Mathematical Models of Reptile Populations Using Delay Differential Equations

California State Polytechnic University, Pomona

and

Loyola Marymount University

Department of Mathematics Technical Report

Tenecia Plummer, Cinthia Vega, Clare Wickman, Michael Zawoiski

David Uminsky,¶Angela Gallegos∥

Applied Mathematical Sciences Summer Institute

Department of Mathematics & Statistics,

California State Polytechnic University, Pomona

3801 W. Temple Ave.

Pomona, CA 91768

3 August 2007

^{*}Albany State University

[†]Loyola Marymount University

[‡]University of Maryland, Baltimore County

[§]City College of New York

[¶]Boston University

Occidental College

Abstract

A well-known phenomenon among reptile species is temperature-dependent sex determination (TSD) in which the temperature of egg incubation determines the sex of the hatchlings. Based on previous work in (Murray, 2002) and (Woodward and Murray, 1993) we develop a delay differential equation (DDE) model describing the nesting habits of crocodilians; the delay accounts for some of the dependence of birth and death rates on the age of the population members. We are able to reasonably account for age structure in the population while finding a nonzero stable equilibrium. Stability of this equilibrium allows us to compare this to the biological data of Smith and Webb (1985, 1987); we obtain very strong agreement. Additionally, we solve our model numerically using a modified Runge-Kutta solver in Matlab and investigate the effects of environmental changes on the population.

1 Introduction

1.1 Biological Background

Crocodilians have been around since the dinosaurs, and have survived essentially unchanged for millions of years (Murray, 2002). A significant difference between the crocodilians and many other species is how the sex of the offspring is determined. Sex determination is a fundamental biological process that varies among species. For example, the sex of offspring in mammals and birds is determined genetically; they have genetic sex determination (GSD). However, among several reptile species the temperature during egg incubation determines the sex of the offspring, a process known as temperature dependent sex determination (TSD). There is general agreement among biologists that temperature exerts its influence on species with TSD by affecting genetic mechanisms. This alters the hormonal environment of the sexually indifferent embryo and direct development in either a male or a female direction (Sarre et al., 2004). Sex determination is an important phenomenon of biological evolution;

not only does it affect population sex ratios, but also the reproductive success of each member. It is likely that a skewed population sex ratio occurs in species which exhibit TSD as a consequence of skewed environmental types (Murray, 2002). For example, slight changes in the egg incubation temperature, as little as one to two degrees, alter the sex gender of the offspring and thus skew the sex ratio.

In crocodiles and alligators, low temperatures generally produce female hatchlings while high temperatures generally produce male hatchlings. This pattern is not true for all reptiles. For example, in several species of turtle, low temperatures generally produce male hatchlings while high temperatures generally produce female hatchlings. Specifically in Alliquitor mississippiensis, temperatures below 30°C yield almost all female hatchlings while temperatures greater than 33°C produce male hatchlings. At approximately 32°C hatchlings are half male and half female. Alligators have three types of nesting sites that roughly correspond to the different temperature zones: wet marsh, dry marsh, and dry levee, depicted in Figure 1. Wet marsh nests are cool while dry levee nests are hot. The dry marsh corresponds to middle range temperatures. For our discussion, we designate the wet marsh as R1, the dry marsh as R2, and the dry leeve as R3. Biologists observe that, for unknown reasons, not all sexually mature females nest in a given year, even if the nesting areas are not filled to capacity (Woodward and Murray, 1993). Female alligators desire to nest in the environment from which they themselves hatched. Thus, while they do not choose the sex of their ospring, their choice of nest site indirectly determines the sex of their offspring (Woodward and Murray, 1993). If there are a limited number of nesting sites within each temperature region, a purely male or female population cannot occur.

Because alligator sex is determined via temperature of the environment, one might think they are particularly susceptible to environmental changes. However, through a skewed sex ratio, TSD may explain how the crocodilians have survived for so long (Woodward and Murray, 1993). It is believed that TSD cannot only protect populations from environmental variability, but also enable them to make use of changing habitats by adjusting their

Nesting Sites Influence the Sex of the Hatchlings

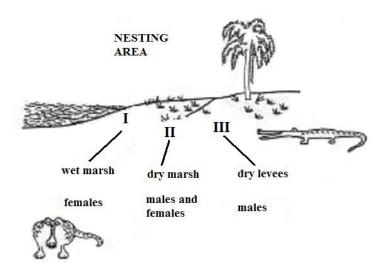


Figure 1: Due to temperature-dependent sex determination, in alligators the choice of nesting site determines the sex of the hatchlings. In wet marsh, cool temperatures produce female hatchlings. In dry levees, hot temperatures produce male hatchlings. In dry marsh, where the temperatures are intermediate, approximately 50 percent of the hatchlings are male, and 50 percent are female. Female alligators desire to nest in the region in which they were hatched. (Graphic taken directly from Murray (2002)).

metabolisms (Murray, 2002). Reproductive fitness of females and males are strongly influenced in different ways by the environment (Murray, 2002). With a warmer temperature the eggs of alligators tend to develop faster, hatch more quickly, and result in larger adults. Accordingly, warm temperatures produce males which are bigger than females. In addition, males control harems of females, and the bigger the male the bigger his harem. Such males mate more often and for longer periods of time. These longer term effects on population members may be more reasons why TSD has persisted in crocodilians.

As can be seen in Figure 2, another key feature in alligator population development is the age-dependence of their birth and death rates. Alligators of age eight or less cannot reproduce and are considered sexually immature; most alligators will be sexually mature by age twelve. The reproductive rate of alligators between ages eight and twelve is roughly 0.286, corresponding to the fact that only some of these alligators are sexually mature. After age twelve it is 0.844. The adults then can reproduce until they die. Egg survivorship is very low due to predation and nesting disturbances. Hatchling survivorship is also low because hatchlings are easy prey; approximately 90% of hatchlings die before they reach one year of age. Between the ages of one and eight, alligator survivorship increases significantly. In middle age, survivorship is very high, almost 100%, likely because very few species pose a threat to mature alligators. Survivorship decreases again after 31 years of age. These changes in birth and death rates cannot be captured by an ordinary differential equation model; thus we need a different type of model to capture more complexity of this biological system.

In this paper we present a delay differential equation (DDE) model for an alligator population. This model incorporates some of the age structure that affects birth and death rates, as mentioned above. First, we describe other models of TSD in alligators. Second, we present our DDE model for an alligator population. Third, we discuss the equilibria of the model including the stability of a nontrivial equilibrium point. We then present numerical simulation results and their implications. We discuss our results in the context of existing

Age-Dependent Birth and Death Rates

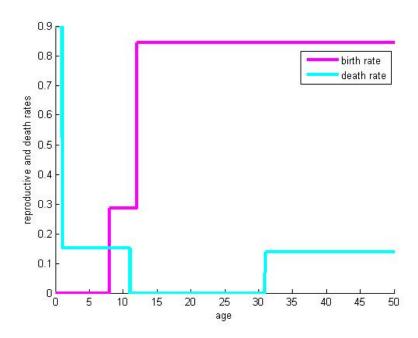


Figure 2: Birth and death rates are highly age-dependent in alligators. The first year of life is particularly perilous for the reptiles, but in their prime, they are practically invulnerable. They reach sexual maturity between 8 and 12 years of age. (Data taken from Smith and Webb (1985, 1987).)

biological knowledge about age distribution and sex ratios in alligators. Finally, we comment on future directions for this work.

1.2 Previous Modeling of TSD in Alligators

We base our model on Murray's ODE model of alligator nesting behavior (Murray, 2002). The driving assumption in his ODE model is that female alligators prefer to nest in the region in which they were hatched; age dependence of birth and death rates is disregarded. The physical size of each region limits the number of females who can nest there. Thus, females from R1 attempt to nest in R1 and move to a warmer region if necessary. Females from R2 do not attempt to nest in R1 but instead try to return to R2; if unable, they try to nest in R3. Murray designates subpopulations of alligators with the number of the region they were born in. Thus, at any time t, the population is divided into four classes: $f_1(t)$ are the female alligators born in R1; $f_2(t)$ are the female alligators born in R2; $m_2(t)$ are the male alligators born in R3. He develops four differential equations to describe these populations and investigates their equilibria. At equilibrium he obtains a male-to-total-population sex ratio of 0.13. This is consistent with the ratio of 0.125 which he cites from (Murray, 2002).

Woodward and Murray (1993) use a partial differential equation (PDE) model to describe the effect of temperature-dependent sex determination on an alligator population; this model also accounts for the age-dependent birth and death rates from Smith and Webb (1985). The PDE model reproduces biologically-observed age distribution. However, it is much harder to analyze, and they give numerical evidence for the existence of a fixed point in their system. This raises the question of how to take age dependence into account and at the same time keep enough simplicity in order to analytically investigate the equilibria. In an attempt to resolve these issues, we propose our DDE model as an alternative. This model is more complex to analyze than an ODE model but less complex than a PDE model. By using a DDE model we hope to capture more realistic behavior in the population and at the

same time maintain enough simplicity to do some significant analysis. Our goal is to offer a new approach to the study of nesting alligator populations. We now discuss some general concepts of DDEs before we introduce our alligator model.

2 Basic Concepts of Delay Differential Equations

Delay differential equations appear similar to ordinary differential equations but with an important difference in their formulation. To solve an ordinary differential equation an initial condition is required. Because a delay differential equation depends on the solution some time, τ , ago, an initial history (i.e. the solution behavior over a time interval of length τ) is instead required. While DDEs can have either countable time delays (a discrete DDE) or uncountable time delays (a continuous DDE) we only consider the discrete case. The general example of such a DDE is

$$\frac{dx(t)}{dt} = f(t, x(t), x(t - \tau_1), \dots, x(t - \tau_n)), \tag{1}$$

where the $\tau_1 > \ldots > \tau_n \ge 0$ are the delays. To solve this DDE an initial history would need to be prescribed over the interval $-\tau_{max} \le t \le 0$ where $\tau_{max} = max(\tau_1, \ldots, \tau_n)$.

To make ourselves more familiar with a DDE model, we have developed a "toy" model for the alligators which incorporates age structure into the population while ignoring other details. We approximate the age structure by dividing the population into "adults", A(t), and "juveniles", J(t). We choose age ten as the dividing line for the population since ten is near the median age that alligators become sexually mature. For this reason we assume the juveniles do not reproduce. In this example, juveniles are born at a rate proportional to the current adult population. Juveniles leave the juvenile population by either dying or becoming adults.

$$\frac{dJ(t)}{dt} = bA(t) - sbA(t-10) - d_jJ(t). \tag{2}$$

The parameter b is the birth rate in the population and is taken in this example to be constant. We assume that juvenile deaths occur at a rate proportional to the current juvenile population. In this case the constraint of proportionality is the juvenile death rate d_j . We also assume that juveniles become adults in proportion to the number born ten years ago. This proportionality constant is the survival probability s, where $s = e^{\int_{t-\tau}^t d_j(w)dw}$, which results from treating the deaths of juvenile alligators as a Poisson process. Each death is considered an arrival, with an arrival rate of d_j , the juvenile death rate, which approximates the probability that a juvenile alligator will die in a particular year. Thus the expected number of juveniles who will die over then length of a delay time τ is:

$$\lambda_T = \int_t^{t+\tau} d_j(w) dw. \tag{3}$$

Therefore, the probability that an alligator born at time t will not die by time $t + \tau$ is:

$$P\{N(t+\tau) - N(t) = 0\} = \frac{\lambda^0}{0!} e^{-\lambda_j}$$
$$= e^{-\lambda_T}. \tag{4}$$

Therefore we take this value as our survival probability. Because we have no further age classes, once in the adult population, an adult can only leave it by dying. We again assume that deaths occur at a rate proportional to the current adult population size; the constant of proportionality is our adult death rate d_a . Thus, the DDE for our adult population is

$$\frac{dA(t)}{dt} = sbA(t-10) - d_aA(t) \tag{5}$$

To complete the formulation of this model, we need to prescribe an initial condition for the juvenile population and an initial history for the adults. A nonzero initial history in this case does not affect the long term behavior of the system, so we take the adult history to be

constant. Thus, the conditions

$$J(0) = J_0, \quad A(t) = A_0 \quad for \quad -10 \le t \le 0$$
 (6)

complete the toy model formulation.

This is a simple model with few parameters. We make use of it, however, to better understand the DDE formulation and to prepare for the development of our more complicated models. We nondimensionalize this model to reduce some parameters. We choose our characteristic time scale to be $(\hat{t} = \frac{1}{b})$. We normalize the juvenile and adult populations by the initial history of the adult population, $\hat{J} = \hat{A} = A_0$. Taking nondimensional variables $t^* = \frac{t}{\hat{t}}, J^* = \frac{J}{\hat{J}}$, and $A^* = \frac{A}{\hat{A}}$ we obtain the following dimensionaless of the model with $a_1 = \frac{d_j}{b}$, $a_2 = \frac{d_a}{b}$, and $\tau = 10b$:

$$\frac{dJ^*}{dt^*} = A^* - a_1 J^*(t^*) - sA^*(t^* - \tau), \tag{7}$$

$$\frac{dA^*}{dt^*} = sA^*(t^* - \tau) - a_2A^*(t^*), \tag{8}$$

$$J^*(0) = \frac{J_0}{A_0}, \quad A^*(t^*) = 1, \quad -\tau \le t \le 0.$$
 (9)

To solve this system numerically, we have used Matlab's dde23, a delay differential equation solver which makes use of a modified second or third order Runge-Kutta method (see appendix). Using this method in our model, we get either exponential growth or decay. A sample result of population is given in figure 3, in this case $s > a_2$. Notice this case results in exponential growth of the population. This is expected given the form of our birth and recruitment function. In addition, there are two equilibria, for which we are able to solve analytically. They first is the trivial fixed point $(J^*, A^*) = (0,0)$. In addition, under the parameter constraint $s = a_2$, we obtain $(J^*, A^*) = (A^*(\frac{1-s}{a_1}), A^*)$.

Numerical experimentation suggests that the second equilibrium given above is stable, although we have been unable to prove this analytically. In addition, the ratio A/J has an

Sample Simulation Results from Toy Model

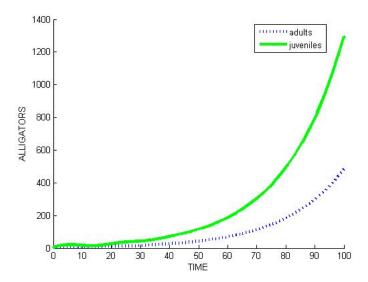


Figure 3: Numerical solution to the toy model. The system tends toward either exponential decay or, in this example, exponential growth.

equilibrium at $\frac{A}{J} = \frac{a_1 - a_2 - s}{s - 1}$. Testing the stability of this equilibrium is trivial; we find that it is stable provided that $s > d_a - d_j$.

3 Delay Differential Equation Model for Alligators

3.1 Three Regions with One Age Delay

We now build on the age structure incorporated in the toy model to create a DDE model that takes into account the nesting behaviors of alligators. We keep the same age classes; thus, our alligator population is divided into a juvenile class (ages 0-10) and an adult class (ages 10-50). Now we incorporate Murray's assumptions: (1) there are three distinct nesting regions with different numbers of nesting sites and (2) females choose to nest in the region in which they hatched. As we are extending the ODE model in (Murray 2002) we keep the notation presented there. However, we now have eight subpopulation since we separate the alligators into subpopulations according to sex, age class, and region of hatchling. We

designate the juvenile females from R1 by $f_1(t)$ and the adult females from R1 by $F_1(t)$. Similarly, from R2 thee are now four subpopulations, the juvenile females, $f_2(t)$, and males, $m_2(t)$, as well as the adult females, $F_2(t)$, and males, $M_2(t)$. Finally, in R3 we track the juvenile and adult males, $m_3(t)$ and $M_3(t)$ respectively; recall no females can be born there.

Since only a fraction, c, of females can nest within each region, we denote by k_i the nesting capacity of the i^{th} region. The fraction must be a function of the nesting capacity and the females desiring to nest in that region. We might assume that $c_1(k_1, F_1)$ is as follows:

$$c_1(k_1, F_1) = \begin{cases} 1, & F_1 \leq k_1 \\ \frac{k_1}{F_1}, & F_1 > k_1. \end{cases}$$

However, because it is likely that females do not fill every last site before moving on, and for algebraic simplicity, we take the approximation

$$c_1(k_1, F_1) = \left(\frac{k_1}{k_1 + F_1}\right),$$

As Murray (2002) notes, the approximate fraction maintains the appropriate behavior for F_1 near 0 and $F_1 \gg k_1$. Also, it is algebraically simple enough for analytic purposes. Additionally, the functions are not too different, as illustrated in Figure 4.

Thus, the number of females who can nest in R1 is given by $c_1(k_1, F_1)F_1$ and therefore the number of juveniles born into R1 is

$$b\frac{k_1}{k_1+F_1}F_1,$$

where b is the birthrate. As before we assume that juvenile alligators die at a rate proportional to the current juvenile population, and that those that do not die survive with corresponding probability s to become adults (see previous section for a description of s). It

Fraction Approximation

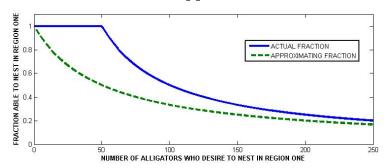


Figure 4: The top line is the actual fraction of female alligators that are able to nest within a region. The bottom line is the approximated function that we input in our equations that approximate the nesting capacity.

follows from these assumptions that the rate of change of juvenile females in R1 is as follows:

$$\frac{df_1}{dt} = bF_1(t) \left(\frac{k_1}{k_1 + F_1(t)}\right) - d_j f_1(t) - sbF_1(t - 10) \left(\frac{k_1}{k_1 + F_1(t - 10)}\right). \tag{10}$$

In this case, b is still the reproductive rate of female adults, and $F_1(t)$ is the number of adult females who were themselves born in R1. Finally k_1 is the nesting capacity, or number of nesting sites, in R1. Notice that, as in the toy model case, the expression describing juvenile graduation into adulthood is the birth function of 10 years ago, modified by the survival probability s. As in the toy model, the adult populations only increase by entrance of juveniles into the adult class. Thus, still assuming a linear death rate in the population, we obtain the following DDE for the adult females from R1:

$$\frac{dF_1}{dt} = sbF_1(t-10)\left(\frac{k_1}{k_1 + F_1(t-10)}\right) - d_aF_1. \tag{11}$$

Notice that the recruitment function appears as it did in equation 10, only now it is positive. Also note that the equation for our $F_1(t)$ population is explicitly independent of $f_1(t)$. Thus, while we describe the populations in order to count them, the $F_1(t)$ population can be explored independently. We make use of this fact in our analysis of the equilibrium points.

The rate of change of the R2 populations is affected by the adult female population in R1

because those who are unable to nest in R1 will try to nest in R2. Again, we are interested in the fraction of adult females who can nest in R2 as well as the number who are interested in nesting in R2. To obtain the fraction of the $F_1(t)$ population seeking to nest in R2, we subtract from one,

$$1 - \frac{k_1}{k_1 + F_1(t)} = \frac{F_1(t)}{k_1 + F_1(t)}.$$

This gives the fraction of females from R1 that could not nest in R1 and now want to nest in R2. This fraction is multiplied by $F_1(t)$ to get the number of $F_1(t)$ that cannot nest in R1:

$$\frac{F_1^2(t)}{k_1 + F_1(t)}.$$

Thus, the total number of females desiring nest sites in R2 is given by:

$$\left(\frac{F_1^2(t)}{k_1 + F_1(t)} + F_2(t)\right).$$

We use the expression

$$\frac{k_2}{k_2 + F_1(t) + F_2(t)}$$

to approximate the fraction of females that can nest in R2. This is clearly an approximation to the actual fraction. We use it for its analytical simplicity as well as to stay consistent with the formulation in (Murray, 2002). Then, assuming the hatchlings in R2 are half female, half

male, and that all populations die linearly, the juveniles in R2 can be described as follows:

$$\frac{df_2}{dt} = \frac{b}{2} \left(\frac{F_1^2(t)}{k_1 + F_1(t)} + F_2(t) \right) \left(\frac{k_2}{k_2 - F_1(t) + F_2(t)} \right) - d_j f_2(t)$$

$$-s \frac{b}{2} \left(\frac{F_1^2(t - 10)}{k_1 + F_1(t - 10)} \right) \left(\frac{k_2}{k_2 + F_1(t - 10) + F_2(t - 10)} \right),$$

$$\frac{dm_2}{dt} = \frac{b}{2} \left(\frac{F_1^2(t)}{k_1 + F_1(t)} + F_2(t) \right) \left(\frac{k_2}{k_2 - F_1(t) + F_2(t)} \right) - d_j m_2(t)$$

$$-s \frac{b}{2} \left(\frac{F_1^2(t - 10)}{k_1 + F_1(t - 10)} + F_2(t - 10) \right) \left(\frac{k_2}{k_2 + F_1(t - 10) + F_2(t - 10)} \right).$$
(12)

The $F_2(t)$ population changes in the same manner as the $F_1(t)$ population. Therefore, their rate of change is given by

$$\frac{dF_2}{dt} = s \frac{b}{2} \left(\frac{F_1^2(t-10)}{k_1 + F_1(t-10)} + F_2(t-10) \right) \left(\frac{k_2}{k_2 + F_1(t-10) + F_2(t-10)} \right) -d_a F_2(t).$$
(14)

The adult males in R2 follow similarly:

$$\frac{dM_2}{dt} = s \frac{b}{2} \left(\frac{F_1^2(t-10)}{k_1 + F_1(t-10)} + F_2(t-10) \right) \left(\frac{k_2}{k_2 + F_1(t-10) + F_2(t-10)} \right)$$

$$-d_a M_2. \tag{15}$$

Similarly the rate of change of males in R3 depends on the R1 and R2 adult females since those unable to nest in R1 or R2 attempt to nest in R3. Again we are interested in who can and who desires to nest in R3. In R3 only males hatch; as a result, we do not have any equations for females in this region. Under similar assumptions, the rate of change for the

juvenile male population from R3 is:

$$\frac{dm_3}{dt} = b \left(\frac{k_3}{k_3 + F_1(t) + F_2(t)} \right) \left(\frac{F_1^2(t)}{k_1 + F_1(t)} + F_2(t) \right) \left(\frac{F_1(t) + F_2(t)}{k_2 + F_1(t) + F_2(t)} \right)
- d_j m_3(t) - sb \left(\frac{k_3}{k_3 + F_1(t - 10) + F_2(t - 10)} \right) \left(\frac{F_1^2(t - 10)}{k_1 + F_1(t - 10)} + F_2(t - 10) \right)
\left(\frac{F_1(t - 10) + F_2(t - 10)}{k_2 + F_1(t - 10) + F_2(t - 10)} \right).$$
(16)

These juveniles are then recruited into the population of adults from R3:

$$\frac{dM_3}{dt} = s \left(\frac{F_1^2(t-10)}{1+F_1(t-10)} + F_2(t-10) \right) \left(\frac{F_1(t-10)+F_2(t-10)}{c_2+F_1(t-10)+F_2(t-10)} \right)$$

$$\left(\frac{c_3}{c_3+F_1(t-10)+F_2(t-10)} \right) - a_2 M_3(t).$$
(17)

Females unable to nest in any of the three regions are neglected and assumed to not reproduce. Notice that the model is driven by the female populations and does not truly account for sexual reproduction. This is not unreasonable in a species which is heavily skewed towards females (Murray, 2002; Woodward and Murray, 1993). To complete the model we need only prescribe initial conditions $f_1(t) = f_{(1,0)}$, $f_2(t) = f_{(2,0)}$, $m_2(t) = m_{(2,0)}$, $m_3(t) = m_{(3,0)}$, $M_2(t) = M_{(2,0)}$, and $M_3(t) = M_{(3,0)}$ and initial histories for $F_1(t)$ and $F_2(t)$. For reasons discussed above we take constant initial histories $F_1(t) = F_{(1,0)}$ and $F_2(t) = F_{(2,0)}$ for $-10 \le t \le 0$. These initial conditions together with equations 10, 11, 12, 13, 14, 15, 16, 17 comprise our DDE model.

3.2 Three Regions with One Delay Nondimensionalized

We recast our model in nondimensional form. We scale time by the birthrate as in the "toy" model, choosing $\hat{t} = \frac{1}{b}$ as the characteristic time scale. All populations are scaled by the nesting capacity of R1, k_1 . Thus,

$$\hat{f}_1 = \hat{F}_1 = \hat{f}_2 = \hat{F}_2 = \hat{m}_2 = \hat{M}_2 = \hat{m}_3 = \hat{M}_3 = k_1.$$

We choose nondimensional variables $t^* = t\hat{t}$, $f_i^* = f_i\hat{f}_i$, $m_i^* = m_i\hat{m}_i$, $F_i^* = F_i\hat{F}_i$ and $M_i^* = M_i\hat{M}_i$. Using these scalings we obtain the following nondimensionalized version of our model, where the nondimensional notation "*" has been dropped for convenience. We list the equations according to region and gender.

• Females from Region 1

$$\frac{df_1}{dt} = F_1(t) \left(\frac{1}{1 + F_1(t)} \right) - sF_1(t - \tau) \left(\frac{1}{1 + F_1(t - \tau)} \right) - a_1 f_1(t) \tag{18}$$

$$\frac{dF_1}{dt} = sF_1(t-\tau) \left(\frac{1}{1+F_1(t-\tau)}\right) - a_2 F_1(t) \tag{19}$$

• Females from Region 2

$$\frac{df_2}{dt} = \frac{1}{2} \left(\frac{F_1^2(t)}{1 + F_1(t)} + F_2(t) \right) \left(\frac{c_2}{c_2 + F_1(t - \tau) + F_2(t - \tau)} \right)
- \frac{s}{2} \left(\frac{F_1^2(t - \tau)}{1 + F_1(t - \tau)} + F_2(t - \tau) \right)
\left(\frac{c_2}{c_2 + F_1(t - \tau) + F_2(t - \tau)} \right) - a_1 f_2$$
(20)

$$\frac{dF_2}{dt} = \frac{s}{2} \left(\frac{F_1^2(t-\tau)}{1+F_1(t-\tau)} + F_2(t-\tau) \right)
\left(\frac{c_2}{c_2+F_1(t-\tau)} + F_2(t-\tau) \right) - a_2 F_2$$
(21)

• Males from Region 2

$$\frac{dm_2}{dt} = \frac{1}{2} \left(\frac{F_1^2(t)}{1 + F_1(t)} + F_2(t) \right) \left(\frac{c_2}{c_2 + F_1(t - \tau) + F_2(t - \tau)} \right) - \frac{s}{2} \left(\frac{F_1^2(t - \tau)}{1 + F_1(t - \tau)} + F_2(t - \tau) \right) \tag{22}$$

$$\left(\frac{c_2}{c_2 + F_1(t - \tau) + F_2(t - \tau)}\right) - a_1 m_2(t)$$

$$\frac{dM_2}{dt} = \frac{s}{2} \left(\frac{F_1^2(t - \tau)}{1 + F_1(t - \tau)} + F_2(t - \tau)\right)$$

$$\left(\frac{c_2}{c_2 + F_1(t - \tau) + F_2(t - \tau)}\right) - a_2 M_2(t)$$
(23)

• Males from Region 3

$$\frac{dm_3}{dt} = \left(\frac{F_1^2(t)}{1 + F_1(t)} + F_2(t)\right) \left(\frac{F_1(t) + F_2(t)}{c_2 + F_1(t) + F_2(t)}\right) \left(\frac{c_3}{c_3 + F_1(t) + F_2(t)}\right)
-s \left(\frac{F_1^2(t - \tau)}{1 + F_1(t - \tau)} + F_2(t - \tau)\right) \left(\frac{F_1(t - \tau) + F_2(t - \tau)}{c_2 + F_1(t - \tau) + F_2(t - \tau)}\right)$$
(24)

$$\left(\frac{c_3}{c_3 + F_1(t - \tau) + F_2(t - \tau)}\right) - a_1 m_3(t)$$

$$\frac{dM_3}{dt} = s \left(\frac{F_1^2(t - \tau)}{1 + F_1(t - \tau)} + F_2(t - \tau)\right) \left(\frac{F_1(t - \tau) + F_2(t - \tau)}{c_2 + F_1(t - \tau) + F_2(t - \tau)}\right)$$

$$\left(\frac{c_3}{c_3 + F_1(t - \tau) + F_2(t - \tau)}\right) - a_2 M_3(t)$$
(25)

The new nondimensional parameter are the juvenile removal rate $a_1 = d_j/b$, the adult removal rate $a_2 = d_a/b$, the nesting capacity ratios $c_2 = k_2/k_1$, $c_3 = k_3/k_1$, and the scaled delay $\tau = 10b$. Notice that the survival probability s remains unchanged by this scaling. We can reformulate it in terms of a, however, $s = e^{-ba_1\tau}$. To complete our nondimesional formulation, we set our initial conditions

$$f_{(1,0)} = f_{(2,0)} = m_{(2,0)} = m_{(3,0)} = 10$$
 and $M_{(2,0)} = M_{(3,0)} = 5$.

We choose constant histories over the time interval $-\tau \le t \le 0$:

$$F_{(1,0)} = 15$$
 and $F_{(2,0)} = 10$.

We picked these numbers for simplicity. A typical result is shown in Figure 5. Notice that we observe the evolution of the population in time as well as the evolution of the sex ratio, shown in Figure 6.

Later we will reformulate the results to discuss them in the context of age structure. Notice that the females from R1 dominate the population. This is unsurprising, given that we use Murray's (2002) values for the proportion of the habitat allocated to each region; R1 accounts for almost eighty percent of the habitat.

Typical Example of Single-Delay Model

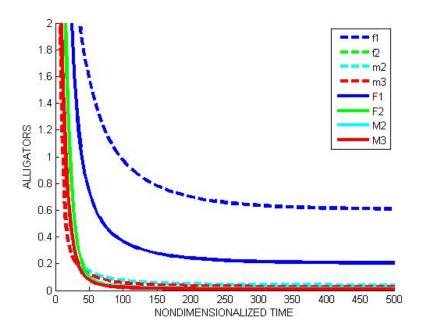


Figure 5: A typical result when our system is solved numerically in Matlab. The system approaches an equilibrium at which the population is dominated by the females from region one.

Evolution of the Male:Population Ratio Over Time

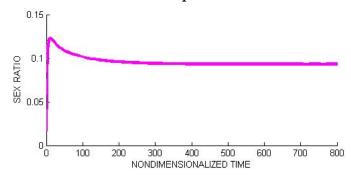


Figure 6: Evolution of the sex ratio over time. The ratio of males to total population approaches a value of .09 as the system nears equilibrium. This is at the low end of what is observed in nature.

3.3 Equilibria of the One Delay Model

A crucial question in any population model is "Under what conditions will the population either die off or reach a nonzero equilibrium?" Our model has three equilibrium points: the trivial equilibrium and two nonzero equilibria. One of the nonzero equilibria has negative values for some of the subpopulations; thus it is biologically irrelevant. In this section we present and discuss the positive equilibrium point. Setting equation ?? to zero and solving for a nonzero constant, F_1^* , yields:

$$F_1^* = \frac{s}{a_2} - 1. (26)$$

From equation 26, F_1^* is positive provided that $s > a_2$. This condition means that the probability of a juvenile reaching adulthood needs to be greater than the rate at which adults are removed from the population. In equation ?? and the steady state value f_1^* is given by

$$f_1^* = \frac{(1-s)(s-a_2)}{sa_1}. (27)$$

The equilibrium value, f_1^* is also positive for $s > a_2$, since s, a probability, is less than one. We stimulate solutions to our system in Matlab. We use its built in solver, dde23 to obtain the numeral results. The solver uses a modified version of Runge Kutta method (see Appendix A). The other equilibria are algebraically very complex, we write them here in terms of F_1^* and F_2^* . We obtain positive equilibrium values for each of the populations. Juveniles in R2 have the equilibrium:

$$f_2^* = m_2^* = 1/2(1-s)c_2\left(\frac{F_1^{*2} + F_2^* + F_2^* F_1^*}{(c_2 + F_1^* + F_2^*)(1 + F_1^*)a_1}\right).$$
 (28)

In R3, the equilibria are given by:

$$m_3^* = \frac{(F_1^* + F_2^*)c_2(F_1^{*2} + F_2^* + F_2^* F_1^*)(1-s)}{(c_1 + F_1^* + F_2^*)(c_2 + F_1^* + F_2^*)(1+F_1^*)a_1},$$
(29)

$$M_3^* = \frac{s(F_1^* + F_2^*)c_2(F_1^{*2} + F_2^* + F_2^* F_1^*)}{(c_1 + F_1^* + F_2^*)(c_2 + F_1^* + F_2^*)(1 + F_1^*)a_2}.$$
(30)

The equilibria in terms of parameter values only are given in appendix B. Thus we have established the existence of positive equilibrium point for the model system. This equilibrium appears to be globally stable; indeed, we can show global stability for our particular values of the parameters. For delay differential equations, global stability implies that the equilibrium values do not depend on the initial histories prescribed. As noted above, the equation for the adult female population from R1 is uncoupled from the rest of the model. We follow the approach in (Castillo-Chavez and Brauer 2001), and to determine the stability of F_1^* , we linearize the equation number around F_1^* . We designate the displacement from the equilibria by $u(t) = F_1(t) - F_1^*$. Castillo-Chavez and Brauer (2001) indicate that for the equation

$$\frac{dx}{dt} = R(x(t-\tau)) - D(x(t))$$

with equilibrium point x^* , the linearization about x^* is

$$\frac{du}{dt} = -D'(x^*)u(t) + R'(x^*)u(t-T). \tag{31}$$

Thus, our linearization is

$$\frac{du}{dt} = s \frac{1}{1 + F_1^*} (F_1(t) - F_1^*) - a_2(F_1(t) - F_1^*). \tag{32}$$

The condition of Castillo-Chavez and Brauer (2002) for an asymptotically stable equilibrium,

 x^* , is $|R'(x^*)| < D'(x^*)$. Hence the fact that

$$|s\frac{1}{(1+F_1^*)^2}| = \frac{(a_2)^2}{s} < a_2$$

since $a_2 < s$, implies that the F_1^* has absolute stability. Once F_1^* reaches its equilibrium, the DDE df_1/dt becomes an ODE. Thus we can calculate the stability of f_1^* by differentiating:

$$\frac{d}{df_1} \left[\frac{df_1}{dt} \right] = \frac{d}{df_1} \left[\frac{F_1^*}{1 + F_1^*} - s \frac{F_1^*}{1 + F_1^*} - a_1 f_1 \right]$$
$$= -a_1.$$

Since $\frac{d}{df_1} \left[\frac{df_1}{dt} \right]$ is always negative in our system, we conclude that f_1^* is globally stable as well. We believe the equilibria for the entire system is stable. We can, in fact, demonstrate this stability for a parameter condition that is overly strict. We are still working on the more general proof.

4 Numerical Results

As mentioned above, our simulations are run in Matlab, using its built-in solver, dde23. By varying certain parameters in the model, we simulate our model population's response to various environmental changes.

4.1 Simulation of Protection of Juveniles

Many states impose regulations on fishing and deer hunting; hunters and fisherman are prohibited from shooting fawns and required to throw back fish below a certain size. These laws recognize the fact that the viability of a population depends on the wellbeing of its sexually-immature members. We consider a similar situation for the juvenile alligators by changing the juvenile removal rate, a_1 , from a constant to a step function. We implement the "hunting ban" at time t = 100. Thus, after t = 100 our removal rate is lower:

$$a_1(t) = \begin{cases} .112, & t \le 100; \\ .012, & t > 100. \end{cases}$$

The lowered removal rate simulates a curb on the hunting of juvenile alligators. Because the survival probability s is directly tied to a_1 , it must change accordingly. We still define s according to a Poisson process but now must account for the nonconstant removal rate. Thus,

$$s = e^{-\int_{t-\tau}^t a_1(w)b \ dw}$$

Limitation on Hunting of Juveniles

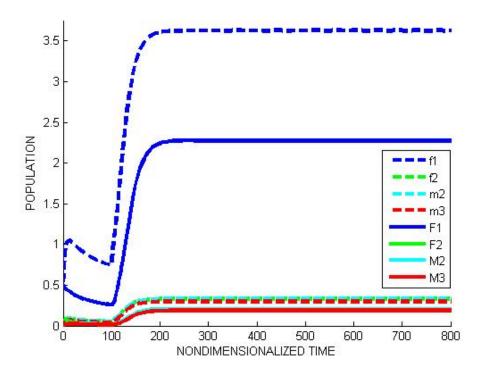


Figure 7: The graph simulates population dynamics resulting from a decrease in the juvenile removal rate when t=100. This reflects a situation resulting from increased protection of the juvenile alligators, perhaps from hunting. This results in larger populations of both juveniles and adults in all regions.

The results of this simulation are depicted in Figure 7. Notice that just before the law is imposed, near 100 units on our characteristic time scale, the population is approaching

equilibrium. The drop in the removal rate causes all populations to increase. This is unsurprising since the growth of the adult populations depends directly on recruitment from the juvenile populations. This simulation supports the idea that to promote a rise in population size, protection of juvenile members is necessary. This is particularly true for alligators since their survivorship is quite high in middle age.

4.2 Simulation of Degradation of Region One Nesting Sites

In the second experiment we decrease the nesting capacity of region one severely, as might happen due to drought or human encroachment on the wet marsh. In our model, the females from R1 dominate the population. This is unsurprising, given that region one accounts for almost eighty percent of the nesting habitat. Thus, we expect that perturbations in the nesting capacity of this region should cause dramatic changes in the population dynamics. Since we scale all populations by k_1 in the nondimensionalized model we return to our original, unscaled model. We implement the "drought" at t = 100. Thus, the nesting capacity of R1, k_1 , becomes:

$$k_1(t) = \begin{cases} 500, & t \le 100; \\ 100, & t > 100. \end{cases}$$

When the decrease in the capacity of the wet-marsh nesting area occurs, an immediate drop in the R1 populations is noticeable, shown in Figure 8. The R2 and R3 populations initially appear to benefit from the habitat change, as more females from R1 are forced to seek out nesting sites in other regions. However, over time this positive effect is damped, reflecting that our model system is truly driven by the wet-marsh population. This gives evidence of the importance of the wet marsh to the alligator population.

4.3 Oscillations in the Nesting Capacity of Region One

We want to investigate how something like periodic flooding in the wet marsh would a ect the alligator population. Thus, we let an oscillating function govern the nesting capacity of

Destruction of Nesting Sites in Region 1

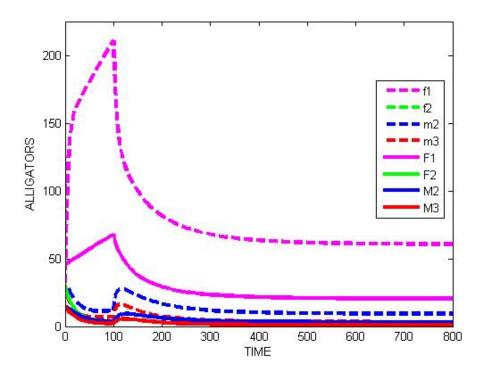


Figure 8: Simulations of population dynamics resulting from a sharp decrease in the number of nesting sites in the wet marsh at time t=100. This could occur as the result of human encroachment, or as a result of a catastrophic event such as a drought.

the region. We implement the flooding after 50 years, so that

$$k_1(t) = \begin{cases} 500, & t \le 50; \\ 500 + 250\sin(t/10), & t > 50. \end{cases}$$

If the wet marsh is flooded, the adult females in this region will move to the next two regions, increasing competition for nesting sites. Overall, the population is resilient enough to be relatively unaffected, although the region two and region three alligators do benefit periodically from the dips in the nesting capacity of region one.

In the flooding depicted in Figure 9, the flooding period is approximately 62 years. We are interested in shortening the period that affects the wet marsh. For example, we might assume that a serious hurrican strikes every six years; therefore, we are not interested in periods less than 2π . The time of the onset of the oscillation remains the same:

Flooding in Region 1

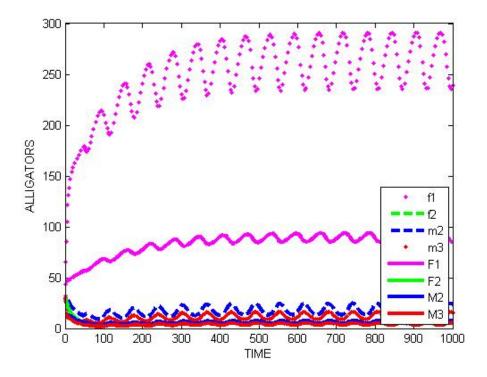


Figure 9: Simulation of the effects of periodic flooding of the wet marsh. The population dynamics remain relatively unchanged.

$$k_1(t) = \begin{cases} 500 & t \le 50 \\ 500 + 250sin(t) & t > 50 \end{cases}.$$

The simulation resulting from these changes in nesting capacity is depicted in figure 10.

These experiments show that an oscillation in k_1 with a longer period has a larger effect on the model population than an oscillation with a shorter period. This may be due to the fact that our shorter period is less than our delay time. Thus, the changes caused by more gradual and long-term flooding are of greater magnitude than those caused by more frequent, short-term flooding, such as might be caused by annual or biennial hurricanes. This needs to be further investigated in cases with delays other than ten years.

More Frequent Flooding in Region 1

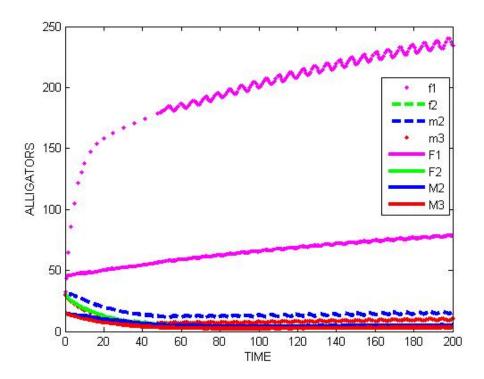


Figure 10: More frequent perturbations in the carrying capacity of R1, which could be due to predictable hurricane or monsoon seasons, cause less disruption in the population dynamics of the system than less frequent perturbations.

4.4 Comparison with Biological Data

Woodward and Murray (1993) cite the birth and death rates of a population of crocodiles studied by Smith and Webb (1985) in the McKinley River area in Australia (Figure 12). Because we use these same birth and death rates in our model, we too compare our results with the biological data gathered by Smith and Webb. The age structure which they observed is shown in Figure 11. The population which they observe is heavily skewed towards juveniles, with over half of the alligators under the age of ten. For age-structure comparisons, we use the equilibrium population distribution from our simulations. Since the model has been nondimensionalized, we cannot compare absolute numbers of adults and juveniles and instead compute the relative proportions of the different age classes in the population. In Figure 13, we display the age structure obtained from our equilibrium state alongside

the corresponding biological data. The graphs have a qualitatively-similar age structure, although the simulation data is more heavily skewed (quantitatively) toward juveniles. This may be a result of smoothing out the extremely high death rate of alligators under one year of age when we use a weighted average of age-dependent death rates.

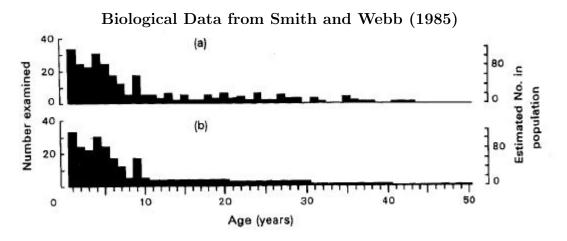


Figure 11: Age-structure data for a population of Australian crocodiles. The top histogram (a) gives the observed data from a random sample of the population which is extrapolated to the total population (right axis) and smoothed for the purposes of modeling (b). (Taken directly from Smith and Webb 1985.)

For the sake of further comparison, we develop DDE models that divide the alligator population into more age groups. The equations are not presented here, but the results are given for discussion; codes are included in appendix C. We first consider a two-delay, three-age-class development. In this case we divide the population into three groups (see Figure 12). Thus, we have a sexually immature class of alligators under age eight. There is a partially sexually mature class of alligators ages eight through eleven. Finally, there is the adult class of alligators over twelve years of age. We again simulate the population dynamics, and observe age structure and sex ratio results at equilibrium. The age structure for the two-delay system is displayed in Figure 14. We get very good agreement between our results and the structure observed by Smith and Webb. Our results are slightly more skewed to adults; this likely results from our choices of age groups. With this model we obtain a sex ratio of 0.13; this agrees quantitatively with the observed value.

Birth and Death Rates Are Age Dependent

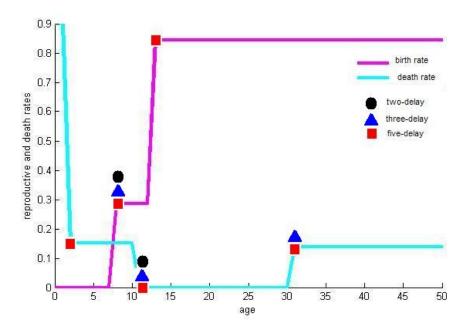


Figure 12: Reproduction and death rates are age dependent. Indicated are the critical changes in these values, which we use as a guideline in choosing where to add delays. (Smith and Webb, 1985)

Age Structure of the One-Delay Model Compared to Biological Data

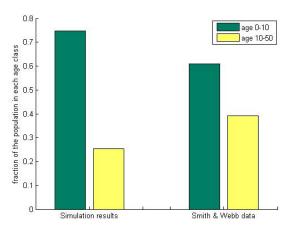


Figure 13: Comparison of simulation results to biological data. On the left, the histograms depict the fraction of the total equilibrium population classified as either juvenile (leftmost column) or adult (next column). The right two bars are the corresponding age classes reported in the population observed by Smith and Webb. The simulation results agree qualitatively with the data in that the juveniles outnumber the adults.

Age structure of the Two-Delay Model Compared to Biological Data

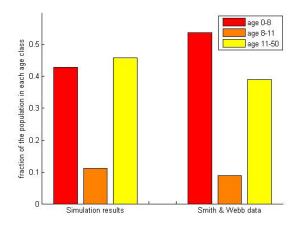


Figure 14: Comparison of simulation results from the two-delay model to biological data. On the left, the histograms depict the fraction of the total equilibrium population classified as either juvenile (leftmost column), teenager (middle column) or adult (next column). The right three bars are the corresponding age classes reported in the population observed by Smith and Webb (1985). The simulation results agree qualitatively with the data in that the juveniles and teenagers outnumber the adults.

We continue to add more age structure to the population, creating models of populations with both four and six age classes. In the four-age-class or three-delay case, we divide the population as follows: alligators from the age of 0 to 8, 8 to 11, 11 to 31, and 31 to death. We choose these divisions in order to capture the fact that 8 and 11 roughly correspond to the ages between which the alligators reach sexual maturity. We are also motivated by the fact that between the ages of 11 and 31, the alligators have a death rate extremely close to zero, and after age 31 the death jumps again, as in Figure 12. In the six-age-class or five-delay model we divide the population in order to account for all differences in birth and death rates in the population, as shown in Figure 12. Therefore, the age divisions are as follows: alligators from the age of 0 to 1, 1 and above to 8, 8 and above to 11, 11 and above to 12, 12 and above to 31, and 31 and above. The age structures for the three-delay and five-delay cases are shown in figures 15 and 16, respectively. Notice that as we increase the number of age groups, we continue to better capture the age structure reported by Smith and Webb. This is unsurprising, as we are using fewer approximations to the birth and death rates each

time.

What is particularly interesting, however, is that the sex ratio worsens in these cases; in the three-delay case, males make up approximately 35 percent of the population, and in the five-delay case, they are 25 percent of the population. The range of sex ratios reported by Smith and Webb (1985, 1987) is 0.125-0.29. Although in most cases our sex ratio falls in this range, we thinks this result could be improved. Possible explanations for this deviation from the observed sex ratios include: (1) as mentioned before, we are not truly accounting for sexual reproduction, and this effect may amplify as we introduce more population age classes; (2) density-dependent factors which would limit the growth of the male population, such as competition for mates and hunting territory, are not taken into consideration in the model.

Age Structure of the Three-Delay Model Compared to Biological Data

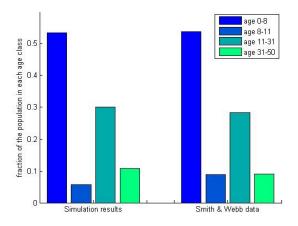


Figure 15: Comparison of simulation results to biological data. On the left, the histograms depict the fraction of the total equilibrium population of our model broken into four age classes. The right four bars are the corresponding age classes reported in the population observed by Smith and Webb. The simulation results agree qualitatively and quantitatively with the data.

It seems clear from a qualitative comparison of our results with the biological data gathered by Smith and Webb that the two-delay model provides results closest to what they observe. Our increased delays, while improving age structure, weaken the highly spanandrous sex ratio which is characteristic of populations which experience TSD.

Age Structure of the Five-Delay Model Compared to Biological Data

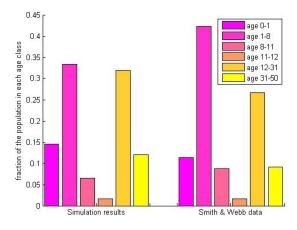


Figure 16: Comparison of simulation results to biological data. On the left, the histograms depict the fraction of the total equilibrium population of our model broken into six age classes. The right six bars are the corresponding age classes reported in the population observed by Smith and Webb. The simulation results agree qualitatively and quantitatively with the data.

5 Discussion and Future Work

Using Murray's ODE model (2002) as a basis, we have developed a model of an alligator population which exhibits temperature-dependent sex determination. Using our delay differential equation formulation, we are able to incorporate the dependence of birth and deathrate parameters on ages without using partial differential equations. For our single-delay model we are able to give an equilibrium point in analytical form. For the population $f_1(t)$ and $F_1(t)$, decoupled from the others in the population, we prove the stability of the equilibrium point (f_1^*, F_1^*) . We use numerical simulation to compare our models' predictions with previous models, as well as with data presented by (Smith and Webb, 1985). We find that we get qualitative agreement in age structure with the results in (Smith and Webb, 1985) in all cases. In particular, in the higher delay models age structure continues to improve, but sex ratio results are off. We also use our single-delay model to experiment with the effects of environmental and policy changes on the alligator population. These results demonstrate some of the ways in which the model can be applied to actual populations, as well as provide a means to explore interesting situations for the alligator population.

Much remains in terms of the future work. We are still working on the stability of the full equilibrium point for the single-delay case. We may use a Lyapunov functional. Because the two-delay model appears to be the "best" in terms of its reflection of biological data, an analysis of the two-delay system should be undertaken. Finally, we hope to use this modeling experience to create a similar type of model for the Kemp's Ridley sea turtle population.

The Kemp's Ridley is the smallest of the world's seven species of sea turtles. Richard Kemp discovered and observed this sea turtle in the 1940s along the Gulf of Mexico, at Rancho Nuevo. All the females in the species nest together in large groups called "arribadas." At the time of discovery, about 40,000 Kemp's Ridley were observed nesting in broad daylight. Since then their numbers have dropped dramatically. Eggs have been collected for human consumption and the adult Kemp Ridleys have been drowned by shrimp trawlers. They are now an endangered species. However, the population is currently rebounding thanks to changes in human behavior (Spotila, 2004).

The Kemp's Ridley turtles also exhibit TSD. Whereas in alligators the temperature of egg incubation is determined by nesting region, the Kemp's Ridley females nest in a single region. The temperature of egg incubation in this case is affected by nesting time. Nesting begins in April and continues for three months. An average female nests two times per season, approximately every one and a half years. Temperatures of 84°F and below yield all males hatchlings, while temperatures above 88°F produce all females. The average temperature of incubation that yields both males and females is approximately 86.4°F. Thus, the female turtles that nest during the cooler month of April will produce male offspring; those nesting in May produce half female, half male hatchlings and those who nest in June will produce all female hatchlings. Delay differential equations may provide a useful framework to study this population as well.

Acknowledgements

This research was conducted at the Applied Mathematical Sciences Summer Institute (AMSSI) and has been partially supported by grants given by the Department of Defense (through its ASSURE program), the National Science Foundation (DMS-0453602), and National Security Agency (MSPF-07IC-043). Substantial financial and moral support was also provided by Don Straney, Dean of the College of Science at California State Polytechnic University, Pomona. Additional financial and moral support was provided by the Department of Mathematics at Loyola Marymount University and the Department of Mathematics & Statistics at California State Polytechnic University, Pomona. The authors are solely responsible for the views and opinions expressed in this research; it does not necessarily reflect the ideas and/or opinions of the funding agencies and/or Loyola Marymount University or California State Polytechnic University, Pomona. Many thanks to Dr. Angela Gallegos and David Uminsky.

Appendix A: Runge-Kutta Methods for DDEs

Matlab's dde23 modified Runge-Kutta methods to solve delay differential equations. A problem emerges when Runge-Kutta is used on delay differential equations. Consider an equation of the form:

$$x'(t) = Rx(t - \tau) + Dx(t)$$

$$x(t) = f(t) \text{ for } t\epsilon(-\tau, 0)$$

As a numerical solver approximates the solution to this DDE, it calculates values at each time-step, where the size of the time-step is chosen to reduce error. However, when calculating the solution to the DDE at the time t_n , the solver must "look back" τ time units earlier to a value between $t_n - \tau$ and $t_{n-1} - \tau$, as can be seen in the DDE above. Since the values of the solution are only calculated at the discrete time-steps, and it may be that no solution point was calculated at the particular value the solver is attempting to recall, some sort of average must be calculated of the solutions at $t_n - \tau$ and $t_{n-1} - \tau$. Averages are calculated in order to account for the "half-step" values used in the Runge-Kutta algorithm. This requires that any solver employing Runge-Kutta must carry a vector of all calculated values of the solution within τ time units of the current point it is trying to evaluate (Wirkus 2003). For a further explanation of the Runge-Kutta method, see Burden and Faires (1989).

Appendix B: Stability of the Equilibria for the Single-Delay Model

In the one-delay model we obtain a stable point at which all populations are positive, provided $s > a_2$. It is easy to show that F_1^* and f_1^* are both greater than 0. But this is more difficult to show for F_2^* . Using Maple we obtain algebraic expressions for F_2^* and F_2^* in terms of parameters:

$$\begin{array}{lcl} F_2^* & = & \displaystyle \frac{1}{4a_2} \left(-2a_2h_1 + 2a_2 + sh_1 - 2s + \sqrt{4a_2^2h_1^2 - 4sh_1^2a_2 - 4sh_1a_2 + 4a_2^2 - 8sa_2 + s^2h_1^2 + 4h_1s^2 + 4s^2} \right) \\ \\ f_2^* & = & \displaystyle \frac{(1-s)h_1(2s^2 - 6sa_2 + 4a_2^2 - 2sh_1a_2 + h_1s^2 + s\sqrt{4a_2^2h_1^2 - 4sh_1^2a_2 - 4sh_1a_2 + 4a_2^2 - 8sa_2 + s^2h_1^2 + 4h_1s^2 + 4s^2})}{2(2a_2h_1 + 2s - 2a_2 + sh_1 + sa_1\sqrt{4a_2^2h_1^2 - 4sh_1^2a_2 - 4sh_1a_2 + 4a_2^2 - 8sa_2 + s^2h_1^2 + 4h_1s^2 + 4s^2}) \end{array}$$

The expression under the radical factors thus:

$$4a_2^2h_1^2 - 4sh_1^2a_2 - 4sh_1a_2 + 4a_2^2 - 8sa_2 + s^2h_1^2 + 4h_1s^2 + 4s^2 = (s - 2a_2)^2h_1^2 + 4s(s - a_2)h_1 + 4(s - a_2)^2.$$

This value is always positive since $0 < h_1$. Furthermore, provided that $0 < a_2 < s < 1$, F_2^* is always real. It should be noted that $s \le 1$ is always true; since s is a probability. Unless the juvenile death rate is zero, $s \ne 1$. Furthermore,

$$\left(\sqrt{4a_2^2h_1^2 - 4sh_1^2a_2 - 4sh_1a_2 + 4a_2^2 - 8sa_2 + s^2h_1^2 + 4h_1s^2 + 4s^2}\right)^2 - \left(-2a_2h_1 + 2a_2 + sh_1 - 2s\right)^2 = 8h_1(s - a_2)^2.$$

Hence it follows that because our parameters have positive values our equilibrium value for F_2^* is always positive as well.

Appendix C: Matlab Codes

Three Region One Delay

 ${\tt \%RegionSolver1Delay_nd.m}$

%This is a script file that calls two function files, RegionDelayFun_nd, %and RegionDelay_hist_nd. The purpose of this file is to numerically solve %the 1 delay alligator model using Matlab's built in dde solver, Runge %Kutta Method, dde23.

%Comments updated for AMSSI 2007 on July 25, 2007

global a1 a2 c1 c2 b s %declare variables as global to allow the dde23 solver

%to access their values, but we only have to change

%them in one place. The global command is to be

%used before you have defined the variables in the

%code.

b=.826; %b is the birth rate and is set at a desired value dJ=.2; %dJ is the death rate of the juveniles and is set at a desired value dA=.0928; %dA is the death rate of the adults and is set at a desired value

k1=.79; %k1 is the carrying capacity of region 1 and is set at a desired value

k2=.15; %k2 is the carrying capacity of region 2 and is set at a desired value

k3=.06; %k3 is the carrying capacity of region 3 and is set at a desired value

a1=(dJ/b); %a1 is the death rate of juveniles divided by the birth rate

a2=(dA/b); %a2 is the death rate of adults divided by the birth rate

c1=(k2/k1); %c1 is the carrying capacity of region 2 divided by the carrying

%capacity of region 1

c2=(k3/k1); %c2 is the carrying capacity of region 3 divided by the carrying

%capacity of region 1

 $s = \exp(-dJ*10); \quad \mbox{\%s is a probability of the survival to maturity}$

tF = 200; %the final time for which we will compute a solution

tspan = [t0 tF]; %vector of initial and final time values for the dde23 solver.

tau=(10*b); %set our time delay value to tau

lags=[tau]; %'lags' is the array that holds the time delay values

 ${\tt Regionsol=dde23(@RegionDelayFun_nd,lags,@RegionDelay_hist_nd,tspan);}$

%this line calls the delay differential equation solver dde23.

%'RegionDelayFun_nd' is the name of the file storing our dde formulas, lags % is the array of delay that we need to use, 'RegionDelay_hist_nd' is the % function file that maintains the system history and 'tspan' feeds in our % initial and final times for computation. The solutions to this system will % be stored in the array'Regionsol'.

%first, separate the output array into its various components

t = Regionsol.x; %assigns the time outputs to a vector 't'

f1= Regionsol.y(1,:); %assigns female juveniles in R1 outputs array

%to a vector named after the variable it

%represents, 'f1'.

f2= Regionsol.y(2,:); %assigns female juveniles in R2 outputs array

%to a vector named after the variable it

%represents, 'f2'.

m3= Regionsol.y(4,:); %assigns male juveniles in R3 outputs array %to a vector named after the variable it %represents, 'm3'.

F1= Regionsol.y(5,:); %assigns female adults in R1 outputs array %to a vector named after the variable it %represents, 'F1'

F2= Regionsol.y(6,:); %assigns female adults in R2 outputs array %to a vector named after the variable it %represents, 'F2'.

M3= Regionsol.y(8,:); %assigns male adults in R3 outputs array %to a vector named after the variable it %represents, 'M3'.

f=f1+f2+F1+F2; %assigns the variable f to be equal to the total female %population

m=m2+m3+M2+M3; %assigns the variable m to be equal to the total male %population

r=(m./(m+f)); %assigns r to be equal to the total male population divided %by the total male population plus the total female population %will give you the ratio of males to total population

q=f1+F1; %assigns q to be equal to the total population of R1

o=f2+F2; %assigns o to be equal to the total population of females in R2 k=m2+M2; %assigns k to be equal to the total population of males in R2

j=m3+M3; %assigns j to be equal to the total population of R3

figure %opens a new figure window

subplot(2,1,1); %able to have 2 graphs in one window

hold on %keeps all the following plots on the same graph

plot(t, f1, 'b-', 'LineWidth',3) %plot the female juveniles in R1 a blue dashed line plot(t, f2, 'g-', 'LineWidth',3) %plot the female juveniles in R2 a green dashed line plot(t, m2, 'c-', 'LineWidth',3) %plot the male juveniles in R2 a light blue dashed line

```
plot(t, m3, 'r-', 'LineWidth',3) %plot the male juveniles in R3 a red dashed line %plot(t, F1, 'b-', 'LineWidth',3) %plot the female adults in R1 a blue solid line %plot(t, F2, 'g-', 'LineWidth',3) %plot the female adults in R2 a green solid line %plot(t, M2, 'c-', 'LineWidth',3) %plot the male adults in R2 a light blue solid line %plot(t, M3, 'r-', 'LineWidth',3) %plot the male adults in R3 a red solid line %plot(time') % creates the label 'time' on the x-axis ylabel('alligators') %creates the label 'alligators' on the y axis title('Three Regions One Delay') %creates a title for the graph legend('FR1', 'FR2', 'MR2', 'MR3') %'AFR1', 'AFR2', 'AMR2', 'AMR3') %creates a legend for the graph
```

figure %opens a new figure window

hold on %keeps all the following plots on the same graph plot(t, q, 'b-', 'LineWidth',3) %plot the total female population of R1 plot(t, o, 'g-', 'LineWidth',3) %plot the total female population of R2 plot(t, k, 'c-', 'LineWidth',3) %plot the total male population of R2 plot(t, j, 'r-', 'LineWidth',3) %plot the total male population of R3 xlabel('time') %creates the label 'time' on the x-axis ylabel('alligators') %creates the label 'alligators' on the y-axis title('Two Delay Three Regions') %creates a title for the graph legend('FR1', 'FR2', 'MR2', 'MR3') %creates a legend for the graph

function dydt=RegionDelayFun_nd(t,y,Z) %function name and variables, time %variable and lags

Lag1=Z(:,1); %a column vector whose rows represent the solution at the %time delay for f1, f2, F1, F2, m2, m3, M2, and M3 respectively.

```
dydt(1) = (1/(1+y(5)))*y(5) - a1*y(1) - s*Lag1(5)*(1/(1+Lag1(5)));
%delay differential equation where F1(t-tau) is represented by Lag1(5).
dydt(2) = (1/2)*(c1/(c1+y(5)+y(6)))*(y(5)^2/(1+y(5)) + y(6))...
-a1*y(2) - (s/2)*((Lag1(5)^2/(1+Lag1(5)))+Lag1(6))*(c1/(c1+Lag1(5)+Lag1(6)));
%delay differential equation where F1(t-tau) is represented by Lag1(5) and
%F2(t-tau) is represented by Lag1(6).
dydt(3) = (1/2)*(c1/(c1+y(5)+y(6)))*(y(5)^2/(1+y(5)) + y(6))...
- a1*y(3) - (s/2)*((Lag1(5)^2/(1+Lag1(5)))+Lag1(6))*(c1/(c1+Lag1(5)+Lag1(6)));
%delay differential equation where F1(t-tau) is represented by Lag1(5) and
%F2(t-tau) is represented by Lag1(6).
\mathtt{dydt}(4) \ = \ (\mathtt{c2/(c2+y(5)+y(6))}) * (\mathtt{y(5)^2/(1+y(5))} \ + \ \mathtt{y(6)}) * ((\mathtt{y(5)+y(6))/(c1+y(5)+y(6))}) \dots
-a1*y(4) - s*(c2/(c2+Lag1(5)+Lag1(6)))*((Lag1(5)^2)/(1+Lag1(5)) + Lag1(6))*((Lag1(5)+Lag1(6))/(c1+Lag1(5)+Lag1(6)));
%delay differential equation where F1(t-tau) is represented by Lag1(5) and
%F2(t-tau) is represented by Lag1(6)
%R1 female adults:y(5), R2 female adults:y(6), R2 male adults:y(7), R3 male adults:y(8)%
%delay differential equation where F1(t-tau) is represented by Lag1(5)
%delay differential equation where F1(t-tau) is represented by Lag1(5) and
%F2(t-tau) is represented by Lag1(6)
%delay differential equation where F1(t-tau) is represented by Lag1(5) and
%F2(t-tau) is represented by Lag1(6)
%delay differential equation where F1(t-tau) is represented by Lag1(5) and
%F2(t-tau) is represented by Lag1(6)
```

%This is a function file that maintains the system histories.

%In this case we are assigning constant values to the variable histories.

f1_hist = 10; %this is the history of the female juvenile population from R1
f2_hist = 10; %this is the history of the female juvenile population from R2
m2_hist = 10; %this is the history of the male juvenile population from R2
m3_hist = 10; %this is the history of the male juvenile population from R3
F1_hist = 15; %this is the history of the female adult population from R1
F2_hist = 10; %this is the history of the female adult population from R2
M2_hist = 5; %this is the history of the male adult population from R2
M3_hist = 5; %this is the history of the male adult population from R3

s = [f1_hist;f2_hist;m2_hist;m3_hist;F1_hist;F2_hist;M2_hist;M3_hist];
%This puts all the histories into a column vector and names it s. This is
%the format that dde23 would like it to be in.

Three Regions Two Delays

%Alli2Solver_Region.m

%This is a script file that calls two function files, Alli2Delay_Region, %and Alli2Delay_hist_region. The purpose of this file is to numerically solve %the 1 delay alligator model using Matlab's built in dde solver, Runge %Kutta Method, dde23.

%Comments updated for AMSSI 2007 on July 27,2007

- t0 = 0; %starting time value
- tF = 200; %the final time for which we will compute a solution tspan = [t0 tF]; %vector of initial and final time values
- b2=.844; %%b is the birth rate and is set at a desired value

tau_3 = 11*b2; %set our delay value tau_3

lags = [tau_2 tau_3]; % 'lags' is the array that holds the time delay values

AlliBirthDivsol = dde23(@Alli2Delay_Region, lags, @Alli2Delay_hist_region, tspan);
%delay differential equation solver dde23. 'Alli2Delay_Region' is the name
%of the file storing out dde formulas, lags is the array of delays that we
%need o use, 'Alli2Delay_his_region' is the function file that maintains
%the system history and 'tspan' feeds in our initial and final times for
%computation. The solutions to this system will be stored in the array
%'AlliBirthDivsol'.

%first, separate the output array into its various components

- t = AlliBirthDivsol.x; %assigns the time outputs to a vector 't'
- Af1 = AlliBirthDivsol.y(1,:); %assigns female juveniles in R1 outputs %array to a vector named after the variable %it represents, 'Af1'.
- Af2 = AlliBirthDivsol.y(2,:); %assigns female juveniles in R2 outputs %array to a vector named after the variable %it represents, 'Af2'.
- Am2 = AlliBirthDivsol.y(3,:); %assigns male juveniles in R2 outputs array %to a vector named after the variable it

%represents, 'Am2'.

- Am3 = AlliBirthDivsol.y(4,:); %assigns male juveniles in R3 outputs array %to a vector named after the variable it %represents, 'Am3'.

- u=Af1+Bf1+Cf1; %assigns the variable 'u' to be equal to the total female %population in R1
- v=Af2+Bf2+Cf2; %assigns the variable 'v' to be equal to the total female %population in R2
- w=Am2+Bm2+Cm2; %assigns the variable 'w' to be equal to the total male
 %population in R2
- q=Am3+Bm3+Cm3; %assigns the variable 'q' to be equal to the total male %population in R3 $\,$

y=u+v; %assigns the variable 'y' to be equal to the total female population z=w+q; %assigns the variable 'z' to be equal to the total male population

r=z./(y+z); %assigns r to be equal to the total male population divided %by the total male population plus the total female population %will give you the ratio of males to total population

figure % opens a new figure window hold on % this keeps all the following plots on the same graph plot(t, Af1, 'g', 'LineWidth',3) %plot the female juveniles in R1 a green dashed line plot(t, Af2, 'r', 'LineWidth',3) %plot the female juveniles in R2 a red dashed line plot(t, Am2, 'y', 'LineWidth',3) %plot the male juveniles in R2 a yellow dashed line plot(t, Am3, 'b', 'LineWidth',3) %plot the male juveniles in R3 a blue dashed line plot(t, Bf1, 'g.', 'LineWidth',3)%plot the female teens in R1 a green dotted line plot(t, Bf2, 'r.', 'LineWidth',3)%plot the female teens in R2 a red dotted line plot(t, Bm2, 'y.', 'LineWidth',3)%plot the male teens in R2 a yellow dotted line plot(t, Bm3, 'b.', 'LineWidth',3)%plot the male teens in R3 a blue dotted line plot(t, Cf1, 'g--', 'LineWidth',3)%plot the female adults in R1 a green solid line plot(t, Cf2, 'r--', 'LineWidth',3)%plot the female adults in R2 a red solid line plot(t, Cm2, 'y--', 'LineWidth',3)%plot the male adults in R2 a yellow solid line plot(t, Cm3, 'b--', 'LineWidth',3)%plot the male adults in R3 a blue solid line xlabel('time') % creates the label 'time' on the x-axis ylabel('alligators') %creates the label 'stuff' on the y axis title('F1 (m) and F2 (c) and M2 (y) M3 (b) J1(solid) J2(dotted) A(dashed)') %creates the title

figure %open a new figure window
hold on %this keeps all the following plots on the same graph
plot(t, u, 'g', 'LineWidth',3) %plot the total female population in R1 a green line
plot(t, v, 'r', 'LineWidth',3) %plot the total female population in R2 a red line
plot(t, w, 'y', 'LineWidth',3) %plot the total male population in R2 a yellow line
plot(t, q, 'b', 'LineWidth',3) %plot the total male population in R3 a blue line

figure %open a new figure window hold on %this keeps all the following plots on the same graph plot(t,r,'r','Linewidth',3) %plot the ratio of males to the total population a red line title('the love graph') %creates the title

function dydt=Alli2Delay_Region(t,y,Z) %function name and variables, time %variables and lags

%declare variables as global to allow the dde23 solver to access their

global d1 d2 d3 b1 b2 s8 s11 k1 k2 k3 c1 c2 r1 a1 a2 a3

%values, but we only have to change them in one place. The global command %is to be used before you have defined the variables in the code. d1=.14; %d1 is the death rate of the juveniles and is set at a desired value d2=.11; %d2 is the death rate of the teens and is set at a desired value d3=.0695: %d3 is the death rate of the adults and is set at a desired value b1=.286: %b1 is the birth rate for the teens and is set at a desired value b2=.844; %bA is the birth rate for the adults and is set at a desired value k1=.79;%k1 is the carrying capacity of R1 and is set at a desired value k2=.15; $\mbox{\ensuremath{\mbox{\sc k2}}}$ is the carrying capacity of R2 and is set at a desired value k3=.06; %k3 is the carrying capacity of R3 and is set at a desired value s8=exp(-d1*8); %s8 is the survival probability to age 8 and is set at a desired value s11 = exp(-d2*3);%s11 is the survival probability to age 11 and is set at a desired value c1=k2/k1; %c1 is the carrying capacity of R2 divided by the carrying capacity of R1 c2=k3/k1; %c2 is the carrying capacity of R3 divided by the carrying capacity of R1 r1=b1/b2; %r1 is the birth rate for the teens divided by the birth rate for adults a1=d1./b2; %a1 is the death rate of the juveniles divided by the birth rate for the adults a2=d2./b2; %a2 is the death rate of the teens divided by the birth rate for the adults a3=d3./b2; %a3 is the death rate of the adults divided by the birth rate for the adults Lag1=Z(:,1); %a column vector whose rows represent the solution at the time delay 1 Lag2=Z(:,2); $\mbox{\ensuremath{\mbox{\sc Ma}}}$ column vector whose rows represent the solution at the time delay 2 Q1=(y(5)+y(9))/(1+y(5)+y(9));%this is the fraction of f1 who can't nest in R1 now Q2=(c1/(c1+y(5)+y(6)+y(9)+y(10)));%this is the fraction of f1s and f2s who can nest in R2 now Q3=(Lag1(5)+Lag1(9))/(1+Lag1(5)+Lag1(9)); %this is the fraction of f1 who couldn't nest in R1 8 years ago Q4=(c1/(c1+Lag1(5)+Lag1(6)+Lag1(9)+Lag1(10)));

%this is the fraction of f1 and f2 who could nest in R2 8 years ago

```
Q5=(c2/(c2+y(5)+y(6)+y(9)+y(10)));
%this is the fraction of f1s and f2s who can nest in R3 now
Q6=(c2/(c2+Lag1(5)+Lag1(6)+Lag1(9)+Lag1(10)));
%this is the fraction of f1s and f2s who could nest in R2 8 years ago
R3=(Lag2(5)+Lag2(9))/(1+Lag2(5)+Lag2(9));
%this is the fraction of f1 who couldn't nest in R1 11 years ago
R4=(c1/(c1+Lag2(5)+Lag2(6)+Lag2(9)+Lag2(10)));
%this is the fraction of f1 and f2 who could nest in R2 11 years ago
R6=(c2/(c2+Lag2(5)+Lag2(6)+Lag2(9)+Lag2(10)));
%this is the fraction of f1s and f2s who could nest in R2 11 years ago
%R1 female juveniles:y(1), R2 female juveniles:y(2), R2 male juveniles:y(3), R3 male juveniles:y(4)%
dydt(1)=r1*(((y(5))*(1-Q1))-s8*r1*(Lag1(5))*(1-Q3))...
   -a1*y(1)+...
   (y(9))*(1-Q1)...
   -s8*(Lag1(9))*(1-Q3);
%delay differential equation for the rate of change of the female juveniles R1
%where Bf1(t-tau_2) is represented by Lag1(5) and Cf1(t-tau_2) is
%represented by Lag1(9).
dydt(2)=(r1/2)*(((y(5)+y(6))*Q1)*Q2...
   -s8*(Lag1(5)+Lag1(6))*Q3*Q4)...
   -a1*y(2)...
   +(1/2)*((y(9)+y(10))*Q1)*Q2...
   -s8*(Lag1(9)+Lag1(10))*Q3*Q4;
%delay differential equation for the rate of change of the female juveniles R2
%where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is represented
%by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9), and Cf2(t-tau_2) is
%represented by Lag1(10).
dydt(3)=(r1/2)*(((y(5)+y(6))*Q1)*Q2...
   -s8*(Lag1(5)+Lag1(6))*Q3*Q4)...
   -a1*y(3)...
   +(1/2)*((y(9)+y(10))*Q1)*Q2...
```

```
-s8*(Lag1(9)+Lag1(10))*Q3*Q4;
%delay differential equation for the rate of change of the male juveniles R2
%where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is represented
%by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9), and Cf2(t-tau_2) is
%represented by Lag1(10).
dydt(4)=r1*(Q5*(y(5)*Q1+y(6))*(1-Q2)...
   -s8*Q6*(Lag1(5)*Q3+Lag1(6))*(1-Q4))...
   -a1*y(4)...
   +Q5*(y(9)*Q1+y(10))*(1-Q2)...
   -s8*Q6*(Lag1(9)*Q3+Lag1(10))*(1-Q4);
%delay differential equation for the rate of change of the male juveniles R3
%where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is represented
%by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9), and Cf2(t-tau_2) is
%represented by Lag1(10).
%R1 female teens:y(5), R2 female teens:y(6), R2 male teens:y(7), R3 male teens:y(8)%
dydt(5)=s8*r1*(Lag1(5))*(1-Q3)...
   +s8*(Lag1(9))*(1-Q3)...
   -a2*y(5)...
   -s8*s11*r1*(Lag2(5))*(1-R3)...
   -s8*s11*(Lag2(9))*(1-R3);
%delay differential equation for the rate of change of the female teens R1
%where Bf1(t-tau_2) is represented by Lag1(5), Cf1(t-tau_2) is represented
%by Lag1(9), Bf1(t-tau_3) is represented by Lag2(5), and Cf1(t-tau_3) is
%represented by Lag2(9).
dydt(6)=s8*(r1/2)*(Lag1(5)+Lag1(6))*Q3*Q4...
    +s8*(Lag1(9)+Lag1(10))*Q3*Q4...
    -a2*y(6)...
    -s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
    -s8*s11*(Lag2(9)+Lag2(10))*R3*R4;
%delay differential equation for the rate of change of the female teens R2
%where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is represented
%by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9), Cf2(t-tau_2) is
%represented by Lag1(10), Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3)
%is represented by Lag2(6), Cf1(t_tau_3) is represented by Lag2(9), and
```

%Cf2(t-tau_3) is represented by Lag2(10).

```
dydt(7)=s8*(r1/2)*(Lag1(5)+Lag1(6))*Q3*Q4...
    +s8*(Lag1(9)+Lag1(10))*Q3*Q4...
    -a2*y(7)...
    -s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
    -s8*s11*(Lag2(9)+Lag2(10))*R3*R4;
%delay differential equation for the rate of change of the male teens R2
%where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is represented
%by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9), Cf2(t-tau_2) is
%represented by Lag1(10), Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3)
%is represented by Lag2(6), Cf1(t_tau_3) is represented by Lag2(9), and
%Cf2(t-tau_3) is represented by Lag2(10).
dydt(8)=s8*Q6*r1*(Lag1(5)*Q3+Lag1(6))*(1-Q4)...
   +s8*Q6*(Lag1(9)*Q3+Lag1(10))*(1-Q4)...
   -a2*y(8)...
   -s8*R6*r1*(Lag2(5)*R3+Lag2(6))*(1-R4)...
   -s8*R6*(Lag2(9)*R3+Lag2(10))*(1-R4);
%delay differential equation for the rate of change of the male teens R3
%where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is represented
%by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9), Cf2(t-tau_2) is
%represented by Lag1(10), Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3)
%is represented by Lag2(6), Cf1(t_tau_3) is represented by Lag2(9), and
%Cf2(t-tau_3) is represented by Lag2(10).
%R1 female adults:y(9), R2 female adults:y(10), R2 male adults:y(11), R3 male adults:y(12)%
dydt(9)=s8*s11*r1*(Lag2(5))*(1-R3)...
   +s8*s11*(Lag2(9))*(1-R3)...
   -a3*y(9);
%delay differential equation for the rate of change of the female adults R1
%where Bf1(t-tau_3) is represented by Lag2(5), and Cf1(t_tau_3) is represented
%by Lag2(9).
dydt(10)=s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
    +s8*s11*(Lag2(9)+Lag2(10))*R3*R4...
    -a3*y(10);
%delay differential equation for the rate of change of the female adults R2
%where Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3) is represented
```

%by Lag2(6), Cf1(t_tau_3) is represented by Lag2(9), and Cf2(t-tau_3) is %represented by Lag2(10).

```
dydt(11)=s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
+s8*s11*(Lag2(9)+Lag2(10))*R3*R4...
-a3*y(11);
```

%delay differential equation for the rate of change of the male adults R2 %where Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3) is represented %by Lag2(6), Cf1(t_tau_3) is represented by Lag2(9), and Cf2(t-tau_3) is %represented by Lag2(10).

```
dydt(12)=s8*R6*r1*(Lag2(5)*R3+Lag2(6))*(1-R4)...
+s8*R6*(Lag2(9)*R3+Lag2(10))*(1-R4)...
-a3*y(12);
```

%delay differential equation for the rate of change of the male adults R3 %where Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3) is represented %by Lag2(6), Cf1(t_tau_3) is represented by Lag2(9), and Cf2(t-tau_3) is %represented by Lag2(10).

dydt=dydt'; %the solver must return a column vector and this sets Matlab
%up to return a row vector, so we take the transpose to keep it
%all the same.

%This is a function file that maintains the system histories.

%In this case we are assigning constant values to the variable histories.

hist_1 = 10; %this is the history of the female juvenile population from R1 hist_2 = 10; %this is the history of the female juvenile population from R2 hist_3 = 10; %this is the history of the male juvenile population from R2

```
hist_4 = 10;
              %this is the history of the male juvenile population from R3
hist_5 = 10;
              %this is the history of the female teen population from R1
hist_6 = 7;
              %this is the history of the female teen population from R2
hist_7 = 4;
              %this is the history of the male teen population from R2
hist_8 = 4;
              %this is the history of the male teen population from R3
hist_9 = 5;
              %this is the history of the female adult population from R1
hist_10 = 3;
            %this is the history of the female adult population from R2
hist_11 = 1;
             %this is the history of the male adult population from R2
hist_12 = 1;
              %this is the history of the male adult population from R3
s = [hist_1; hist_2; hist_3; hist_4; hist_5; hist_6; hist_7; hist_8; hist_9; hist_10; hist_11; hist_12];
%This puts all the histories into a column vector and names it s. This is
%the format that dde23 would like it to be in.
Three Regions Three Delay
%Alli3Solver_Region.m
%This is a script file that calls two function files, Alli3Delay_Region,
%and Alli3Delay_hist_region. The purpose of this file is to numerically solve
%the 1 delay alligator model using Matlab's built in dde solver, Runge
%Kutta Method, dde23.
%Comments updated for AMSSI 2007 on July 27,2007
t0 = 0;
          %starting time value
tF = 200; %the final time for which we will compute a solution
tspan = [t0 tF]; %vector of initial and final time values
b2=.844;
          %%b is the birth rate and is set at a desired value
%tau_1 = 1*b2; %set our delay value tau_1
tau_3 = 11*b2; %set our delay value tau_2
%tau_4 = 12*b2; %set our delay value tau_2
tau_5 = 31*b2; %set our delay value tau_2
```

lags = [tau_2 tau_3 tau_5]; %'lags' is the array that holds the time delay values

AlliBirthDivsol = dde23(@Alli3Delay_Region, lags, @Alli3Delay_hist_region, tspan);
%delay differential equation solver dde23. 'Alli3Delay_Region' is the name
%of the file storing out dde formulas, lags is the array of delays that we
%need o use, 'Alli3Delay_his_region' is the function file that maintains
%the system history and 'tspan' feeds in our initial and final times for
%computation. The solutions to this system will be stored in the array
%'AlliBirthDivsol'.

t = AlliBirthDivsol.x; %assigns the time outputs to a vector 't'

- Af1 = AlliBirthDivsol.y(1,:); %assigns females between ages 0-8 in R1 outputs %array to a vector named after the variable %it represents, 'Af1'.
- Af2 = AlliBirthDivsol.y(2,:); %assigns females between ages 0-8 in R2 outputs %array to a vector named after the variable %it represents, 'Af2'.
- Am2 = AlliBirthDivsol.y(3,:); %assigns males between ages 0-8 in R2 outputs array %to a vector named after the variable it %represents, 'Am2'.
- Am3 = AlliBirthDivsol.y(4,:); %assigns males between ages 0-8 in R3 outputs array %to a vector named after the variable it %represents, 'Am3'.

- Bm2 = AlliBirthDivsol.y(7,:); %assigns males between ages 8-11 in R2 outputs %array to a vector named after the variable %it represents, 'Bm2'.
- Cf1 = AlliBirthDivsol.y(9,:); %assigns females between ages 11-31 in R1 outputs %array to a vector named after the variable

%it represents, 'Cf1'.

- Df1 = AlliBirthDivsol.y(13,:); %assigns females between the ages 31+ in R1 %outputs array to a vector named after the %variable it represents, 'Df1'.
- Df2 = AlliBirthDivsol.y(13,:); %assigns females between the ages 31+ in R2 %outputs array to a vector named after the %variable it represents, 'Df2'.

- u=Af1+Bf1+Cf1+Df1; %assigns the variable 'u' to be equal to the total female %population in R1 $\,$
- v=Af2+Bf2+Cf2+Df2; %assigns the variable 'v' to be equal to the total female %population in R2
- w=Am2+Bm2+Cm2+Dm2; %assigns the variable 'w' to be equal to the total male %population in R2
- q=Am3+Bm3+Cm3+Dm3; %assigns the variable 'q' to be equal to the total male %population in R3
- y=u+v; %assigns the variable 'y' to be equal to the total female population z=w+q; %assigns the variable 'z' to be equal to the total male population
- r=z./(y+z); %assigns r to be equal to the total male population divided %by the total male population plus the total female population %will give you the ratio of males to total population

figure % opens a new figure window hold on % this keeps all the following plots on the same graph π 0 for π 1, 'r-', 'LineWidth',3) % L will be red and solid of weight 3

```
plot(t, Af1, 'g-', 'LineWidth',3) %plot the females between ages 0-8 in R1 a green dashed line
plot(t, Af2, 'r-', 'LineWidth',3) %plot the females between ages 0-8 in R2 a red dashed line
plot(t, Am2, 'y-', 'LineWidth',3) %plot the males between ages 0-8 in R2 a yellow dashed line
plot(t, Am3, 'b-', 'LineWidth',3) %plot the males between ages 0-8 in R3 a blue dashed line
plot(t, Bf1, 'g.', 'LineWidth',3)%plot the females between ages 8-11 in R1 a green dotted line
plot(t, Bf2, 'r.', 'LineWidth',3)%plot the females between ages 8-11 in R2 a red dotted line
plot(t, Bm2, 'y.', 'LineWidth',3)%plot the males between ages 8-11 in R2 a yellow dotted line
plot(t, Bm3, 'b.', 'LineWidth',3)%plot the males between ages 8-11 in R3 a blue dotted line
plot(t, Cf1, 'g-.', 'LineWidth',3)%plot the females between ages 11-31 in R1 a green dashed dotted line
plot(t, Cf2, 'r-.', 'LineWidth',3)%plot the females between ages 11-31 in R2 a red dashed dotted line
plot(t, Cm2, 'y-.', 'LineWidth',3)%plot the males between ages 11-31 in R2 a yellow dashed dotted line
plot(t, Cm3, 'b-.', 'LineWidth',3)%plot the males between ages 11-31 in R3 a blue dashed dotted line
plot(t, Df1, 'g', 'LineWidth',3)%plot the females between ages 31+ in R1 a green solid line
plot(t, Df1, 'r', 'LineWidth',3)\% plot the females between ages 31+ in R2 a red solid line
plot(t, Df1, 'y', 'LineWidth',3)%plot the males between ages 31+ in R2 a yellow solid line
plot(t, Df1, 'b', 'LineWidth',3)%plot the males between ages 31+ in R3 a blue solid line
xlabel('time') % creates the label 'time' on the x-axis
vlabel('alligators') %creates the label 'stuff' on the y axis
title('F1 (m) and F2 (c) and M2 (y) M3 (b) J1(solid) J2(dotted) A(dashed)') %creates the title
```

figure %open a new figure window

hold on %this keeps all the following plots on the same graph

plot(t, u, 'g', 'LineWidth',3) %plot the total female population in R1 a green line plot(t, v, 'r', 'LineWidth',3) %plot the total female population in R2 a red line plot(t, w, 'y', 'LineWidth',3) %plot the total male population in R2 a yellow line plot(t, q, 'b', 'LineWidth',3) %plot the total male population in R3 a blue line

figure %open a new figure window

hold on %this keeps all the following plots on the same graph plot(t,r,'r','Linewidth',3) %plot the ratio of males to the total population a red line title('the love graph') %creates the title

%is to be used before you have defined the variables in the code. d1=.245: %d1 is the death rate between the ages 0-8 and is set at a desired value d2=.151; %d2 is the death rate between the ages 8-11 and is set at a desired value d_new=.001; %d_new is the death rate between the ages 11-31 and is set a desired value %we gave the age group 11-31 a very low death rate since biological data %states that it was 0. d3=.139: %d3 is the death rate between the ages 31+ and is set at a desired value b1=.286: %b1 is the birth rate for the teens and is set at a desired value %bA is the birth rate for the adults and is set at a desired value b2=.844: k1=.79*1.5; %k1 is the carrying capacity of R1 and is set at a desired value k2=.15*1.5; %k2 is the carrying capacity of R2 and is set at a desired value k3=.06*1.5; %k3 is the carrying capacity of R3 and is set at a desired value s8=exp(-d1*8); %s8 is the survival probability to age 8 and is set at a desired value s11 =exp(-d2*3);%s11 is the survival probability from age 8 to age 11 and is set at a desired value s31=exp(-d_new*20); %s31 is the survival probability from age 11 to age 31 and is set at a desired value c1=k2/k1; %c1 is the carrying capacity of R2 divided by the carrying capacity of R1 c2=k3/k1; %c2 is the carrying capacity of R3 divided by the carrying capacity of R1 r1=b1/b2; %r1 is the birth rate for the teens divided by the birth rate for adults a1=d1./b2; %a1 is the death rate between the ages 0-8 divided by the birth rate for the adults a2=d2./b2; %a2 is the death rate between the ages 8-11 divided by the birth rate for the adults a_new=d_new/b2; %a_new is the death rate between the ages 11-31 divided by the birth rate for the adults a3=d3./b2; %a3 is the death rate between the ages 31+ divided by the birth rate for the adults Lag1=Z(:,1); % 2000 = 10000 = 1000 = 1000 = 1000 = 1000 = 1000 = 10000 = 10000 = 10000 = 1Lag2=Z(:,2); %a column vector whose rows represent the solution at the time delay 2 Lag3=Z(:,3); %a column vector whose rows represent the solution at the time delay 3 Q1=(y(5)+y(9)+y(13))/(1+y(5)+y(9)+y(13));%this is the fraction of f1 who can't nest in R1 now Q2=(c1/(c1+y(5)+y(6)+y(9)+y(10)+y(13)+y(14)));%this is the fraction of f1s and f2s who can nest in R2 now Q3=(Lag1(5)+Lag1(9)+Lag1(13))/(1+Lag1(5)+Lag1(9)+Lag1(13)); %this is the fraction of f1 who couldn't nest in R1 8 years ago

global d1 d2 d3 b1 b2 s8 s11 k1 k2 k3 c1 c2 r1 a1 a2 a3

%declare variables as global to allow the dde23 solver to access their %values, but we only have to change them in one place. The global command

```
Q4=(c1/(c1+Lag1(5)+Lag1(6)+Lag1(9)+Lag1(10)+Lag1(13)+Lag1(14)));
%this is the fraction of f1 and f2 who could nest in R2 8 years ago
Q5=(c2/(c2+y(5)+y(6)+y(9)+y(10)+y(13)+y(14)));
%this is the fraction of f1s and f2s who can nest in R3 now
Q6=(c2/(c2+Lag1(5)+Lag1(6)+Lag1(9)+Lag1(10)+Lag1(13)+Lag1(14)));
%this is the fraction of f1s and f2s who could nest in R2 8 years ago
R3=(Lag2(5)+Lag2(9)+Lag2(13))/(1+Lag2(5)+Lag2(9)+Lag2(13));
%this is the fraction of f1 who couldn't nest in R1 11 years ago
R4=(c1/(c1+Lag2(5)+Lag2(6)+Lag2(9)+Lag2(10)+Lag2(13)+Lag2(14)));
%this is the fraction of f1 and f2 who could nest in R2 11 years ago
R6=(c2/(c2+Lag2(5)+Lag2(6)+Lag2(9)+Lag2(10)+Lag2(13)+Lag2(14)));
%this is the fraction of f1s and f2s who could nest in R2 11 years ago
S3=(Lag3(5)+Lag3(9)+Lag3(13))/(1+Lag3(5)+Lag3(9)+Lag3(13));
%this is the fraction of f1 who couldn't nest in R1 11 years ago
S4=(c1/(c1+Lag3(5)+Lag3(6)+Lag3(9)+Lag3(10)+Lag3(13)+Lag3(14)));
%this is the fraction of f1 and f2 who could nest in R2 11 years ago
S6=(c2/(c2+Lag3(5)+Lag3(6)+Lag3(9)+Lag3(10)+Lag3(13)+Lag3(14)));
%this is the fraction of f1s and f2s who could nest in R2 11 years ago
%R1 females between 0-8:y(1), R2 females between 0-8:y(2), R2 males between 0-8:y(3), R3 males between 0-8:y(4)%
dydt(1)=r1*(y(5)*(1-Q1))...
   -s8*r1*(Lag1(5))*(1-Q3)...
   -a1*y(1)...
   +(y(9)+y(13))*(1-Q1)...
   -s8*(Lag1(9)+Lag1(13))*(1-Q3);
%delay differential equation for the rate of change of the females between
%ages 0-8 R1 where Bf1(t-tau_2) is represented by Lag1(5), Cf1(t-tau_2) is
%represented by Lag1(9), and Df1(t-tau_2) is represented by Lag1(13).
dydt(2)=(r1/2)*(((y(5)+y(6))*Q1)*Q2...
```

```
-s8*(Lag1(5)+Lag1(6))*Q3*Q4)...
   -a1*y(2)...
   +(1/2)*((y(9)+y(10)+y(13)+y(14))*Q1)*Q2...
   -s8*(Lag1(9)+Lag1(10)+Lag1(13)+Lag1(14))*Q3*Q4;
%delay differential equation for the rate of change of the females between
%ages 0-8 in R2 where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2)
%is represented by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9),
\mbox{Cf2}(t-tau_2) is represented by Lag1(10), Df1(t-tau_2) is represented by
Lag1(13), and Df1(t-tau_2) is represented by Lag1(14).
dydt(3)=(r1/2)*(((y(5)+y(6))*Q1)*Q2...
   -s8*(Lag1(5)+Lag1(6))*Q3*Q4)...
   -a1*y(3)...
   +(1/2)*((y(9)+y(10)+y(13)+y(14))*Q1)*Q2...
   -s8*(Lag1(9)+Lag1(10)+Lag1(13)+Lag1(14))*Q3*Q4;
%delay differential equation for the rate of change of the males between
%ages 0-8 R2 where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is
%represented by Lag1(6),Cf1(t-tau_2) is represented by Lag1(9),
%Cf2(t-tau_2) is represented by Lag1(10), Df1(t-tau_2) is represented by
%Lag1(13), and Df1(t-tau_2) is represented by Lag1(14).
dydt(4)=r1*(Q5*(y(5)*Q1+y(6))*(1-Q2)...
   -s8*Q6*(Lag1(5)*Q3+Lag1(6))*(1-Q4))...
   -a1*y(4)...
   +Q5*((y(9)+y(13))*Q1+y(10)+y(14))*(1-Q2)...
   -s8*Q6*((Lag1(9)+Lag1(13))*Q3+Lag1(10)+Lag1(14))*(1-Q4);
%delay differential equation for the rate of change of the males between
%ages 0-8 R3 where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is
%represented by Lag1(6),Cf1(t-tau_2) is represented by Lag1(9),
%Cf2(t-tau_2) is represented by Lag1(10), Df1(t-tau_2) is represented by
%Lag1(13), and Df1(t-tau_2) is represented by Lag1(14).
%R1 females between 8-11:y(5), R2 females between 8-11:y(6), R2 males between 8-11:y(7), R3 males between 8-11:y(8)%
dydt(5)=s8*r1*(Lag1(5))*(1-Q3)...
   +s8*(Lag1(9)+Lag1(13))*(1-Q3)...
   -a2*y(5)...
   -s8*s11*r1*(Lag2(5))*(1-R3)...
   -s8*s11*(Lag2(9)+Lag2(13))*(1-R3);
```

```
%delay differential equation for the rate of change of the females between
%ages 8-11 R1 where Bf1(t-tau_2) is represented by Lag1(5), Cf1(t-tau_2)
%is represented by Lag1(9), Df1(t-tau_2) is represented by Lag1(13), Bf1(t-tau_3)
%is represented by Lag2(5), and Cf1(t-tau_3) is represented by Lag2(13).
dydt(6)=s8*(r1/2)*(Lag1(5)+Lag1(6))*Q3*Q4...
     +s8*(Lag1(9)+Lag1(10)+Lag1(13)+Lag1(14))*Q3*Q4...
     -a2*y(6)...
     -s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
     -s8*s11*(Lag2(9)+Lag2(10)+Lag2(13)+Lag2(14))*R3*R4;
%delay differential equation for the rate of change of females between ages
%8-11 R2 where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is
%represented by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9),
%Cf2(t-tau_2) is represented by Lag1(10), Df1(t-tau_2) is represented by
Lag1(13), Df2(t-tau_2) is represented by Lag1(14), Bf1(t-tau_3) is
%represented by Lag2(5), Bf2(t-tau_3) is represented by Lag2(6), Cf1(t-tau_3)
%is represented by Lag2(9), Cf2(t-tau_3) is represented by Lag2(10),
%Df1(t-tau_3) is represented by Lag2(13), Df2(t-tau_3) is represented by
%Lag2(14).
dydt(7)=s8*(r1/2)*(Lag1(5)+Lag1(6))*Q3*Q4...
     +s8*(Lag1(9)+Lag1(10)+Lag1(13)+Lag1(14))*Q3*Q4...
     -a2*y(7)...
     -s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
     -s8*s11*(Lag2(9)+Lag2(10)+Lag2(13)+Lag2(14))*R3*R4;
%delay differential equation for the rate of change of males between ages
%8-11 R2 where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is
%represented by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9),
\mbox{Cf2}(t-tau_2) is represented by Lag1(10), Df1(t-tau_2) is represented by
Lag1(13), Df2(t-tau_2) is represented by Lag1(14), Bf1(t-tau_3) is
%represented by Lag2(5), Bf2(t-tau_3) is represented by Lag2(6), Cf1(t-tau_3)
%is represented by Lag2(9), Cf2(t-tau_3) is represented by Lag2(10),
%Df1(t-tau_3) is represented by Lag2(13), Df2(t-tau_3) is represented by
%Lag2(14).
dydt(8)=s8*Q6*r1*(Lag1(5)*Q3+Lag1(6))*(1-Q4)...
   +s8*Q6*((Lag1(9)+Lag1(13))*Q3+Lag1(10)+Lag1(14))*(1-Q4)...
   -a2*y(8)...
   -s8*s11*R6*r1*(Lag2(5)*R3+Lag2(6))*(1-R4)...
   -s8*s11*R6*((Lag2(9)+Lag2(13))*R3+Lag2(10)+Lag2(14))*(1-R4);
%delay differential equation for the rate of change of males between ages
```

```
\%8-11 R3 where Bf1(t-tau_2) is represented by Lag1(5), Bf2(t-tau_2) is
%represented by Lag1(6), Cf1(t-tau_2) is represented by Lag1(9),
%Cf2(t-tau_2) is represented by Lag1(10), Df1(t-tau_2) is represented by
Lag1(13), Df2(t-tau_2) is represented by Lag1(14), Bf1(t-tau_3) is
%represented by Lag2(5), Bf2(t-tau_3) is represented by Lag2(6), Cf1(t-tau_3)
%is represented by Lag2(9), Cf2(t-tau_3) is represented by Lag2(10),
%Df1(t-tau_3) is represented by Lag2(13), Df2(t-tau_3) is represented by
%Lag2(14).
%R1 females between 11-31:y(9), R2 females between 11-31:y(10), R2 males between 11-31:y(11), R3 males between 11-31:y(12)%
dydt(9)=s8*s11*r1*(Lag2(5))*(1-R3)...
   +s8*s11*(Lag2(9)+Lag2(13))*(1-R3)...
   -a_new*y(9)...
   -s8*s11*s31*r1*(Lag3(5))*(1-S3)...
   -s8*s11*s31*(Lag3(9)+Lag3(13))*(1-S3);
%delay differential equation for the rate of change of females between ages
%11-31 R1 where Bf1(t-tau_3) is represented by Lag2(5), Cf1(t-tau_3) is
%represented by Lag2(9), Df1(t-tau_3) is represented by Lag2(13), Bf1(t-tau_5)
%is represented by Lag3(5), Cf1(t-tau_5) is represented by Lag3(9),
%Df1(t-tau_5) is represented by Lag3(13).
dydt(10)=s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
    +s8*s11*(Lag2(9)+Lag2(10)+Lag2(13)+Lag2(14))*R3*R4...
    -a_new*y(10)...
    -s8*s11*s31*(r1/2)*(Lag3(5)+Lag3(6))*S3*S4...
    -s8*s11*s31*(Lag3(9)+Lag3(10)+Lag3(13)+Lag3(14))*S3*S4;
%delay differential equation for the rate of change of females between ages
%11-31 R2 where Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3) is
%represented by Lag2(6), Cf1(t-tau_3) is represented by Lag2(9),
%Cf2(t-tau_3) is represented by Lag2(10), Df1(t-tau_3) is represented by
%Lag2(13), Df2(t-tau_3) is represented by Lag2(14), Bf1(t-tau_5)
%is represented by Lag3(5), Bf2(t-tau_5) is represented by Lag3(6) Cf1(t-tau_5)
%is represented by Lag3(9), Cf2(t-tau_5) is represented by Lag3(10),
%Df1(t-tau_5) is represented by Lag3(13), and Df2(t-tau_5) is represented by Lag3(14).
dydt(11)=s8*s11*(r1/2)*(Lag2(5)+Lag2(6))*R3*R4...
    +s8*s11*(Lag2(9)+Lag2(10)+Lag2(13)+Lag2(14))*R3*R4...
    -a_new*y(11)...
```

```
-s8*s11*s31*(r1/2)*(Lag3(5)+Lag3(6))*S3*S4...
    -s8*s11*s31*(Lag3(9)+Lag3(10)+Lag3(13)+Lag3(14))*S3*S4;
%delay differential equation for the rate of change of males between ages
%11-31 R2 where Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3) is
%represented by Lag2(6), Cf1(t-tau_3) is represented by Lag2(9),
%Cf2(t-tau_3) is represented by Lag2(10), Df1(t-tau_3) is represented by
%Lag2(13), Df2(t-tau_3) is represented by Lag2(14), Bf1(t-tau_5)
%is represented by Lag3(5), Bf2(t-tau_5) is represented by Lag3(6) Cf1(t-tau_5)
%is represented by Lag3(9), Cf2(t-tau_5) is represented by Lag3(10),
Df1(t-tau_5) is represented by Lag3(13), and Df2(t-tau_5) is represented
%by Lag3(14).
dydt(12)=s8*s11*R6*r1*(Lag2(5)*R3+Lag2(6))*(1-R4)...
   +s8*s11*R6*((Lag2(9)+Lag2(13))*R3+Lag2(10)+Lag2(14))*(1-R4)...
   -a_new*y(12)...
   -s8*s11*s31*S6*r1*(Lag3(5)*S3+Lag3(6))*(1-S4)...
   -s8*s11*s31*S6*((Lag3(9)+Lag3(13))*S3+Lag3(10)+Lag3(14))*(1-S4);
%delay differential equation for the rate of change of males between ages
%11-31 R3 where Bf1(t-tau_3) is represented by Lag2(5), Bf2(t-tau_3) is
%represented by Lag2(6), Cf1(t-tau_3) is represented by Lag2(9),
%Cf2(t-tau_3) is represented by Lag2(10), Df1(t-tau_3) is represented by
%Lag2(13), Df2(t-tau_3) is represented by Lag2(14), Bf1(t-tau_5)
%is represented by Lag3(5), Bf2(t-tau_5) is represented by Lag3(6) Cf1(t-tau_5)
%is represented by Lag3(9), Cf2(t-tau_5) is represented by Lag3(10),
%Df1(t-tau_5) is represented by Lag3(13), and Df2(t-tau_5) is represented
%by Lag3(14).
%R1 females between 11-31:y(9), R2 females between 11-31:y(10), R2 males between 11-31:y(11), R3 males between 11-31:y(12)%
dydt(13)=s8*s11*s31*r1*(Lag3(5))*(1-S3)...
   +s8*s11*s31*(Lag3(9)+Lag3(13))*(1-S3)...
   -a3*y(13);
%delay differential equation for the rate of change of females between ages
%31+ R1 where Bf1(t-tau_5) is represented by Lag3(5), Cf1(t-tau_5) is
%represented by Lag3(9), and Df1(t-tau_5) is represented by Lag3(13).
dydt(14)=s8*s11*s31*(r1/2)*(Lag3(5)+Lag3(6))*S3*S4...
    +s8*s11*s31*(Lag3(9)+Lag3(10)+Lag3(13)+Lag3(14))*S3*S4...
    -a3*y(14);
```

%delay differential equation for the rate of change of females between ages %31+ R2 where Bf1(t-tau_5) is represented by Lag3(5), Bf2(t-tau_5) is %represented by Lag3(6), Cf1(t-tau_5) is represented by Lag3(9), %Cf2(t-tau_5) is represented by Lag3(10), Df1(t-tau_5) is represented by %Lag3(13), and Df2(t-tau_5) is represented by Lag3(14).

dydt(15)=s8*s11*s31*(r1/2)*(Lag3(5)+Lag3(6))*S3*S4...
+s8*s11*s31*(Lag3(9)+Lag3(10)+Lag3(13)+Lag3(14))*S3*S4...
-a3*y(15);

%delay differential equation for the rate of change of males between ages %31+ R2 where Bf1(t-tau_5) is represented by Lag3(5), Bf2(t-tau_5) is %represented by Lag3(6), Cf1(t-tau_5) is represented by Lag3(9), %Cf2(t-tau_5) is represented by Lag3(10), Df1(t-tau_5) is represented by %Lag3(13), and Df2(t-tau_5) is represented by Lag3(14).

dydt(16)=s8*s11*s31*S6*r1*(Lag3(5)*S3+Lag3(6))*(1-S4)...
+s8*s11*s31*S6*((Lag3(9)+Lag3(13))*S3+Lag3(10)+Lag3(14))*(1-S4)...
-a3*y(16);

%delay differential equation for the rate of change of males between ages %31+ R3 where Bf1(t-tau_5) is represented by Lag3(5), Bf2(t-tau_5) is %represented by Lag3(6), Cf1(t-tau_5) is represented by Lag3(9), %Cf2(t-tau_5) is represented by Lag3(10), Df1(t-tau_5) is represented by %Lag3(13), and Df2(t-tau_5) is represented by Lag3(14).

%This is a function file that maintains the system histories.

%In this case we are assigning constant values to the variable histories.

```
hist_1 = 10;
               \%this is the history of the females between ages 0-8 population from R1
hist_2 = 10;
               %this is the history of the females between ages 0-8 population from R2
hist_3 = 10;
               %this is the history of the males between ages 0-8 population from R2
hist_4 = 10;
               %this is the history of the males between ages 0-8 population from R3
hist_5 = 10;
               %this is the history of the females between ages 8-11 population from R1
hist_6 = 7;
               \%this is the history of the females between ages 8-11 population from R2
hist_7 = 4;
               \%this is the history of the males between ages 8-11 population from R2
hist_8 = 4;
               %this is the history of the males between ages 8-11 population from R3
hist_9=2.5;
               %this is the history of the females between ages 11-31 population from R1
hist_10 = 1.5; %this is the history of the females between ages 11-31 population from R2
hist 11=1:
               %this is the history of the males between ages 11-31 population from R2
hist_12=1;
               \%this is the history of the males between ages 11-31 population from R3
hist_13=2.5;
               %this is the history of the females between ages 31+ population from R1
hist_14 = 1.5; %this is the history of the females between ages 31+ population from R2
hist_15=1;
               %this is the history of the males between ages 31+ population from R2
hist_16=1;
               %this is the history of the males between ages 31+ population from R3
```

```
s = [hist_1; hist_2; hist_3; hist_4; hist_5; hist_6; hist_7; hist_8; hist_9;
hist_10; hist_11; hist_12; hist_13; hist_14; hist_15; hist_16];
%This puts all the histories into a column vector and names it s. This is
%the format that dde23 would like it to be in.
```

Three Regions Five Delay

```
%Alli3Solver_Region.m
```

%This is a script file that calls two function files, Alli3Delay_Region, %and Alli3Delay_hist_region. The purpose of this file is to numerically solve %the 1 delay alligator model using Matlab's built in dde solver, Runge %Kutta Method, dde23.

%Comments updated for AMSSI 2007 on July 27,2007

b2=.844; %b is the birth rate and is set at a desired value

lags = [tau_1 tau_2 tau_3 tau_4 tau_5]; % 'lags' is the array that holds the time delay values

%options = ddeset('RelTol',ie-4,'AbsTol',ie-7,'InitialY',[3 5 2 2 4 0 0 0 0 0 0 0 2 2 1 0 0 0 0 0 0 0 0 0]);
AlliBirthDivsol = dde23(@Alli6Delay_Region, lags, @Alli6Delay_hist_region, tspan);% options); %this line calls the %delay differential equation solver dde23. 'Alli6Delay_Region' is the name
%of the file storing out dde formulas, lags is the array of delays that we
%need to use, 'Alli6Delay_his_region' is the function file that maintains
%the system history and 'tspan' feeds in our initial and final times for
%computation. The solutions to this system will be stored in the array
%'AlliBirthDivsol'.

 $\mbox{\ensuremath{\mbox{\%}}first},$ separate the output array into its various components

t = AlliBirthDivsol.x; %assigns the time outputs to a vector 't'

Af1 = AlliBirthDivsol.y(1,:); %assigns females between ages 0-1 in R1 outputs %array to a vector named after the variable %it represents, 'Af1'.

Af2 = AlliBirthDivsol.y(2,:); %assigns females between ages 0-1 in R2 outputs %array to a vector named after the variable %it represents, 'Af2'.

Am2 = AlliBirthDivsol.y(3,:); %assigns males between ages 0-1 in R2 outputs array %to a vector named after the variable it %represents, 'Am2'.

Am3 = AlliBirthDivsol.y(4,:); %assigns males between ages 0-1 in R3 outputs array %to a vector named after the variable it %represents, 'Am3'.

%assigns females between ages 1-8 in R1 outputs Bf1 = AlliBirthDivsol.y(5,:); %array to a vector named after the variable %it represents, 'Bf1'. Bf2 = AlliBirthDivsol.y(6,:); %assigns females between ages 1-8 in R2 outputs %array to a vector named after the variable %it represents, 'Bf2'. Bm2 = AlliBirthDivsol.y(7,:); %assigns males between ages 1-8 in R2 outputs %array to a vector named after the variable %it represents, 'Bm2'. Bm3 = AlliBirthDivsol.y(8,:); %assigns males between ages 1-8 in R3 outputs %array to a vector named after the variable %it represents, 'Bm3'. %assigns females between ages 8-11 in R1 outputs Cf1 = AlliBirthDivsol.y(9,:); %array to a vector named after the variable %it represents, 'Cf1'. Cf2 = AlliBirthDivsol.y(10,:); %assigns females between ages 8-11 in R2 outputs %array to a vector named after the variable %it represents, 'Cf2'. Cm2 = AlliBirthDivsol.y(11,:); %assigns males between ages 8-11 in R2 outputs %array to a vector named after the variable %it represents, 'Cm2'. Cm3 = AlliBirthDivsol.y(12,:); %assigns males between ages 8-11 in R3 outputs %array to a vector named after the variable %it represents, 'Cm3'. Df1 = AlliBirthDivsol.y(13,:); %assigns females between the ages 11-12 in R1 %outputs array to a vector named after the %variable it represents, 'Df1'. Df2 = AlliBirthDivsol.y(13,:); %assigns females between the ages 11-12 in R2 %outputs array to a vector named after the %variable it represents, 'Df2'. Dm2 = AlliBirthDivsol.y(13,:); %assigns males between the ages 11-12 in R2 %outputs array to a vector named after the %variable it represents, 'Dm2'. Dm3 = AlliBirthDivsol.y(13,:); %assigns males between the ages 11-12 in R3 %outputs array to a vector named after the %variable it represents, 'Dm3'. Ef1 = AlliBirthDivsol.y(17,:); %assigns females between the ages 12-31 in R1 %outputs array to a vector named after the %variable it represents, 'Ef1'.

Ef2 = AlliBirthDivsol.y(18,:); %assigns females between the ages 12-31 in R2

%outputs array to a vector named after the

```
%variable it represents, 'Ef2'.
Em2 = AlliBirthDivsol.y(19,:); %assigns males between the ages 12-31 in R2
                                                                                     %outputs array to a vector named after the
                                                                                     %variable it represents, 'Em2'.
Em3 = AlliBirthDivsol.y(20,:); %assigns males between the ages 12-31 in R3
                                                                                     %outputs array to a vector named after the
                                                                                     %variable it represents, 'Em3'.
Ff1 = AlliBirthDivsol.y(21,:); %assigns females between the ages 31+ in R1
                                                                                     %outputs array to a vector named after the
                                                                                     %variable it represents, 'Ff1'.
Ff2 = AlliBirthDivsol.y(22,:); %assigns females between the ages 31+ in R2
                                                                                     %outputs array to a vector named after the
                                                                                     %variable it represents, 'Ff2'.
Fm2 = AlliBirthDivsol.y(23,:); %assigns males between the ages 31+ in R2
                                                                                     % \frac{1}{2} = \frac{
                                                                                     %variable it represents, 'Fm2'.
Fm3 = AlliBirthDivsol.y(24,:); %assigns males between the ages 31+ in R3
                                                                                     %outputs array to a vector named after the
                                                                                     %variable it represents, 'Fm3'.
u=Af1+Bf1+Cf1+Df1+Ef1+Ff1; %assigns the variable 'u' to be equal to the total female
                                                                          %population in R1
v = Af2 + Bf2 + Cf2 + Df2 + Ef2 + Ff2; \quad \mbox{\it `assigns the variable 'v' to be equal to the total female}
                                                                          %population in R2
w=Am2+Bm2+Cm2+Dm2+Em2+Fm2; %assigns the variable 'w' to be equal to the total male
                                                                          %population in R2
x=Am3+Bm3+Cm3+Dm3+Em3+Fm3; %assigns the variable 'x' to be equal to the total male
                                                                          %population in R3
y=u+v; %assigns the variable 'y' to be equal to the total female population
z=w+x; %assigns the variable 'z' to be equal to the total male population
r=z./(y+z); %assigns r to be equal to the total male population divided
                                %by the total male population plus the total female population
                                %will give you the ratio of males to total population
final=size(t);
Af1(final(2));
Bf1(final(2));
```

Cf1(final(2));
Df1(final(2));

```
Ef1(final(2));
Ff1(final(2));
Af2(final(2));
Bf2(final(2));
Cf2(final(2));
Df2(final(2));
Ef2(final(2));
Ff2(final(2));
Am2(final(2));
Bm2(final(2));
Cm2(final(2));
Dm2(final(2));
Em2(final(2));
Fm2(final(2));
Am3(final(2));
Bm3(final(2));
Cm3(final(2));
Dm3(final(2));
Em3(final(2));
Fm3(final(2));
figure % opens a new figure window
hold on % this keeps all the following plots on the same graph
\protect\ (t, x, y, 'r-', 'LineWidth',3) \protect\ L will be red and solid of weight 3
plot(t, Af1, 'g-', 'LineWidth',3) %plot the females between ages 0-1 in R1 a green dashed line
plot(t, Af2, 'r-', 'LineWidth',3) %plot the females between ages 0-1 in R2 a red dashed line
plot(t, Am2, 'y-', 'LineWidth',3) %plot the males between ages 0-1 in R2 a yellow dashed line
plot(t, Am3, 'b-', 'LineWidth',3) %plot the males between ages 0-1 in R3 a blue dashed line
plot(t, Bf1, 'g.', 'LineWidth',3)%plot the females between ages 1-8 in R1 a green dotted line
plot(t, Bf2, 'r.', 'LineWidth',3)%plot the females between ages 1-8 in R2 a red dotted line
plot(t, Bm2, 'y.', 'LineWidth',3)%plot the males between ages 1-8 in R2 a yellow dotted line
plot(t, Bm3, 'b.', 'LineWidth',3)%plot the males between ages 1-8 in R3 a blue dotted line
plot(t, Cf1, 'g-.', 'LineWidth',3)%plot the females between ages 8-11 in R1 a green dashed dotted line
plot(t, Cf2, 'r-.', 'LineWidth',3)%plot the females between ages 8-11 in R2 a red dashed dotted line
plot(t, Cm2, 'y-.', 'LineWidth',3)%plot the males between ages 8-11 in R2 a yellow dashed dotted line
plot(t, Cm3, 'b-.', 'LineWidth',3)%plot the males between ages 8-11 in R3 a blue dashed dotted line
plot(t, Df1, 'g', 'LineWidth',3)%plot the females between ages 11-12 in R1 a green solid line
```

```
plot(t, Df1, 'r', 'LineWidth',3)%plot the females between ages 11-12 in R2 a red solid line
plot(t, Df1, 'y', 'LineWidth',3)%plot the males between ages 11-12 in R2 a yellow solid line
plot(t, Df1, 'b', 'LineWidth',3)%plot the males between ages 11-12 in R3 a blue solid line
xlabel('time') % creates the label 'time' on the x-axis
ylabel('alligators') %creates the label 'stuff' on the y axis
title('Population of ages 0-12') %creates the title
figure %opens a new figure window
hold on %keeps all the following plots on the same graph
plot(t,Ef1,'g-','Linewidth',3);
                                    %plot the females between ages 12-31 in R1 a green dashed line
plot(t,Ef2,'r-', 'Linewidth',3);
                                    %plot the females between ages 12-31 in R2 a red dashed line
plot(t,Em2,'y-','Linewidth',3);
                                    %plot the males between ages 12-31 in R2 a yellow dashed line
plot(t,Em3,'b-','Linewidth',3);
                                    %plot the males between ages 12-31 in R3 a blue dashed line
plot(t,Ff1,'g','Linewidth',3);
                                    %plot the females between ages 31+ in R1 a green solid line
plot(t,Ff2,'r', 'Linewidth',3);
                                    \mbox{\ensuremath{\upmu}{l}}\mbox{plot} the females between ages 31+ in R2 a red solid line
plot(t,Fm2,'y','Linewidth',3);
                                    %plot the males between ages 31+ in R2 a yellow solid line
plot(t,Fm3,'b','Linewidth',3);
                                    %plot the males between ages 31+ in R3 a blue solid line
xlabel('time') % creates the label 'time' on the x-axis
ylabel('alligators') %creates the label 'stuff' on the y axis
title('Population of ages 12+') %creates the title
figure %open a new figure window
hold on %this keeps all the following plots on the same graph
plot(t, r,'m','Linewidth',3) %plot the ratio of males to the total population a red line
title('the love graph') %creates the title
%total_f1_pde=3070.45;
%total_f2_pde=466.385;
%total_m2_pde=252.79;
%total_m3_pde=233.705;
%bargraphvector1=[(u(final(2))/(u(final(2))+v(final(2))+w(final(2))+x(final(2))))...
% (v(final(2))/(u(final(2))+v(final(2))+w(final(2))+x(final(2))))...
   (w(final(2))/(u(final(2))+v(final(2))+w(final(2))+x(final(2))))...
   (x(final(2))/(u(final(2))+v(final(2))+w(final(2))+x(final(2))))]
%bargraphvector2=[total_f1_pde/(total_f1_pde+total_f2_pde+total_m2_pde+total_m3_pde)...
% total_f2_pde/(total_f1_pde+total_f2_pde+total_m2_pde+total_m3_pde)...
% total_m2_pde/(total_f1_pde+total_f2_pde+total_m2_pde+total_m3_pde)...
% total_m3_pde/(total_f1_pde+total_f2_pde+total_m2_pde+total_m3_pde)]
```

%figure

%bar([bargraphvector1; bargraphvector2],'group')

%colormap spring

%legend('F1','F2','M2','M3')

% creates the label 'time' on the x-axis

%ylabel('percentage of total population') %creates the label 'stuff' on the y axis

%This is a function code that stores all the delay differential equations %formulas in another file to be called by the script file

function dydt=Alli6Delay_Region(t,y,Z) %function name and variables, time $\label{eq:condition} \mbox{\% variables and lags}$

Current size(Z) = [3,2]

%col 1 of Z: solutions with time delay

%tau_1. col 2 of Z represents solutions

%with time delay tau_2.

%row 1 of Z: delay value for x

%row 2 of Z: delay value for y

%row 3 of Z: delay value for y

 $\verb|global| d1 d2 d3 b1 b2 s1 s8 s11 s12 s31 k1 k2 k3 c1 c2 r1 a1 a2 a3|\\$

%declare variables as global to allow the dde23 solver to access their

 $\mbox{\ensuremath{\mbox{\sc w}}}$ values, but we only have to change them in one place. The global command

 $\mbox{\ensuremath{\mbox{\sc h}}}\mbox{\sc is}$ to be used before you have defined the variables in the code.

d1=.9; %d1 is the death rate between the ages 0-8 and is set at a desired value

d2=.151; %d2 is the death rate between the ages 8-11 and is set at a desired value

 $d_{new}=.001;%d_{new}$ is the death rate between the ages 11-31 and is set a desired value

%we gave the age group 11-31 a very low death rate since biological data

%states that it was 0.

d3=.139; %d3 is the death rate between the ages 31+ and is set at a desired value

b1=.286; %b1 is the birth rate for the teens and is set at a desired value

b2=.844; %b2 is the birth rate for the adults and is set at a desired value

k1=.79*1.5; %k1 is the carrying capacity of R1 and is set at a desired value

k2=.15*1.5; %k2 is the carrying capacity of R2 and is set at a desired value

 $\mbox{k3=.6*1.5};$ %k3 is the carrying capacity of R3 and is set at a desired value

s1=exp(-d1);%s1 is the survival probability to age 1 and is set at a desired value

```
s8=exp(-d2.*7); %s8 is the survival probability from age 1 to age 8 and is set at a desired value
s11 =exp(-d2.*3); %s11 is the survival probability from age 8 to age 11 and is set at a desired value
s12 =exp(-d_new); %s12 is the survival probability from age 11 to age 12 and is set at a desired value
s31 =exp(-d_new*19);%s31 is the survival probability from age 12 to age 31+ and is set at a desired value
c1=k2/k1; %c1 is the carrying capacity of R2 divided by the carrying capacity of R1
c2=k3/k1; %c2 is the carrying capacity of R3 divided by the carrying capacity of R1
r1=b1/b2; %r1 is the birth rate for the teens divided by the birth rate for adults
a1=d1./b2; %a1 is the death rate between the ages 0-8 divided by the birth rate for the adults
a2=d2./b2; %a2 is the death rate between the ages 8-11 divided by the birth rate for the adults
a_new=d_new/b2; %a_new is the death rate between the ages 11-31 divided by the birth rate for the adults
a3=d3./b2; %a3 is the death rate between the ages 31+ divided by the birth rate for the adults
Lag1=Z(:,1);
              %a column vector whose rows represent the solution at the time delay 1
Lag2=Z(:,2);
             %a column vector whose rows represent the solution at the time delay 2
Lag3=Z(:,3);
             %a column vector whose rows represent the solution at the time delay 3
Lag4=Z(:,4);
             %a column vector whose rows represent the solution at the time delay 4
Lag5=Z(:,5);
              %a column vector whose rows represent the solution at the time delay 5
Q1=(y(9)+y(13)+y(17)+y(21))/(1+y(9)+y(13)+y(17)+y(21));
%this is the fraction of f1 who can't nest in R1 now
Q2=(c1/(c1+y(9)+y(13)+y(17)+y(21)+y(10)+y(14)+y(18)+y(22)));
%this is the fraction of f1s and f2s who can nest in R2 now
Q3=(Lag1(9)+Lag1(13)+Lag1(17)+Lag1(21))/(1+Lag1(9)+Lag1(13)+Lag1(17)+Lag1(21));
%this is the fraction of f1 who couldn't nest in R1 1 year ago
Q4=(c1/(c1+Lag1(9)+Lag1(13)+Lag1(17)+Lag1(21)+Lag1(10)+Lag1(14)+Lag1(18)+Lag1(22)));
%this is the fraction of f1 and f2 who could nest in R2 1 year ago
Q5=(c2/(c2+y(9)+y(13)+y(17)+y(21)+y(10)+y(14)+y(18)+y(22)));
%this is the fraction of f1s and f2s who can nest in R3 now
Q6=(c2/(c2+Lag1(9)+Lag1(13)+Lag1(17)+Lag1(21)+Lag1(10)+Lag1(14)+Lag1(18)+Lag1(22)));
%this is the fraction of f1s and f2s who could nest in R2 1 year ago
R3=(Lag2(9)+Lag2(13)+Lag2(17)+Lag2(21))/(1+Lag2(9)+Lag2(13)+Lag2(17)+Lag2(21));
%this is the fraction of f1 who couldn't nest in R1 8 years ago
R4 = (c1/(c1 + Lag2(9) + Lag2(13) + Lag2(17) + Lag2(21) + Lag2(10) + Lag2(14) + Lag2(18) + Lag2(22)));
```

```
%this is the fraction of f1 and f2 who could nest in R2 8 years ago
R6 = (c2/(c2+Lag2(9)+Lag2(13)+Lag2(17)+Lag2(21)+Lag2(10)+Lag2(14)+Lag2(18)+Lag2(22)));
%this is the fraction of f1s and f2s who could nest in R2 8 years ago
S3=(Lag3(9)+Lag3(13)+Lag3(17)+Lag3(21))/(1+Lag3(9)+Lag3(13)+Lag3(17)+Lag3(21));
%this is the fraction of f1 who couldn't nest in R1 11 years ago
S4 = (c1/(c1+Lag3(9)+Lag3(13)+Lag3(17)+Lag3(21)+Lag3(10)+Lag3(14)+Lag3(18)+Lag3(22)));
%this is the fraction of f1 and f2 who could nest in R2 11 years ago
S6=(c2/(c2+Lag3(9)+Lag3(13)+Lag3(17)+Lag3(21)+Lag3(10)+Lag3(14)+Lag3(18)+Lag3(22)));
%this is the fraction of f1s and f2s who could nest in R3 11 years ago
T3 = (Lag4(9) + Lag4(13) + Lag4(17) + Lag4(21)) / (1 + Lag4(9) + Lag4(13) + Lag4(17) + Lag4(21));
%this is the fraction of f1 who couldn't nest in R1 12 years ago
T4=(c1/(c1+Lag4(9)+Lag4(13)+Lag4(17)+Lag4(21)+Lag4(10)+Lag4(14)+Lag4(18)+Lag4(22)));
%this is the fraction of f1 and f2 who could nest in R2 12 years ago
T6 = (c2/(c2 + Lag4(9) + Lag4(13) + Lag4(17) + Lag4(21) + Lag4(10) + Lag4(14) + Lag4(18) + Lag4(22)));
%this is the fraction of f1s and f2s who could nest in R2 12 years ago
U3=(Lag5(9)+Lag5(13)+Lag5(17)+Lag5(21))/(1+Lag5(9)+Lag5(13)+Lag5(17)+Lag5(21));
%this is the fraction of f1 who couldn't nest in R1 31 years ago
U4=(c1/(c1+Lag5(9)+Lag5(13)+Lag5(17)+Lag5(21)+Lag5(10)+Lag5(14)+Lag5(18)+Lag5(22)));
%this is the fraction of f1 and f2 who could nest in R2 31 years ago
 \begin{tabular}{l} U6=(c2/(c2+Lag5(9)+Lag5(13)+Lag5(17)+Lag5(21)+Lag5(10)+Lag5(14)+Lag5(18)+Lag5(22))); \\ (4) & + Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag5(18)+Lag
%this is the fraction of f1s and f2s who could nest in R2 31 years ago
%R1 females between 0-1:y(1), R2 females between 0-1:y(2), R2 males between 0-1:y(3), R3 males between 0-1:y(4)%
dydt(1)=r1*((y(9)+y(13))*(1-Q1))-s1.*r1*(Lag1(9)+Lag1(13))*(1-Q3)...
      -a1*y(1)+...
       (y(17)+y(21))*(1-Q1)...
       -s1.*(Lag1(17)+Lag1(21))*(1-Q3);
```

%delay differential equation for the rate of change of the females between

```
%ages 0-1 R1 where Cf1(t-tau_1) is represented by Lag1(9), Df1(t-tau_1) is
%represented by Lag1(13), Ef1(t-tau_1) is represented by Lag1(17), and
%Ff1(t-tau_1) is represented by Lag1(21).
dydt(2)=(r1/2)*((y(10)+y(14)+(y(9)+y(13))*Q1)*Q2...
   -s1.*(Lag1(10)+Lag1(14)+(Lag1(9)+Lag1(13))*Q3)*Q4)...
   -a1*y(2)...
   +(1/2)*((y(18)+y(22)+((y(17)+y(21))*Q1)*Q2)...
   -s1.*(Lag1(18)+Lag1(22)+(Lag1(17)+Lag1(21))*Q3)*Q4);
%delay differential equation for the rate of change of the females between
%ages 0-1 R2 where Cf2(t-tau_1) is represented by Lag1(10), Df2(t-tau_1) is
%represented by Lag1(14), Cf1(t-tau_1) is represented by Lag1(9),
%Df1(t-tau_1) is represented by Lag1(13), Ef2(t-tau_1) is represented by
%Lag1(18), Ff2(t-tau_1) is represented by Lag1(22), Ef1(t-tau_1) is
%represented by Lag1(17), Ff1(t-tau_1) is represented by Lag1(22).
dydt(3) = (r1/2)*((y(10)+y(14)+(y(9)+y(13))*Q1)*Q2...
   -s1.*(Lag1(10)+Lag1(14)+(Lag1(9)+Lag1(13))*Q3)*Q4)...
   -a1*v(3)...
   +(1/2)*((y(18)+y(22)+((y(17)+y(21))*Q1)*Q2)...
   -s1.*(Lag1(18)+Lag1(22)+(Lag1(17)+Lag1(21))*Q3)*Q4);
%delay differential equation for the rate of change of the males between
%ages 0-1 R3 where Cf2(t-tau_1) is represented by Lag1(10), Df2(t-tau_1) is
%represented by Lag1(14), Cf1(t-tau_1) is represented by Lag1(9),
%Df1(t-tau_1) is represented by Lag1(13), Ef2(t-tau_1) is represented by
%Lag1(18), Ff2(t-tau_1) is represented by Lag1(22), Ef1(t-tau_1) is
%represented by Lag1(17), Ff1(t-tau_1) is represented by Lag1(22).
dydt(4)=r1*(Q5*((y(9)+y(13))*Q1+y(10)+y(14))*(1-Q2)...
   -s1.*Q6*((Lag1(9)+Lag1(13))*Q3+Lag1(10)+Lag1(14))*(1-Q4))...
   -a1*y(4)...
   +Q5*((y(17)+y(21))*Q1+y(18)+y(22))*(1-Q2)...
    -s1.*Q6*((Lag1(17)+Lag1(21))*Q3+Lag1(18)+Lag1(22))*(1-Q4);
%delay differential equation for the rate of change of the males between
%ages 0-1 R3 where Cf1(t-tau_1) is represented by Lag1(9), Df1(t-tau_1) is
%represented by Lag1(13), Cf2(t-tau_1) is represented by Lag1(10),
%Df2(t-tau_1) is represented by Lag1(14), Ef1(t-tau_1) is represented by
%Lag1(17), Ff1(t-tau_1) is represented by Lag1(21), Ef2(t-tau_1) is
%represented by Lag1(18), Ff1(t-tau_1) is represented by Lag1(22).
```

```
dydt(5)=s1.*r1*(Lag1(9)+Lag1(13))*(1-Q3)+...
   s1.*(Lag1(17)+Lag1(21))*(1-Q3)...
   -a2*y(5)-...
   s1.*s8.*r1*(Lag2(9)+Lag2(13))*(1-R3)-...
   s1.*s8.*(Lag2(17)+Lag2(21))*(1-R3);
%delay differential equation for the rate of change of the females between
%ages 1-8 R1 where Cf1(t-tau_1) is represented by Lag1(9), Df1(t-tau_1) is
%represented by Lag1(13), Ef1(t-tau_1) is represented by Lag1(17),
%Ff1(t-tau_1) is represented by Lag1(21), Cf1(t-tau_2) is represented by
%Lag2(9), Df1(t-tau_2) is represented by Lag2(13), Ef1(t-tau_2) is
%represented by Lag2(17), and Ff1(t-tau_2) is represented by Lag2(21).
(1/2)*s1.*(Lag1(18)+Lag1(22)+(Lag1(17)+Lag1(21))*Q3)*Q4...
   -a2*v(6)-...
    (r1/2)*s1.*s8.*(Lag2(10)+Lag2(14)+(Lag2(9)+Lag2(13))*R3)*R4-...
    (1/2)*s1.*s8.*(Lag2(18)+Lag2(22)+(Lag2(17)+Lag2(21))*R3)*R4;
%delay differential equation for the rate of change of the females between
%ages 1-8 R2 where Cf2(t-tau_1) is represented by Lag1(10), Df2(t-tau_1) is
%represented by Lag1(14), Cf1(t-tau_1) is represented by Lag1(9),
%Df1(t-tau_1) is represented by Lag1(13), Ef2(t-tau_1) is represented by
Lag1(18), Ff2(t-tau_1) is represented by Lag1(22), Ef1(t-tau_1) is
%represented by Lag1(17), Ff1(t-tau_1) is represented by Lag1(21),
%Cf2(t-tau_2) is represented by Lag2(10), Df2(t-tau_2) is
%represented by Lag2(14), Cf1(t-tau_2) is represented by Lag2(9),
%Df1(t-tau_2) is represented by Lag2(13), Ef2(t-tau_2) is represented by
Lag2(18), Ff2(t-tau_2) is represented by Lag2(22), Ef1(t-tau_2) is
%represented by Lag2(17), and Ff1(t-tau_2) is represented by Lag2(21).
dydt(7)=(r1/2)*s1.*(Lag1(10)+Lag1(14)+(Lag1(9)+Lag1(13))*Q3)*Q4+...
   (1/2)*s1.*(Lag1(18)+Lag1(22)+(Lag1(17)+Lag1(21))*Q3)*Q4...
   -a2*y(7)-...
    (r1/2)*s1.*s8.*(Lag2(10)+Lag2(14)+(Lag2(9)+Lag2(13))*R3)*R4-...
    (1/2)*s1.*s8.*(Lag2(18)+Lag2(22)+(Lag2(17)+Lag2(21))*R3)*R4;
%delay differential equation for the rate of change of the males between
%ages 1-8 R2 where Cf2(t-tau_1) is represented by Lag1(10), Df2(t-tau_1) is
%represented by Lag1(14), Cf1(t-tau_1) is represented by Lag1(9),
%Df1(t-tau_1) is represented by Lag1(13), Ef2(t-tau_1) is represented by
```

```
Lag1(18), Ff2(t-tau_1) is represented by Lag1(22), Ef1(t-tau_1) is
%represented by Lag1(17), Ff1(t-tau_1) is represented by Lag1(21),
%Cf2(t-tau_2) is represented by Lag2(10), Df2(t-tau_2) is
%represented by Lag2(14), Cf1(t-tau_2) is represented by Lag2(9),
%Df1(t-tau_2) is represented by Lag2(13), Ef2(t-tau_2) is represented by
%Lag2(18), Ff2(t-tau_2) is represented by Lag2(22), Ef1(t-tau_2) is
%represented by Lag2(17), and Ff1(t-tau_2) is represented by Lag2(21).
\label{eq:dydt(8)=r1*s1.*Q6*((Lag1(9)+Lag1(13))*Q3+Lag1(10)+Lag1(14))*(1-Q4)+...}
   s1.*Q6*((Lag1(17)+Lag1(21))*Q3+Lag1(18)+Lag1(22))*(1-Q4)-...
   a2*y(8)-...
   r1*s1.*s8.*R6*((Lag2(9)+Lag2(13))*R3+Lag2(10)+Lag2(14))*(1-R4)-...
   s1.*s8.*R6*((Lag2(17)+Lag2(21))*R3+Lag2(18)+Lag2(22))*(1-R4);
%delay differential equation for the rate of change of the males between
%ages 1-8 R3 where Cf1(t-tau_1) is represented by Lag1(9), Df1(t-tau_1) is
%represented by Lag1(13), Cf2(t-tau_1) is represented by Lag1(10),
%Df2(t-tau_1) is represented by Lag1(14), Ef1(t-tau_1) is represented by
%Lag1(17), Ff1(t-tau_1) is represented by Lag1(21), Ef2(t-tau_1) is
%represented by Lag1(18), Ff2(t-tau_1) is represented by Lag1(22),
%Cf1(t-tau_2) is represented by Lag2(9), Df1(t-tau_2) is
%represented by Lag2(13), Cf2(t-tau_2) is represented by Lag2(10),
%Df2(t-tau_2) is represented by Lag2(14), Ef1(t-tau_2) is represented by
Lag2(17), Ff1(t-tau_2) is represented by Lag2(21), Ef2(t-tau_2) is
%represented by Lag2(18), and Ff2(t-tau_2) is represented by Lag2(22).
%R1 females between 8-11:y(9), R2 females between 8-11:y(10), R2 males between 8-11:y(11), R3 males between 8-11:y(12)%
dydt(9)= s1.*s8.*r1*(Lag2(9)+Lag2(13))*(1-R3)+...
   s1.*s8.*(Lag2(17)+Lag2(21))*(1-R3)...
   -a2*y(9)-...
   s1.*s8.*s11.*r1*(Lag3(9)+Lag3(13))*(1-S3)-...
   s1.*s8.*s11.*(Lag3(17)+Lag3(21))*(1-S3);
%delay differential equation for the rate of change of the females between
%ages 8-11 R1 where Cf1(t-tau_2) is represented by Lag2(9), Df1(t-tau_2) is
%represented by Lag2(13), Ef1(t-tau_2) is represented by Lag2(17),
%Ff1(t-tau_2) is represented by Lag2(21), Cf1(t-tau_3) is represented by
%Lag3(9), Df1(t-tau_3) is represented by Lag3(13), Ef1(t-tau_3) is
%represented by Lag3(17), and Ff1(t-tau_3) is represented by Lag3(21).
```

```
(1/2)*s1.*s8.*(Lag2(18)+Lag2(22)+(Lag2(17)+Lag2(21))*R3)*R4...
   -a2*y(10)...
   -(r1/2)*s1.*s8.*s11.*(Lag3(10)+Lag3(14)+(Lag3(9)+Lag3(13))*S3)*S4-...
    (1/2)*s1.*s8.*s11.*(Lag3(18)+Lag3(22)+(Lag3(17)+Lag3(21))*S3)*S4;
%delay differential equation for the rate of change of the females between
%ages 8-11 R2 where Cf2(t-tau_2) is represented by Lag2(10), Df2(t-tau_2) is
%represented by Lag2(14), Cf1(t-tau_2) is represented by Lag2(9),
Df1(t-tau_2) is represented by Lag2(13), Ef2(t-tau_2) is represented by
Lag2(18), Ff2(t-tau_2) is represented by Lag2(22), Ef1(t-tau_2) is
%represented by Lag2(17), Ff1(t-tau_2) is represented by Lag2(21),
%Cf2(t-tau_3) is represented by Lag3(10), Df2(t-tau_3) is
%represented by Lag3(14), Cf1(t-tau_3) is represented by Lag3(9),
%Df1(t-tau_3) is represented by Lag3(13), Ef2(t-tau_3) is represented by
Lag3(18), Ef2(t-tau_3) is represented by Lag3(22), Ef1(t-tau_3) is
%represented by Lag3(17), and Ff1(t-tau_3) is represented by Lag3(21).
dydt(11)=(r1/2)*s1.*s8.*(Lag2(10)+Lag2(14)+(Lag2(9)+Lag2(13))*R3)*R4+...
    (1/2)*s1.*s8.*(Lag2(18)+Lag2(22)+(Lag2(17)+Lag2(21))*R3)*R4...
   -a2*v(11)...
   -(r1/2)*s1.*s8.*s11.*(Lag3(10)+Lag3(14)+(Lag3(9)+Lag3(13))*S3)*S4-...
    (1/2)*s1.*s8.*s11.*(Lag3(18)+Lag3(22)+(Lag3(17)+Lag3(21))*S3)*S4;
%delay differential equation for the rate of change of the males between
%ages 8-11 R2 where Cf2(t-tau_2) is represented by Lag2(10), Df2(t-tau_2) is
%represented by Lag2(14), Cf1(t-tau_2) is represented by Lag2(9),
Df1(t-tau_2) is represented by Lag2(13), Ef2(t-tau_2) is represented by
%Lag2(18), Ff2(t-tau_2) is represented by Lag2(22), Ef1(t-tau_2) is
%represented by Lag2(17), Ff1(t-tau_2) is represented by Lag2(21),
\Cf2(t-tau_3) is represented by Lag3(10), Df2(t-tau_3) is
%represented by Lag3(14), Cf1(t-tau_3) is represented by Lag3(9),
%Df1(t-tau_3) is represented by Lag3(13), Ef2(t-tau_3) is represented by
Lag3(18), Ff2(t-tau_3) is represented by Lag3(22), Ef1(t-tau_3) is
%represented by Lag3(17), and Ff1(t-tau_3) is represented by Lag3(21).
dydt(12)=r1*s1.*s8.*R6*((Lag2(9)+Lag2(13))*R3+Lag2(10)+Lag2(14))*(1-R4)+...
   s1.*s8.*R6*((Lag2(17)+Lag2(21))*R3+Lag2(18)+Lag2(22))*(1-R4)...
   -a2*y(12)...
   -r1*s1.*s8.*s11.*S6*((Lag3(9)+Lag3(13))*S3+Lag3(10)+Lag3(14))*(1-S4)...
   -s1.*s8.*s11.*S6*((Lag3(17)+Lag3(21))*S3+Lag3(18)+Lag3(22))*(1-S4);
%delay differential equation for the rate of change of the males between
%ages 8-11 R3 where Cf1(t-tau_2) is represented by Lag2(9), Df1(t-tau_2) is
%represented by Lag2(13), Cf2(t-tau_2) is represented by Lag2(10),
```

```
%Df2(t-tau_2) is represented by Lag2(14), Ef1(t-tau_2) is represented by
Lag2(17), Ff1(t-tau_2) is represented by Lag2(21), Ef2(t-tau_2) is
%represented by Lag2(18), Ff2(t-tau_2) is represented by Lag2(22),
%Cf1(t-tau_3) is represented by Lag3(9), Df1(t-tau_3) is
%represented by Lag3(13), Cf2(t-tau_3) is represented by Lag3(10),
%Df2(t-tau_3) is represented by Lag3(14), Ef1(t-tau_3) is represented by
%Lag3(17), Ff1(t-tau_3) is represented by Lag3(21), Ef2(t-tau_3) is
%represented by Lag3(18), and Ff2(t-tau_3) is represented by Lag3(22).
%R1 females between 11-12:y(13), R2 females between 11-12:y(14), R2 males between 11-12:y(15), R3 males between 11-12:y(16)%
dydt(13)=s1.*s8.*s11.*r1*(Lag3(9)+Lag3(13))*(1-S3)+...
   s1.*s8.*s11.*(Lag3(17)+Lag3(21))*(1-S3)...
   -a_new*y(13)...
   -s1.*s8.*s11.*s12*r1*(Lag4(9)+Lag4(13))*(1-T3)-...
   s1.*s8.*s11.*s12*(Lag4(17)+Lag4(21))*(1-T3);
%delay differential equation for the rate of change of the females between
%ages 11-12 R1 where Cf1(t-tau_3) is represented by Lag3(9), Df1(t-tau_3) is
%represented by Lag3(13), Ef1(t-tau_3) is represented by Lag3(17),
%Ff1(t-tau_3) is represented by Lag3(21), Cf1(t-tau_4) is represented by
Lag4(9), Df1(t-tau_4) is represented by Lag4(13), Ef1(t-tau_4) is
%represented by Lag4(17), and Ff1(t-tau_4) is represented by Lag4(21).
(1/2)*s1.*s8.*s11.*(Lag3(18)+Lag3(22)+(Lag3(17)+Lag3(21))*S3)*S4...
   -a_new*y(14)...
   -(r1/2)*s1.*s8.*s11.*s12*(Lag4(10)+Lag4(14)+(Lag4(9)+Lag4(13))*T3)*T4-...
   (1/2)*s1.*s8.*s11.*s12*(Lag4(18)+Lag4(22)+(Lag4(17)+Lag4(21))*T3)*T4;
%delay differential equation for the rate of change of the females between
%ages 11-12 R2 where Cf2(t-tau_3) is represented by Lag3(10), Df2(t-tau_3) is
%represented by Lag3(14), Cf1(t-tau_3) is represented by Lag3(9),
%Df1(t-tau_3) is represented by Lag3(13), Ef2(t-tau_3) is represented by
Lag3(18), Ff2(t-tau_3) is represented by Lag3(22), Ef1(t-tau_3) is
%represented by Lag3(17), Ff1(t-tau_3) is represented by Lag3(21),
%Cf2(t-tau_4) is represented by Lag4(10), Df2(t-tau_4) is
%represented by Lag4(14), Cf1(t-tau_4) is represented by Lag4(9),
%Df1(t-tau_4) is represented by Lag4(13), Ef2(t-tau_4) is represented by
%Lag4(18), Ff2(t-tau_4) is represented by Lag4(22), Ef1(t-tau_4) is
%represented by Lag4(17), and Ff1(t-tau_4) is represented by Lag4(21).
```

```
dydt(15)=(r1/2)*s1.*s8.*s11.*(Lag3(10)+Lag3(14)+(Lag3(9)+Lag3(13))*S3)*S4+...
   (1/2)*s1.*s8.*s11.*(Lag3(18)+Lag3(22)+(Lag3(17)+Lag3(21))*S3)*S4...
   -a_new*y(15)...
   -(r1/2)*s1.*s8.*s11.*s12*(Lag4(10)+Lag4(14)+(Lag4(9)+Lag4(13))*T3)*T4-...
   (1/2)*s1.*s8.*s11.*s12*(Lag4(18)+Lag4(22)+(Lag4(17)+Lag4(21))*T3)*T4;
%delay differential equation for the rate of change of the males between
%ages 11-12 R2 where Cf2(t-tau_3) is represented by Lag3(10), Df2(t-tau_3) is
%represented by Lag3(14), Cf1(t-tau_3) is represented by Lag3(9),
%Df1(t-tau_3) is represented by Lag3(13), Ef2(t-tau_3) is represented by
Lag3(18), Ff2(t-tau_3) is represented by Lag3(22), Ef1(t-tau_3) is
%represented by Lag3(17), Ff1(t-tau_3) is represented by Lag3(21),
%Cf2(t-tau_4) is represented by Lag4(10), Df2(t-tau_4) is
%represented by Lag4(14), Cf1(t-tau_4) is represented by Lag4(9),
%Df1(t-tau_4) is represented by Lag4(13), Ef2(t-tau_4) is represented by
Lag4(18), Ff2(t-tau_4) is represented by Lag4(22), Ef1(t-tau_4) is
%represented by Lag4(17), and Ff1(t-tau_4) is represented by Lag4(21).
dydt(16)=r1*s1.*s8.*s11.*S6*((Lag3(9)+Lag3(13))*S3+Lag3(10)+Lag3(14))*(1-S4)+...
   s1.*s8.*s11.*S6*((Lag3(17)+Lag3(21))*S3+Lag3(18)+Lag3(22))*(1-S4)...
   -a_new*y(16)...
   -r1*s1.*s8.*s11.*s12*T6*((Lag4(9)+Lag4(13))*T3+Lag4(10)+Lag4(14))*(1-T4)...
   -s1.*s8.*s11.*s12*T6*((Lag4(17)+Lag4(21))*T3+Lag4(18)+Lag4(22))*(1-T4);
%delay differential equation for the rate of change of the males between
%ages 11-12 R3 where Cf1(t-tau_3) is represented by Lag3(9), Df1(t-tau_3) is
%represented by Lag3(13), Cf2(t-tau_3) is represented by Lag3(10),
Df2(t-tau_3) is represented by Lag3(14), Ef1(t-tau_3) is represented by
%Lag3(17), Ff1(t-tau_3) is represented by Lag3(21), Ef2(t-tau_3) is
%represented by Lag3(18), Ff2(t-tau_3) is represented by Lag3(22),
\Cf1(t-tau_4) is represented by Lag4(9), Df1(t-tau_4) is
%represented by Lag4(13), Cf2(t-tau_4) is represented by Lag4(10),
%Df2(t-tau_4) is represented by Lag4(14), Ef1(t-tau_4) is represented by
Lag4(17), Ff1(t-tau_4) is represented by Lag4(21), Ef2(t-tau_4) is
%represented by Lag4(18), and Ff2(t-tau_4) is represented by Lag4(22).
%R1 females between 12-31:y(17), R2 females between 12-31:y(18), R2 males between 12-31:y(19), R3 males between 12-31:y(20)%
dydt(17)=s1.*s8.*s11.*s12*r1*(Lag4(9)+Lag4(13))*(1-T3)+...
   s1.*s8.*s11.*s12*(Lag4(17)+Lag4(21))*(1-T3)...
   -a_new*y(17)...
   -s1.*s8.*s11.*s12*s31*r1*(Lag5(9)+Lag5(13))*(1-U3)-...
```

```
s1.*s8.*s11.*s12*s31*(Lag5(17)+Lag5(21))*(1-U3);
%delay differential equation for the rate of change of the females between
%ages 12-31 R1 where Cf1(t-tau_4) is represented by Lag4(9), Df1(t-tau_4) is
%represented by Lag4(13), Ef1(t-tau_4) is represented by Lag4(17),
%Ff1(t-tau_4) is represented by Lag4(21), Cf1(t-tau_5) is represented by
%Lag5(9), Df1(t-tau_5) is represented by Lag5(13), Ef1(t-tau_5) is
%represented by Lag5(17), and Ff1(t-tau_5) is represented by Lag5(21).
dydt(18)=(r1/2)*s1.*s8.*s11.*s12*(Lag4(10)+Lag4(14)+(Lag4(9)+Lag4(13))*T3)*T4+...
    (1/2)*s1.*s8.*s11.*s12*(Lag4(18)+Lag4(22)+(Lag4(17)+Lag4(21))*T3)*T4-...
   a_new*y(18)...
   -(r1/2)*s1.*s8.*s11.*s12*s31*(Lag5(10)+Lag5(14)+(Lag5(9)+Lag5(13))*U3)*U4-...
    (1/2)*s1.*s8.*s11.*s12*s31*(Lag5(18)+Lag5(22)+(Lag5(17)+Lag5(21))*U3)*U4;
%delay differential equation for the rate of change of the females between
%ages 12-31 R2 where Cf2(t-tau_4) is represented by Lag4(10), Df2(t-tau_4) is
%represented by Lag4(14), Cf1(t-tau_4) is represented by Lag4(9),
%Df1(t-tau_4) is represented by Lag4(13), Ef2(t-tau_4) is represented by
%Lag4(18), Ff2(t-tau_4) is represented by Lag4(22), Ef1(t-tau_4) is
%represented by Lag4(17), Ff1(t-tau_4) is represented by Lag4(21),
%Cf2(t-tau_5) is represented by Lag5(10), Df2(t-tau_5) is
%represented by Lag5(14), Cf1(t-tau_5) is represented by Lag5(9),
%Df1(t-tau_5) is represented by Lag5(13), Ef2(t-tau_5) is represented by
Lag5(18), Ff2(t-tau_5) is represented by Lag5(22), Ef1(t-tau_5) is
%represented by Lag5(17), and Ff1(t-tau_5) is represented by Lag5(21).
dydt(19)=(r1/2)*s1.*s8.*s11.*s12*(Lag4(10)+Lag4(14)+(Lag4(9)+Lag4(13))*T3)*T4+...
    (1/2)*s1.*s8.*s11.*s12*(Lag4(18)+Lag4(22)+(Lag4(17)+Lag4(21))*T3)*T4-...
   a_new*y(19)...
   -(r1/2)*s1.*s8.*s11.*s12*s31*(Lag5(10)+Lag5(14)+(Lag5(9)+Lag5(13))*U3)*U4-...
    (1/2)*s1.*s8.*s11.*s12*s31*(Lag5(18)+Lag5(22)+(Lag5(17)+Lag5(21))*U3)*U4;
%delay differential equation for the rate of change of the males between
%ages 12-31 R2 where Cf2(t-tau_4) is represented by Lag4(10), Df2(t-tau_4) is
%represented by Lag4(14), Cf1(t-tau_4) is represented by Lag4(9),
%Df1(t-tau_4) is represented by Lag4(13), Ef2(t-tau_4) is represented by
Lag4(18), Ff2(t-tau_4) is represented by Lag4(22), Ef1(t-tau_4) is
%represented by Lag4(17), Ff1(t-tau_4) is represented by Lag4(21),
%Cf2(t-tau_5) is represented by Lag5(10), Df2(t-tau_5) is
%represented by Lag5(14), Cf1(t-tau_5) is represented by Lag5(9),
%Df1(t-tau_5) is represented by Lag5(13), Ef2(t-tau_5) is represented by
%Lag5(18), Ff2(t-tau_5) is represented by Lag5(22), Ef1(t-tau_5) is
%represented by Lag5(17), and Ff1(t-tau_5) is represented by Lag5(21).
```

```
+s1.*s8.*s11.*s12*T6*((Lag4(17)+Lag4(21))*T3+Lag4(18)+Lag4(22))*(1-T4)...
   -a_new*y(20)...
   -r1*s1.*s8.*s11.*s12*s31*U6*((Lag5(9)+Lag5(13))*U3+Lag5(10)+Lag5(14))*(1-U4)...
   -s1.*s8.*s11.*s12*s31*U6*((Lag5(17)+Lag5(21))*U3+Lag5(18)+Lag5(22))*(1-U4);
%delay differential equation for the rate of change of the males between
%ages 12-31 R3 where Cf1(t-tau_4) is represented by Lag4(9), Df1(t-tau_4) is
%represented by Lag4(13), Cf2(t-tau_4) is represented by Lag4(10),
%Df2(t-tau_4) is represented by Lag4(14), Ef1(t-tau_4) is represented by
%Lag4(17), Ff1(t-tau_4) is represented by Lag4(21), Ef2(t-tau_4) is
%represented by Lag4(18), Ff2(t-tau_4) is represented by Lag4(22),
%Cf1(t-tau_5) is represented by Lag5(9), Df1(t-tau_5) is
%represented by Lag5(13), Cf2(t-tau_5) is represented by Lag5(10),
\mbox{Df2(t-tau_5)} is represented by Lag5(14), Ef1(t-tau_5) is represented by
Lag5(17), Ff1(t-tau_5) is represented by Lag5(21), Ef2(t-tau_5) is
%represented by Lag5(18), and Ff2(t-tau_5) is represented by Lag5(22).
%R1 females between 31+:y(21), R2 females between 31+:y(22), R2 males between 31+:y(23), R3 males between 31+:y(24)%
s1.*s8.*s11.*s12*s31*(Lag5(17)+Lag5(21))*(1/(1+Lag5(9)+Lag5(13)+Lag5(17)+Lag5(21)))...
   -a3*y(21);
%delay differential equation for the rate of change of the females between
%ages 31+ R1 where Cf1(t-tau_5) is represented by Lag5(9), Df1(t-tau_5) is
%represented by Lag5(13), Ef1(t-tau_5) is represented by Lag5(17), and
%Ff1(t-tau_5) is represented by Lag5(21).
dydt(22)=(r1/2)*s1.*s8.*s11.*s12*s31*(Lag5(10)+Lag5(14)+(Lag5(9)+Lag5(13))*U3)*U4+...
   (1/2)*s1.*s8.*s11.*s12*s31*(Lag5(18)+Lag5(22)+(Lag5(17)+Lag5(21))*U3)*U4...
   -a3*y(22);
%delay differential equation for the rate of change of the females between
%ages 31+ R2 where Cf2(t-tau_5) is represented by Lag5(10), Df2(t-tau_5)
%is represented by Lag5(14), Cf1(t-tau_5) is represented by Lag5(9),
%Df1(t-tau_5) is represented by Lag5(13), Ef2(t-tau_5) is represented by
Lag5(18), Ff2(t-tau_5) is represented by Lag5(22), Ef1(t-tau_5) is
%represented by Lag5(17), and Ff1(t-tau_5) is represented by Lag5(21).
dydt(23)=(r1/2)*s1.*s8.*s11.*s12*s31*(Lag5(10)+Lag5(14)+(Lag5(9)+Lag5(13))*U3)*U4+...
   (1/2)*s1.*s8.*s11.*s12*s31*(Lag5(18)+Lag5(22)+(Lag5(17)+Lag5(21))*U3)*U4...
```

-a3*y(23);

%delay differential equation for the rate of change of the males between %ages 31+ R2 where Cf2(t-tau_5) is represented by Lag5(10), Df2(t-tau_5) %is represented by Lag5(14), Cf1(t-tau_5) is represented by Lag5(9), %Df1(t-tau_5) is represented by Lag5(13), Ef2(t-tau_5) is represented by %Lag5(18), Ff2(t-tau_5) is represented by Lag5(22), Ef1(t-tau_5) is %represented by Lag5(17), and Ff1(t-tau_5) is represented by Lag5(21).

dydt(24)=r1*s1.*s8.*s11.*s12*s31*U6*((Lag5(9)+Lag5(13))*U3+Lag5(10)+Lag5(14))*(1-U4)...
+s1.*s8.*s11.*s12*s31*U6*((Lag5(17)+Lag5(21))*U3+Lag5(18)+Lag5(22))*(1-U4)...
-a3*y(24);

%delay differential equation for the rate of change of the males between %ages 31+ R3 where Cf1(t-tau_5) is represented by Lag5(9), Df1(t-tau_5) %is represented by Lag5(13), Cf2(t-tau_5) is represented by Lag5(10), %Df2(t-tau_5) is represented by Lag5(14), Ef1(t-tau_5) is represented by %Lag5(17), Ff1(t-tau_5) is represented by Lag5(21), Ef2(t-tau_5) is %represented by Lag5(18), and Ff2(t-tau_5) is represented by Lag5(22).

 $\mbox{\ensuremath{\mbox{\scriptsize M}}} This is a function file that maintains the system histories.$

%In this case we are assigning constant values to the variable histories.

hist_1 = 5; %this is the history of the females between ages 0-1 population from R1 hist_2 = 5; %this is the history of the females between ages 0-1 population from R2 hist_3 = 5; %this is the history of the males between ages 0-1 population from R2 hist_4 = 5; %this is the history of the males between ages 0-1 population from R3

```
hist_5 = 5;
              \%this is the history of the females between ages 1-8 population from R1
hist_6 = 5;
              %this is the history of the females between ages 1-8 population from R2
hist_7 = 5;
              %this is the history of the males between ages 1-8 population from R2
hist_8 = 5;
              %this is the history of the males between ages 1-8 population from R3
               %this is the history of the females between ages 8-11 population from R1
hist_9 = 5;
hist_10 = 3.5; %this is the history of the females between ages 8-11 population from R2
hist_11 = 2;
               \%this is the history of the males between ages 8-11 population from R2
hist_12 =2;
               \%this is the history of the males between ages 8-11 population from R3
hist_13 = 5;
               %this is the history of the females between ages 11-12 population from R1
hist_14 = 3.5; %this is the history of the females between ages 11-12 population from R2
              %this is the history of the males between ages 11-12 population from R2
hist 15 = 2:
hist_16 = 2;
             %this is the history of the males between ages 11-12 population from R3
hist_17 = 2.5; %this is the history of the females between ages 12-31 population from R1
hist_18 = 1.5; %this is the history of the females between ages 12-31 population from R2
hist_20 = 1;
             %this is the history of the males between ages 12-31 population from R3
hist_21 = 2.5; %this is the history of the females between ages 31+ population from R1
hist_22 = 1.5; %this is the history of the females between ages 31+ population from R2
hist_23 = 1;
             %this is the history of the males between ages 31+ population from R2
hist_24 = 1; %this is the history of the males between ages 31+ population from R3
```

s = [hist_1; hist_2; hist_3; hist_4; hist_5; hist_6; hist_7; hist_8; hist_9; hist_10; hist_11; hist_12;
hist_13; hist_14; hist_15; hist_16; hist_17; hist_18; hist_19; hist_20; hist_21; hist_22; hist_23; hist_24];
%This puts all the histories into a column vector and names it s. This is
%the format that dde23 would like it to be in.

References

- [Brauer and Castillo-Chavez, 2001] Brauer, F. and Castillo-Chavez, C. (2001). *Mathematical Models in Population Biology* and *Epidemiology*, chapter Continuous Single-Species Population Models with Delays, pages 95–107. Springer-Verlag, New York.
- [Burden and Faires, 1989] Burden, R. L. and Faires, J. (1989). *Numerical Analysis*, chapter Runge-Kutta Methods, pages 240–247. PWS-KENT, Boston, fourth edition.
- [Helms, 1997] Helms, H. (1997). Introduction to Probability Theory, chapter Continuous Parameter Markov Processes, pages 267–299. W.H. Freeman and Co., New York.
- [Keshet, 2005] Keshet, L. E. (2005). An Introduction to Continuous Models, section Continuous Parameter Markov Processes, pages 115–163. SIAM, Philadelphia.
- [Murray, 2002] Murray, J. (2002). *Mathematical Biology*, section Temperature-Dependent Sex Determination (TSD): Crocodilian Survivorship, pages 119–144. Springer-Verlag, New York, third edition.
- [Roussel, 2004] Roussel, M. (2004). Delay-differential equations. pre-print.
- [Sarre et al., 2004] Sarre, S. D., Georges, A., and Quinn, A. (2004). The ends of a continuum: genetic and temperature-dependent sex determination in reptiles. *BioEssays*, 26(6):639–645.
- [Smith and Webb, 1985] Smith, A. and Webb, G. (1985). *Crocodylus johnstoni* in the mckinley river area, n.t. vii. a population simulation model. *Australian Wildlife Research*, 12:541–554.
- [Smith and Webb, 1987] Smith, A. and Webb, G. (1987). Wildlife Management: Crocodiles and Alligators, chapter Life history parameters, population dynamics, and the management of crocodilians, pages 199–210. Surrey-Beatty, Sydney, third edition.
- [Spotila, 2004] Spotila, J. R. (2004). Sea Turtles: A Complete Guide to Their Biology, Behavior, and Conservation. The Johns Hopkins University Press and Oakwood Arts, Baltimore.
- [Strogatz, 1994] Strogatz, S. H. (1994). Nonlinear Dynamics and Chaos, section Bifurcations, pages 44–92. Perseus Books, Cambridge, MA.
- [Wirkus, 2003] Wirkus, S. (2003). Numerical solutions of differential and delay-differential equations.
- [Woodward and Murray, 1993] Woodward, D. and Murray, J. (1993). On the effect of temperature-dependent sex determination on sex ratio and survivorship in crocodilians. *Biological Sciences*, 253(1344):149–155.