}$$

In this system, the linear part is $\begin{bmatrix} \dot{u} \\ \dot{w} \end{bmatrix} = A \begin{bmatrix} u \\ w \end{bmatrix}$. If we let $m = \sqrt{\frac{c-1}{2} - \mu^2 - \mu}$, then we obtain that

$$L = \begin{bmatrix} -m/c & -\mu/c \\ 0 & 1 \end{bmatrix}.$$

Computing L^{-1} we get $L^{-1} = \begin{bmatrix} -c/m & -\mu/m \\ 0 & 1 \end{bmatrix}$. The original system is $\begin{bmatrix} \dot{u} \\ \dot{w} \end{bmatrix} = A \begin{bmatrix} u \\ w \end{bmatrix} + G(u, w)$, where the non-linear part of the system is $G(u, w) = \begin{bmatrix} -uw \\ -w^2 + hw^2 \end{bmatrix}$. We obtain

$$\begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} = L^{-1} \begin{bmatrix} \dot{u} \\ \dot{w} \end{bmatrix} = L^{-1} A \begin{bmatrix} u \\ w \end{bmatrix} + L^{-1} G \left(L \begin{bmatrix} x \\ y \end{bmatrix} \right).$$

After simplification,

$$L^{-1} G \left(L \begin{bmatrix} x \\ y \end{bmatrix} \right) = \begin{bmatrix} -xy - \frac{\mu hy^2}{m} \\ -y^2 + hy^2 \end{bmatrix}.$$

Thus we obtain that

$$\begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} = \begin{bmatrix} \mu & m \\ -m & \mu \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} + \begin{bmatrix} -xy - \frac{\mu hy^2}{m} \\ -y^2 + hy^2 \end{bmatrix}.$$

Using the notation $f = -xy - \mu hy^2/m$, $g = -y^2 + hy^2$, we have to compute the quantity

$$\begin{aligned} a &= \frac{1}{16} (f_{xxx} + g_{xxy} + f_{xyy} + g_{yyy}) + \\ &+ \frac{1}{16\omega} (f_{xy}(f_{xx} + f_{yy}) - g_{xy}(g_{xx} + g_{yy}) - f_{xx}g_{xx} + f_{yy}g_{yy}) \end{aligned}$$

to identify whether we have a Hopf bifurcation. With the above f and g , we obtain $a = 2\mu h(3 - 2h)/m$, which is 0 when $\mu = 0$ so we do not have a regular Hopf bifurcation in the system.

A degenerate Hopf bifurcation occurs when one or more of the conditions of a Hopf bifurcation is not satisfied. This can result in many different outcomes; often there is still a periodic solution, sometimes there are multiple periodic solutions. If a transversality condition is not satisfied, the equilibrium point may not change stability. We know from [1] that a degenerate Hopf happens when $c > h > 1$ and $2h - c - 1$ changes signs. There is a spiral source at the equilibrium $(K(1 - h/c), 1)$ when $2h - c - 1 > 0$: the trajectories of nearby solutions diverge away from the equilibrium point causing a growing oscillation. When $2h - c - 1 < 0$, we have a spiral sink and the trajectories of nearby solutions spiral inward, toward the equilibrium point.

1.6 Lyapunov Functions

Lyapunov functions are used to establish the stability properties of equilibrium solutions of differential equations. Basener and Ross used the following Lyapunov function to obtain a full description of the various stability properties exhibited by their model:

$$V(z, \xi) = z^{2h-2} \left(\frac{K}{2c} \xi^2 - \frac{K}{c} \xi + \frac{z}{2h-1} + \frac{K}{2c} - \frac{K(1-h/c)}{2h-2} \right).$$

When $2h = c + 1$, we obtain that

$$V(z, \xi) = z^{c-1} \left(\frac{K}{2c} \xi^2 - \frac{K}{c} \xi + \frac{z}{c} \right).$$

In this case, we get that $\dot{V} = 0$, thus V is constant along trajectories of the system. The level sets of this function can be seen on Figure 2 around the equilibrium point $((1 - h/c)K, 1)$. This establishes the existence of periodic solutions for $2h = c + 1$.

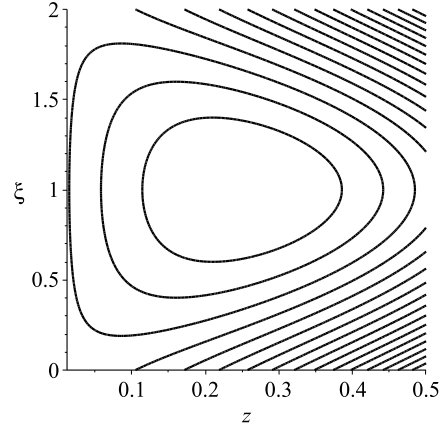


Figure 2: Level sets of V , $c = 2$.

The computation in the previous subsection gives an insight how a modified model might exhibit a non-degenerate Hopf bifurcation.

2 A DDE Modification of the Basener-Ross Model

One of the facts that was not taken into account in the Basener-Ross (B-R) model is that reproduction is not instantaneous. There is a time delay between the fertilization of an egg and the birth of a child. In an attempt to improve upon the B-R model, we introduce delay differential equations (DDEs). The delay τ is used to represent the gestational period of a human female, which is known to be about nine months. This is a fairly common use of delay differential equations [13]. We will use a combination of analytic methods and numerical simulations to investigate how the original model changes with the introduction of this delay.

Recall that the original model is given by

$$\begin{aligned}\frac{dP}{dt} &= aP\left(1 - \frac{P}{R}\right) \\ \frac{dR}{dt} &= cR\left(1 - \frac{R}{K}\right) - hP.\end{aligned}$$

The modification we introduce to the system takes into account the gestational period for humans; the new system describing this will take the form of the DDE

$$\frac{dP}{dt} = aP(t - \tau)\left(1 - \frac{P(t - \tau)}{R(t - \tau)}\right) \quad (3)$$

$$\frac{dR}{dt} = cR\left(1 - \frac{R}{K}\right) - hP. \quad (4)$$

Observe that the rate of change of the population now depends on the size of the population (and resources) τ time ago. This is a standard assumption in delay differential equation population models.

2.1 Scaling

First, we reduce the number of parameters by scaling time and the functions in the equations. Let us introduce the scaled time $\tilde{t} = bt$, i.e. $t = \tilde{t}/b$. Also, denote $P(t) = P(\tilde{t}/b) = \tilde{P}(\tilde{t})$, and $R(t) = R(\tilde{t}/b) = \tilde{R}(\tilde{t})$. We compute to obtain

$$\begin{aligned}\frac{d\tilde{P}(\tilde{t})}{d\tilde{t}} &= \frac{dP(\tilde{t}/b)}{d\tilde{t}} = \frac{dP(t)}{d\tilde{t}} = \frac{dP(t)}{dt} \cdot \frac{dt}{d\tilde{t}} = aP(t - \tau)\left(1 - \frac{P(t - \tau)}{R(t - \tau)}\right) \cdot \frac{1}{b} = \\ &= \frac{a}{b}\tilde{P}(\tilde{t} - b\tau)\left(1 - \frac{\tilde{P}(\tilde{t} - b\tau)}{\tilde{R}(\tilde{t} - b\tau)}\right).\end{aligned}$$

Thus if we choose $b = a$ and the new time $\tilde{t} = at$, we obtain

$$\frac{d\tilde{P}}{d\tilde{t}} = \tilde{P}(\tilde{t} - a\tau)\left(1 - \frac{\tilde{P}(\tilde{t} - a\tau)}{\tilde{R}(\tilde{t} - a\tau)}\right),$$

and

$$\begin{aligned}\frac{d\tilde{R}}{d\tilde{t}} &= \frac{dR(\tilde{t}/a)}{d\tilde{t}} = \frac{dR(t)}{d\tilde{t}} = \frac{dR(t)}{dt} \cdot \frac{dt}{d\tilde{t}} = \left(cR\left(1 - \frac{R}{K}\right) - hP\right) \cdot \frac{1}{a} = \\ &= \frac{c}{a} \cdot \tilde{R} \left(1 - \frac{\tilde{R}}{K}\right) - \frac{h}{a} \cdot \tilde{P}.\end{aligned}$$

Let us rename now these new functions and constants to be the original: $P = \tilde{P}$, $R = \tilde{R}$, $\tau = a\tau$, $c = c/a$, and $h = h/a$. We obtain

$$\begin{aligned}\frac{dP}{dt} &= P(t - \tau) \left(1 - \frac{P(t - \tau)}{R(t - \tau)}\right) \\ \frac{dR}{dt} &= cR \left(1 - \frac{R}{K}\right) - hP.\end{aligned}$$

Now we will rescale P and R using the carrying capacity K of the resources. Let $\hat{R} = R/K$, i.e. $R = \hat{R}K$ and $\hat{P} = P/K$, i.e. $P = \hat{P}K$. Then

$$\begin{aligned}\frac{d\hat{R}}{dt} &= \frac{dR}{dt} \cdot \frac{1}{K} = \left(cR \left(1 - \frac{R}{K}\right) - hP\right) \cdot \frac{1}{K} = c \frac{R}{K} \left(1 - \frac{R}{K}\right) - \frac{hP}{K} = \\ &= c\hat{R}(1 - \hat{R}) - h\hat{P}.\end{aligned}$$

Further,

$$\frac{d\hat{P}}{dt} = \frac{dP}{dt} \cdot \frac{1}{K} = P(t - \tau) \left(1 - \frac{P(t - \tau)}{R(t - \tau)}\right) \cdot \frac{1}{K} = \hat{P}(t - \tau) \left(1 - \frac{\hat{P}(t - \tau)}{\hat{R}(t - \tau)}\right)$$

Again, if we let $\hat{R} = R$ and $\hat{P} = P$ we have

$$\frac{dP}{dt} = P(t - \tau) \left(1 - \frac{P(t - \tau)}{R(t - \tau)}\right) \quad (5)$$

$$\frac{dR}{dt} = cR(1 - R) - hP \quad (6)$$

We are now left with the two parameters c and h ; also, P and R are measured

against the carrying capacity of the resources.

Our new time shift is coming from the equation $P(t - \tau) = P(\tilde{t}/a - \tau) = P((\tilde{t} - a\tau)/a) = \tilde{P}(\tilde{t} - a\tau)$; this slows down time. Since the gestation period for humans is nine months, in the original time variable (where we measure time in years) $\tau = 3/4$. Using the estimated value of $a = 0.004$, the new time shift for the numerical simulation is $\tilde{\tau} = a\tau = 3/4(0.004) = 0.003$.

2.2 The Singularity at the Origin

We obtained the following set of equations:

$$\begin{aligned}\frac{dP}{dt} &= P(t - \tau) \left(1 - \frac{P(t - \tau)}{R(t - \tau)} \right) \\ \frac{dR}{dt} &= cR(1 - R) - hP.\end{aligned}$$

The system has a singularity at $R(t - \tau) = 0$. In an attempt to remedy this situation we will try to utilize the singularity blow-up transformation of [1]. We let $z = P$ and $\xi = P/R$; therefore $R\xi = P = z$ and $R = z/\xi$. Substituting into the above equations we obtain

$$\dot{z} = \dot{P} = z(t - \tau)(1 - \xi(t - \tau)).$$

Using the chain rule, from $z = R\xi$ we get $\dot{z} = \dot{R}\xi + R\dot{\xi}$, thus

$$[cR(1 - R) - hP] \cdot \xi + R\dot{\xi} = z(t - \tau)(1 - \xi(t - \tau)).$$

Then

$$\left[c \frac{z}{\xi} \left(1 - \frac{z}{\xi} \right) - hz \right] \xi + \frac{z}{\xi} \dot{\xi} = z(t - \tau)(1 - \xi(t - \tau)),$$

and this gives

$$cz \left(1 - \frac{z}{\xi} \right) - hz\xi + \frac{z}{\xi} \dot{\xi} = z(t - \tau)(1 - \xi(t - \tau)).$$

Multiplication by ξ gives

$$cz\xi - cz^2 - hz\xi^2 + z\dot{\xi} = \xi z(t - \tau)(1 - \xi(t - \tau)).$$

Solving for $\dot{\xi}$ we get

$$\dot{\xi} = \xi(1 - \xi(t - \tau)) \frac{z(t - \tau)}{z(t)} + cz - c\xi + h\xi^2,$$

and our new system is

$$\dot{z} = z(t - \tau)(1 - \xi(t - \tau)) \quad (7)$$

$$\dot{\xi} = \xi(1 - \xi(t - \tau)) \frac{z(t - \tau)}{z(t)} + cz - c\xi + h\xi^2. \quad (8)$$

We can see that the delay terms will not allow the removal of the singularity in this case. For our numerical simulations we will use the above form of the equation nevertheless; we can see that the numerics will be suspect only when z gets close to 0.

3 Hopf Bifurcation in the DDE Model

3.1 General Theory

We established that in the Basener-Ross population model

$$\begin{aligned} \dot{z} &= z(1 - \xi) \\ \dot{\xi} &= \xi(1 - \xi) + c(z - \xi) + h\xi^2 \end{aligned}$$

a degenerate Hopf bifurcation happens as $c > h > 1$, and $2h - c - 1$ changes sign.

In the case of delay differential equations, the test for linearized stability takes a different form [13]. Suppose that for a general DDE with a single delay in the

form

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}(t), \mathbf{x}(t - \tau)),$$

we have an equilibrium solution at $\mathbf{x}(t) \equiv \mathbf{x}^*$, i.e.

$$\mathbf{f}(\mathbf{x}^*, \mathbf{x}^*) = 0.$$

In the case of ODEs, the assumption for linearized stability analysis is that a small perturbation is made in the finite dimensional phase space from the equilibrium. DDEs are handled in an analogous way, but in this case the phase space is an infinite dimensional function space, which will have to be taken into account. We will use the common practice of indicating the instantaneous variables without a subscript (i.e. $\mathbf{x}(t) = \mathbf{x}$), while the delayed variables are denoted by the subscripted value of the delay (i.e. $\mathbf{x}(t - \tau) = \mathbf{x}_\tau$). Let us disturb now the equilibrium \mathbf{x}^* by a small perturbation which lasts from $t = t_0 - \tau$ to t_0 . Let $\delta\mathbf{x}(t)$ be the displacement from equilibrium; then $\mathbf{x} = \mathbf{x}^* + \delta\mathbf{x}$ and

$$\dot{\mathbf{x}} = \dot{\delta\mathbf{x}} = \mathbf{f}(\mathbf{x}^* + \delta\mathbf{x}, \mathbf{x}^* + \delta\mathbf{x}_\tau).$$

Using the Taylor series now for this function, and taking into account that $\mathbf{f}(\mathbf{x}^*, \mathbf{x}^*) = 0$, we obtain

$$\dot{\delta\mathbf{x}} = \mathbf{J}_0 \delta\mathbf{x} + \mathbf{J}_\tau \delta\mathbf{x}_\tau.$$

Here \mathbf{J}_0 is the usual Jacobian with respect to \mathbf{x} , and \mathbf{J}_τ is the Jacobian with respect to \mathbf{x}_τ , both evaluated at \mathbf{x}^* . Similarly to linear ODEs, we assume that the linearized DDE has a solution in the form $\delta\mathbf{x}(t) = Ae^{\lambda t}$. Substituting this into the linearization we get

$$\lambda A = (\mathbf{J}_0 + e^{-\lambda\tau} \mathbf{J}_\tau)A.$$

In order to get a nonzero solution A , we need that

$$\det(\mathbf{J}_0 + e^{-\lambda\tau} \mathbf{J}_\tau - \lambda I) = 0.$$

This is the characteristic equation in case of DDEs; observe that because of the exponential function involved, this is not a polynomial but a quasipolynomial, and as such, it can easily have infinitely many solutions. Checking the form of the assumed solution $\delta \mathbf{x}$, we can see that the stability property will change as the real part of the rightmost solutions of the characteristic equation cross over the imaginary axis on the complex plane.

3.2 The Modified System

We will now test the DDE for a Hopf bifurcation. As before, we will let $z_\tau = z(t - \tau)$. Our system of equations of the DDE model is:

$$\begin{aligned}\dot{z} &= z_\tau(1 - \xi_\tau) \\ \dot{\xi} &= \xi(1 - \xi_\tau)\frac{z_\tau}{z} + cz - c\xi + h\xi^2.\end{aligned}$$

The Jacobian with respect to the non-shifted variables ξ and z is

$$J_0 = \begin{bmatrix} 0 & 0 \\ \xi(1 - \xi_\tau)(-z_\tau/z^2) + c & (1 - \xi_\tau)(z_\tau/z) - c + 2h\xi \end{bmatrix}.$$

The Jacobian at the constant equilibrium $(1 - h/c, 1)$ is

$$J_0 = \begin{bmatrix} 0 & 0 \\ c & -c + 2h \end{bmatrix}.$$

Now we find the time shifted Jacobian, J_τ , by taking the derivatives of the equations with respect to the time shifted variables:

$$J_\tau = \begin{bmatrix} 1 - \xi_\tau & -z_\tau \\ \xi(1 - \xi_\tau)/z & -\xi z_\tau/z \end{bmatrix}.$$

This Jacobian at the equilibrium point $(1 - h/c, 1)$ is

$$J_\tau = \begin{bmatrix} 0 & \frac{h}{c} - 1 \\ 0 & -1 \end{bmatrix}.$$

Now we find the eigenvalues of this system by solving $\det(J_0 + e^{-\lambda\tau}J_\tau - \lambda I) = 0$.

We obtain the equation

$$\begin{vmatrix} -\lambda & e^{-\lambda\tau}(\frac{h}{c} - 1) \\ c & -c + 2h - e^{-\lambda\tau} - \lambda \end{vmatrix} = 0,$$

which gives

$$\lambda^2 + \lambda e^{-\lambda\tau} + (c - 2h)\lambda - (h - c)e^{-\lambda\tau} = 0.$$

This is a transcendental equation in λ , thus we can't get an algebraic solution. We are interested in the case when λ crosses over from the negative complex half-plane to the positive half-plane, i.e. when $\lambda = i\theta$. We can see that if λ solves this equation, then $\bar{\lambda}$ also solves it.

Substituting $\lambda = i\theta$ gives

$$-\theta^2 + i\theta(\cos(\theta\tau) - i\sin(\theta\tau)) + (c - 2h)i\theta - (h - c)(\cos(\theta\tau) - i\sin(\theta\tau)) = 0.$$

We consider the real and imaginary parts of this equation:

$$-\theta^2 + \theta \sin(\theta\tau) - (h - c)\cos(\theta\tau) = 0$$

$$\theta \cos(\theta\tau) + (c - 2h)\theta + (h - c)\sin(\theta\tau) = 0.$$

In the ODE model, the degenerate Hopf bifurcation takes place when $2h = c + 1$; we can see that when $\tau = 0$, the imaginary part of equation gives $2h = c + 1$, and then the eigenvalue is $\lambda = i\theta = \sqrt{c - h} = \sqrt{(c - 1)/2}$ as in Section 1.5. The presence of the delay will move the location of the Hopf bifurcation curve $2h = c + 1$. The Hopf bifurcation curve can be found by eliminating θ from the above two

equations and obtaining a connection between h and c . Because of the structure of the equations, we can't eliminate θ algebraically, but we can use θ as a parameter to graph all the c and h values satisfying the above equation. The equations can be written as

$$\begin{aligned}\cos(\theta\tau)c - \cos(\theta\tau)h &= \theta^2 - \theta \sin(\theta\tau) \\ (\theta - \sin(\theta\tau))c + (\sin(\theta\tau) - 2\theta)h &= -\theta \cos(\theta\tau),\end{aligned}$$

thus we obtain

$$\begin{aligned}c &= \frac{\begin{vmatrix} \theta^2 - \theta \sin(\theta\tau) & -\cos(\theta\tau) \\ -\theta \cos(\theta\tau) & \sin(\theta\tau) - 2\theta \end{vmatrix}}{\begin{vmatrix} \cos(\theta\tau) & -\cos(\theta\tau) \\ \theta - \sin(\theta\tau) & \sin(\theta\tau) - 2\theta \end{vmatrix}} = \frac{-3\theta \sin(\theta\tau) + 2\theta^2 + 1}{\cos(\theta\tau)}, \\ h &= \frac{\begin{vmatrix} \cos(\theta\tau) & \theta^2 - \theta \sin(\theta\tau) \\ \theta - \sin(\theta\tau) & -\theta \cos(\theta\tau) \end{vmatrix}}{\begin{vmatrix} \cos(\theta\tau) & -\cos(\theta\tau) \\ \theta - \sin(\theta\tau) & \sin(\theta\tau) - 2\theta \end{vmatrix}} = \frac{-2\theta \sin(\theta\tau) + \theta^2 + 1}{\cos(\theta\tau)}.\end{aligned}$$

Figure 3 shows the location of the Hopf bifurcation for different values of τ : $\tau = 0$ (i.e. no delay) is just the line $2h = c + 1$ as can be checked easily. This is the leftmost curve on the figure; the subsequent curves correspond to the values $\tau = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6$ and 0.7 , respectively. We can compare this figure to Figure 1 and see that as τ increases, the Hopf bifurcation curve in the h - c parameter plane moves down; also, for big enough τ values the curve even dips below $h = 1$, thus possibly changing a "survival for all" situation into a "death for all" scenario.

In the next section, we investigate the behavior of the system numerically.

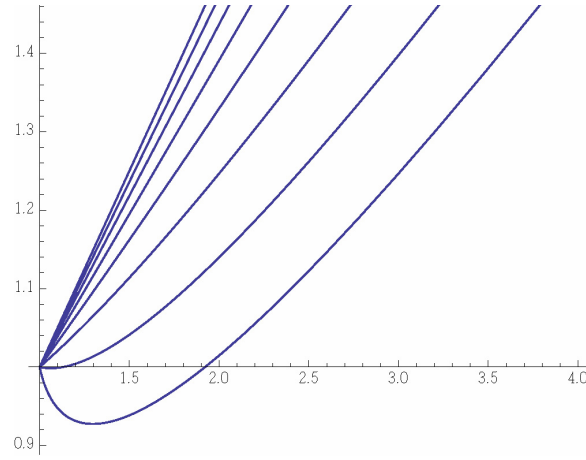


Figure 3: Location of Hopf bifurcation: c - h plane

4 Numerical Simulations

Numerical simulations for delay differential equations are always incomplete, because the initial conditions are chosen from an infinite dimensional function space. In some cases it is possible to prove that an equilibrium is stable or unstable, but these proofs are very involved exactly because of the infinite dimensionality of the underlying phase space.

The choice of initial conditions for a given numerical approximation of a solution of a delay differential equation can be the subject of a lengthy discussion. For simplicity, we chose constant history functions for our numerical simulations, i.e. we assumed that $z(t) = z_0$ and $\xi(t) = \xi_0$ for $-\tau \leq t \leq 0$. We were interested in the question of how the bifurcation diagram in [1] is changing with the introduction of delays in the system.

The numerical simulations were performed using the *dde23* routine of MATLAB [14]. We included the simple code files in the Appendix.

We have chosen our initial conditions and constants to mimic those in [1]. Because of the scaling performed in Section 2.1, the only parameters we have to identify are c , h and τ . As stated before, in the original system a feasible value

of the time delay is $\tau = 3/4$; the time is measured in years in the original ODE system. We will identify a feasible τ value for our system, and run simulations using this value, but we will also change this time delay to illustrate how the delay feature can have a dramatic effect on the behavior of the solutions.

The constants involved are estimated in [1]; the constant which can be estimated with the most confidence is the population growth rate a . The widely accepted value is $a = 0.004$, and we will use this in our computations. The constants c and h , the growth rate for the resources and the effect of harvesting, are harder to estimate, but [1] uses values close to $c = 0.01$ and $h = 0.005$.

The scaling performed in Section 2.1 changes these values. As we mentioned there, the new time shift is: $P(t - \tau) = P(\tilde{t}/a - \tau) = P((\tilde{t} - \tau a)/a) = \tilde{P}(\tilde{t} - \tau a)$; the scaling, in effect, "slows down" time. Now considering the above mentioned values for a , c and h , some possible values for the constants are $\tilde{c} = c/a = 0.01/0.004 = 2.5$, $\tilde{h} = h/a = 0.005/0.004 = 1.25$ and $\tilde{\tau} = \tau a = 3/4(0.004) = 0.003$. We will consider values close to these "base estimate" values, as well as different ones of course, because we want to explore the different regions of the parameter plane for different types of behavior of the system.

We will use the transformed DDE system (7)-(8) for our numerical simulations; recall that $z = P$ (the size of the population). Our graphs show the behavior of this function. Recall also that P and R are scaled against K , the carrying capacity of the resources.

We will refer to the notations of the bifurcation diagram Figure 1; we try to investigate parameter values close to the boundaries of the regions specified there, to identify how the delay might change the behavior of the system.

First, we will choose $\tau = 0.003$, and investigate the boundary between regions 5 and 4, i.e. the regions where survival is ensured for all initial conditions and where extinction and survival are both possible, respectively.

Let us choose the initial conditions to be $z(t) = 0.3$, $\xi(t) = 0.8$ for $-\tau \leq t \leq 0$.

Figures 4 and 5 below show some possible behavior as c is fixed at 1.5, and h is changed. The original ODE model predicts that as h increases over the value 1,

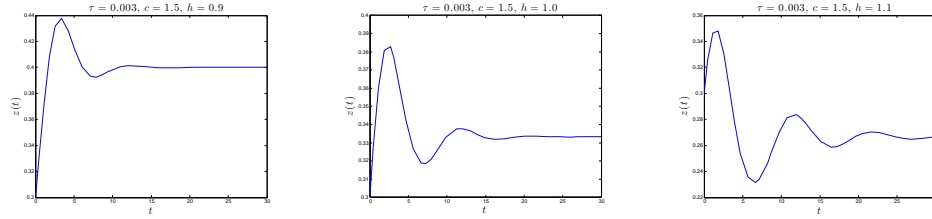


Figure 4: Fixed $\tau = 0.003$, $c = 1.5$, changing h .

there are initial conditions so that $z(t)$ converges to 0 (extinction). This is certainly not the case for the initial condition $z(t) = 0.3$, $-\tau \leq t \leq 0$ for the DDE system; raising this value will give us extinction, but for a lot higher initial condition than [1] gives for the ODE. It seems that the delay acts as a "damping" on the system and does not allow the solution to approach the extinction regime for a while.

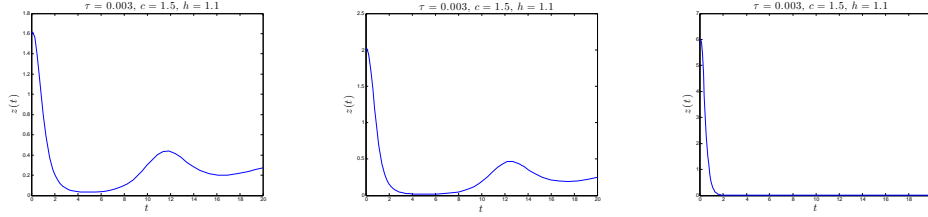


Figure 5: Fixed $\tau = 0.003$, $c = 1.5$, $h = 1.1$; changing the initial condition

Let us consider now the boundary between regions 3 and 4 (the location of the Hopf bifurcation) when $c = 2$. When the initial population is low (0.1) and the initial population/resource ratio is high (0.8), then varying the value of h from 1.3 to 1.7 produces the numerical approximations shown on Figure 6. We can see that we go through the Hopf bifurcation predicted earlier. For this small value of τ , the Hopf bifurcation is taking place fairly close to the ODE result $2h = c + 1$, but certainly a little before; looking at the amplitude on the middle figure (where $2h = 2 \cdot 1.5 = 2 + 1 = c + 1$), we can see that it is already growing, thus we captured a situation where the coexistence equilibrium is already unstable.

As Figure 3 suggests, raising the value of c will give us a bigger gap between the ODE and DDE Hopf bifurcation values. Let us illustrate this with choosing the values $c = 4$ and $h = 2.495$, $h = 2.499$ and $h = 2.500$. The value of τ is still small, thus the difference will not be big, but we can check that the Hopf bifurcation takes place before the ODE predicted value $h = 2.5$. The results are shown on Figure 7.

The effect of the delay becomes very pronounced when we start to raise the value of τ . As predicted on Figure 3, for higher values of the delay, the location of the Hopf bifurcation can even enter the part where the ODE predicted survival for

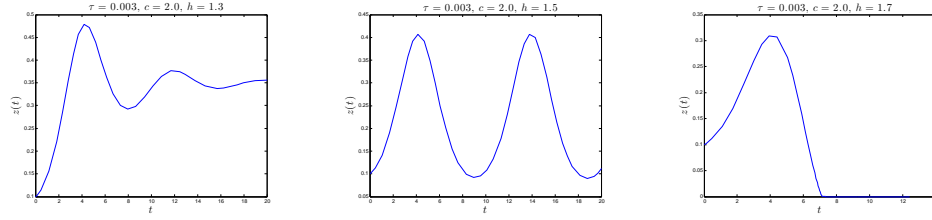


Figure 6: Fixed $\tau = 0.003$, $c = 2$, changing h .

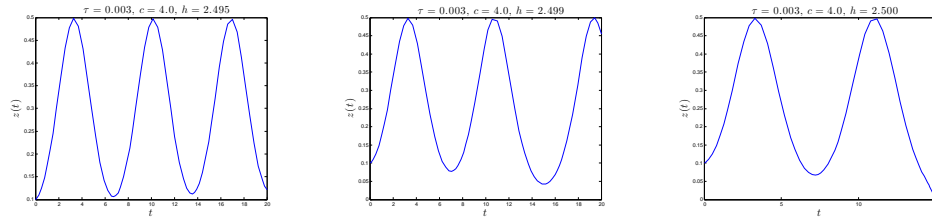


Figure 7: Fixed $\tau = 0.003$, $c = 4$, changing h .

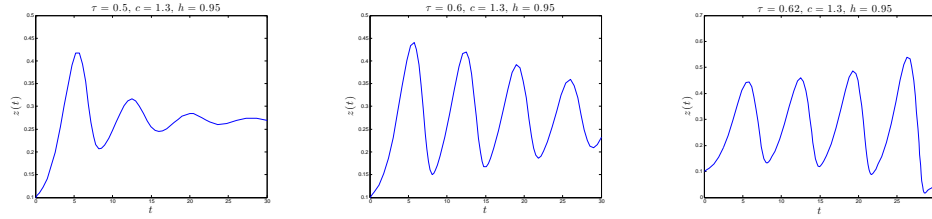


Figure 8: Fixed $c = 1.3$, $h = 0.95$, changing τ .

all. We show this effect on Figure 8. We choose $c = 1.3$, $h = 0.95$; this is clearly in region 5 for the ODE model. Raising the value of τ , we can see from Figure 3 that somewhere between $\tau = 0.6$ and $\tau = 0.62$ the stability of the attractor at $(1 - h/c, 1)$ will be lost, resulting in a solution signifying extinction.

A Appendix

- Delay differential equation file: system right hand side.

```
function v = righthands(t,y,Z,h,c)
% System (7)–(8).

% y(1) = z(t)      population size at time t
% y(2) = xi(t)     resource/population ratio at time t
% Z(1) = z(t-tau)  population size, time shifted
% Z(2) = xi(t-tau) resource/population ratio, time shifted

v = zeros(2,1);

%z derivative
v(1) = Z(1)*(1-Z(2));
%xi derivative
v(2) = y(2)*(1-Z(2))*(Z(1)/y(1))+c*y(1)-c*y(2)+h*y(2)*y(2);
```

- History file: initial condition functions.

```
function u = hist(t,h,c)
% Initial (constant) function for model (7)–(8).
% u(1) is the initial population size, scaled against K.

u = zeros(2,1);

%initial population
u(1) = 0.3;      % 'real size'=0.3K
%initial resource/population ratio
u(2) = 0.8;
```

- Script file using *dde23*.


```

% Solves and plots approximating solutions of (7)–(8).
% Calls righthts.m and hist.m via dde23.

c = 1.5;           % resource reproduction rate
h = 1.0;           % harvesting constant

tau = 0.003;       % delay

Tscale = [0 30];   %30/0.004 = 7500 years

sol = dde23(@righthts,tau,@hist,Tscale,[],h,c);

figure(1);clf;
plot(sol.x,sol.y(1,:));

ylabel('z(t)', 'interpreter', 'latex');
xlabel('t', 'interpreter', 'latex');
title('τ=0.003, c=1.5, h=1.0', 'interpreter', 'latex');

```

References

- [1] Basener, W., and Ross, D. S. *Booming and Crashing Populations and Easter Island*. SIAM Journal on Applied Mathematics 65.2 (2004): 684.
- [2] Bod, R., Hay, J., and Jannedy, S. *Probabilistic Linguistics* Cambridge, MA: MIT, 2003.
- [3] Diamond, J. M. *Collapse: How Societies Choose to Fail or Succeed*. New York: Penguin, 2005.
- [4] Fischer, S. R. *Island at the End of the World: The Turbulent History of Easter Island*. The American Historical Review 111.2 (2006): 455-56.
- [5] Gershenfeld, N. A. *The Nature of Mathematical Modeling*. Cambridge: Cambridge UP, 1999.
- [6] Heyerdahl, T. *Aku-Aku: The Secret of Easter Island*. American Anthropologist 61.4 (1959): 708-10.
- [7] Kingsland, S. E. *Modeling Nature: Episodes in the History of Population Ecology*. Chicago: University of Chicago, 1995.
- [8] Malthus, T. R. *An Essay on the Principle of Population Or, A View of Its past and Present Effects on Human Happiness; with an Inquiry into Our Prospects Respecting the Future Removal or Mitigation of the Evils Which It Occasions*. London: J. Murray, 1826.
- [9] Ravindran, S. *Book Reviews : J. E. Cohen, How Many People Can the Earth Support?* New York and London: Norton, 1995, 532 Pp.
- [10] Turchin, P. *Complex Population Dynamics: A Theoretical/empirical Synthesis*. Princeton, NJ: Princeton UP, 2003.
- [11] Turchin, P. *Does Population Ecology Have General Laws?* Oikos 94.1 (2001): 17-26.
- [12] Van Der Heijden, G. *Hopf Bifurcation*. Encyclopedia of Nonlinear Science. Ed. Alwyn Scott. New York: Routledge, 2005.

- [13] Driver, R. D. Ordinary and Delay Differential Equations, Springer Verlag, 1977.
- [14] Shampine, L.F., and Thompson, S. *Solving DDEs in MATLAB*, Appl. Numer. Math., 37 (2001), pp. 441-458.