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UNIVERSITY OF ALBERTA

TIME DELAY MODELS OF POPULATION GROWTH WITH STAGE STRUCTURE

BY

WALTER G. AIELLO ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in

Applied Mathematics

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled

Time Delay Models of Population Growth with Stage Structure

submitted by Walter G. Aiello in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Applied Mathematics.

H. I. Freedman

H.I. Freedman
Supervisor

John W. Macki

J.W. Macki

W. Allegretto

W. Allegretto

S. Busenberg

J.C. Holmes

J. So

October 5, 1990
date

DEDICATION

To my father,

who stimulated in me the desire

to better understand the Universe

ABSTRACT

In this thesis we investigate the modelling of stage structured population growth using systems of ordinary differential equations with time delays. We study four models; stage structured single species growth with constant time delay, competition between two stage structured species, a stage structured predator prey model, and finally, stage structured single species growth with a state dependent time delay. For each system we establish that we have a model that make sense both biologically and mathematically. As well, we investigate the existence and stability of equilibria, and we establish criteria for extinction or nonextinction of a species. For each model we study the global behavior of solutions, and for the predator prey model we look at the possibility of a Hopf bifurcation. Finally we present numerous computer simulations that illustrate the behavior of some of the models.

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CHAPTER I

INTRODUCTION

1.1 Background

Modelling population growth has a long history in mathematics, but the modern developments in the field of population dynamics can be said to have started with the simple model of single-species growth used by Malthus in 1798,

$$\dot{x}(t) = gx(t)$$

where g is a constant. This very simple expression, which is still utilized by some even today, suffers from the obvious deficiency of unrestrained, unlimited growth. Observing that the mathematical expression for the model should reflect competition for space and food, Verhulst in 1838 proposed the logistic equation,

$$\dot{x}(t) = gx(t) - dx^2(t) \tag{1.1}$$

to more realistically describe single-species growth. Here the constant g represents the intrinsic growth rate of the species, and d represents the logistic death rate. This differential equation has a stable equilibrium at the point $K = g/d$, and populations with $x(0) > K$ decrease monotonically to K, while those with $x(0) < K$ increase monotonically to K. Those populations for which $x(0) = K$ remain at K. The constant K is called the carrying capacity of the environment since, when the population is at this level, the ability of the environment to sustain increased numbers is exhausted, and the total number of births into the population is matched by the total number of deaths.

Then in the 1920's Lotka (1925) and Volterra (1927) independently considered a model for predator-prey interactions. In this model, prey growth was Malthusian but the growth rate was reduced by a factor proportional to the predator density. The predator growth rate was proportional to the prey density, and the predator death rate was constant; in the absence of prey the predator population would decrease exponentially to zero. The Lotka-Volterra predator-prey model was expressed as,

$$\begin{aligned} \dot{x} &= \alpha x - \beta x y \\ \dot{y} &= \delta x y - \gamma y \qquad \alpha, \beta, \gamma, \delta > 0 \end{aligned} \tag{1.2}$$

For initial conditions $x(0) > 0$ and $y(0) > 0$ all solutions of equation (1.2) are periodic, and the solution $(x(t), y(t)) \equiv (\gamma/\delta, \alpha/\beta)$ is a center interior equilibrium. This would seem to indicate that predator-prey systems are inherently periodic, an observation that seems to be well-known by zoologists and to be corroborated by trapping records kept by the Hudson's Bay Company (cited in Gilpin, 1973), and by field reports (cited in Gilpin, 1973).

The Lotka-Volterra system (1.2) has the disadvantage of oversimplification; all solutions except the equilibrium are periodic with period $\theta > 0$. Thus in 1967 Samuelson modified system (1.2) to include increasing and decreasing returns, whereby the growth rate of a species is either augmented or decremented by increased population density. In the case of increasing returns, interior nonequilibrium solutions spiral away from the interior equilibrium, and interior nonequilibrium solutions of the system with decreasing returns spiral inward toward the equilibrium.

Thus far, the systems we have discussed have solutions that are either periodic, or are of such a nature that no solution that does not start at the interior equilibrium is periodic. As well, the Lotka-Volterra model and the model with increasing returns both suffer the fault of Malthusian growth of the prey in the absence of a predator. The systems with increasing returns also suffer the obvious deficiency of unlimited growth of both prey and predator.

In 1967 Samuelson, and more recently in 1975 Freedman and Waltman (1975a, 1975b) proposed a more realistic perturbed model,

$$\begin{aligned} \dot{x}(t) &= \alpha x - \beta xy - \varepsilon f_1(x,y) \\ \dot{y}(t) &= \delta xy - \gamma y - \varepsilon f_2(x,y) \end{aligned} \tag{1.3}$$

where ε, f_1, and f_2 satisfied conditions that gave the system increasing returns for values near the equilibrium point and decreasing returns for values sufficiently distant from the equilibrium. The existence of a stable limit cycle could then be shown using the Poincaré-Bendixon theorem, which is discussed in Coddington and Levison's 1984 book.

A thorough discussion of just what conditions ε, f_1, and f_2 must satisfy in order to give system (1.3) a stable limit cycle is given in Freedman (1987). A more general model of predator-prey population dynamics is the following:

$$\begin{aligned} \dot{x}(t) &= xg(x) - yp(x) \\ \dot{y}(t) &= yq(x) - \gamma y \end{aligned} \tag{1.4}$$

where $g(x)$ is the growth rate of prey in the absence of predators and $p(x)$ is the predator response function for y with respect to the particular prey x. This system, as well as the even more generalized Kolmogorov model, is discussed by Freedman in his 1987 book.

Lotka's and Volterra's concept for modelling single species growth has also been applied to systems of competing species. For example, the system

$$\begin{aligned} \dot{x}_1(t) &= \alpha_1 x_1 - \alpha_1 x_1^2/k_1 - \beta_1 x_2 \\ \dot{x}_2(t) &= \alpha_2 x_2 - \alpha_2 x_2^2/k_2 - \beta_2 x_1 \end{aligned} \tag{1.5}$$

is an example of a competition model where each species in the absence of the other demonstrates logistic growth. If an interior equilibrium exists, it can be either globally asymptotically stable, or an unstable saddle point. If it is unstable, all solutions approach one of the two boundary equilibria $(k_1, 0)$ or $(0, k_2)$ except those on the separatrix Γ formed by the stable manifold of the interior equilibrium. If no interior equilibrium exists, all nonboundary solutions approach $(k_1, 0)$ or they all approach $(0, k_2)$, depending on the parameters.

One can also consider three dimensional systems of two competitors and a predator. A Lotka-Volterra example would be,

$$\begin{aligned} \dot{x}_1(t) &= x_1(h_1 - a_{11}x_1 - a_{12}x_2 - p_1 y) \\ \dot{x}_2(t) &= x_2(h_2 - a_{21}x_1 - a_{22}x_2 - p_2 y) \\ \dot{y}(t) &= y(-s + c_1 p_1 x_1 + c_2 p_2 x_2) \end{aligned} \tag{1.6}$$

In this model, the two prey species x_1 and x_2 display logistic growth in the absence of the other prey and the predator. For there to exist a stable interior equilibrium, there must exist a stable competition equilibrium $(\widehat{x}_1, \widehat{x}_2, 0)$ such that $c_1 p_x \hat{x}_1 + c_2 p_2 \hat{x}_2 > s$ holds. If $c_1 p_1 \hat{x}_1 + c_2 p_2 \hat{x}_2 \leq s$ the predator cannot survive on the available prey, and if the interior competition equilibrium were not stable, one of the prey would go extinct.

However, by making the predator response constants p_1 and p_2 into suitable functions of x_1 and x_2 it is possible to stabilize a bistable competition equilibrium by predator switching. As the numbers of a given prey species decreases, the predator can switch to the other prey, allowing the first prey to replenish itself.

All of the population dynamics models discussed thus far suffer the inadequacy that they assume the birth and death processes to be age independent. Lotka and Sharpe in 1911, and McKendrick in 1926 formulated models where the birth and death processes were linear functions of population densities and of age. Such models as were developed in this period were linear; they did not consider crowding or other environmental constraints.

One such age-dependent model that arises out of work done by Lotka (1925) and Von Foerster (1959) is given by the system

$$X(t) = \int_0^\infty \rho(a,t)da \tag{17a}$$

$$D\rho(a,t) + \gamma(a)\rho(a,t) = 0 \tag{17b}$$

$$\rho(0,t) = \int_0^\infty b(a)\rho(a,t)da. \tag{17c}$$

Equation 17a simply states that $X(t)$, the total population at a given time t, is the sum total of the populations $\rho(a,t)$ of members of the species in the age interval $(a, a + da)$.

In addition there is a death function $d(a,t)$ giving the number of individuals of age a who die per unit time t. One can then assume that $d(a,t) = \gamma(a)\rho(a,t)$, where $\gamma(a)$ is a death rate for individuals of age a per unit population at age a. With this model the rate at which the number of individuals of age a at time t changes with time, plus the number of individuals $d(a,t)$ per unit age and time who die at time t, must equal zero. This relationship gives us that

$$D\rho(a,t) = \lim_{h\to 0} \frac{1}{h}(\rho(a+h,t+h) - \rho(a,t)) = -d(a,t)$$

which is just equation (17b).

As well, there is a birth function $b(a)$ which gives the average number of immatures produced per unit time by an individual of age a. The total number of births at time t is then expressed by equation 17c.

The system (1.7a, 1.7b, and 1.7c), when combined with the initial condition $\rho(a,0) = \phi(a)$ constitute what is called the Lotka-Von Foerster model. Note that equation (1.7c) will not hold at $t = 0$ unless the initial function $\phi(a)$ satisfies the compatibility criterion that the initial data be consistent with the birth process.

In 1974 Gurtin & MacCamy generalized this model to correct the deficiency that the birth and death processes were independent of total population.

The Gurtin-MacCamy model became,

$$\begin{aligned} &D\rho(a,t) + \gamma(a,X)\rho(a,t) = 0 \\ &X(t) = \int_0^\infty \rho(a,t)da \\ &\rho(0,t) = \int_0^\infty b(a,X)\rho(a,t)da \end{aligned} \tag{1.8}$$

coupled with the initial condition $\rho(a,0) = \phi(a)$. Gurtin and MacCamy gave sufficient conditions for existence and uniqueness of solutions, and gave necessary and sufficient conditions for the existence of an equilibrium solution $\rho(a,t)$ independent of time. The stability of such solutions was also discussed.

Then in 1983 Gyllenberg considered a more general model that included several previous extensions to the Lotka-Von Foerster model. He gave a criterion for local asymptotic stability of equilibrium solutions and then applied his results to the Gurtin-MacCamy model, and also to models considered by Rorres in 1979, and to a previous model of his own (Gyllenberg, 1981, 1982).

Also in 1983 Gurney, Nisbet and Lawton analyzed a lumped age class model based on the Lotka-Von Foerster model that avoided the mathematical intractability of the continuous model, and illustrated its use as applied to Nicholson's famous blowflies (1954, 1957) and to Pielou's larval competition model of the Indian mealmoth (1969).

In the 1985 work of Nisbet, Blythe and Gurney and of Murphy in 1983, some stage-structured models where development in any stage depends not only on age, but on other factors such as size were discussed.

Another development of the Lotka-Von Foerster model of stage-structured growth was done by Zachmann in 1987. His model applied to population where no individual lives past age $a = L$ and where immature individuals of age $0 < a < L^* < L$ are cannibalized by older individuals of age $L^* < a < L$. Some results concerning existence and uniqueness of equilibrium solutions were obtained.

Thus one branch of development of the study of stage-structured growth of populations has developed out of the Lotka-Von Foerster model using integral equations. However these models are characterized by a degree of mathematical intractability that precludes all but a fairly restricted analysis. Another direction the modeling of population dynamics has taken has been from Verhulst's logistic growth equation using differential rather than integral equations. Coleman (1979) and Coleman, Hseih and Knowles (1979) analysed a model where both the intrinsic growth rate g and the carrying capacity $K = g/d$ in equation (1.1) both vary with time. Further in this direction, Arrigoni and Steiner in 1985 obtained some results in the area of fluctuating environments by explicitly solving the logistic equation

$$\dot{x}(t) = g(t)x(t)(1 - x^n(t)/K)$$

which incorporates not only a time dependent growth coefficient but a generalized nonlinearity as well.

In another investigation into nonlinear forms of the logistic equation, in 1973 Gilpin and Ayala investigated the theta-selection model

$$\dot{x}(t) = gx(t)\left[1 - \left(\frac{x(t)}{K}\right)^{\theta}\right]$$

which was used to simulate the growth of *Drosophila* populations. This theta-selection model was further investigated by Gilpin, Case, and Ayala in 1976, by Mueller and Ayala in 1981, and by Rosen in 1987.

These models which were developed from the logistic equation that we have discussed thus far do not incorporate stage-structure into the system, nor do they take into account such factors as gestation or time to maturity. For this reason time delays were introduced into the logistic equation to give a retarded functional differential equation. The delay logistic equation

$$\dot{x}(t) = gx(t)\left[1 - \frac{x(t-\tau)}{K}\right]$$

is known as Hutchinson's equation, and has served as the basis for several models of single species growth. Wright in 1955, Kakutani and Markus in 1958, Jones in 1962, and May in 1973 have all contributed to the investigation of Hutchinson's equation. A generalized form of Hutchinson's equation where both the growth rate g and the time delay τ are functions of time was considered in 1988 by Zhang and Gopalsamy, where sufficient conditions for oscillation and nonoscillation of solutions were obtained. In another development in the area of generalizations of Hutchinson's equation, Aiello (1990) obtained sufficient conditions for nonoscillatory solutions of a nonlinear form of the retarded logistic equation to exist.

We see that, in general, the study of population dynamics models has been characterised by the use of integral equations with their flexibility, generality, and mathematical intractability, or by application of ordinary differential equations with their relative mathematical simplicity and restrictiveness.

1.2 Thesis Outline

In an attempt to achieve the generality gained by including stage structure into the model yet retain enough mathematical simplicity to enable us to do a thorough analysis of the model, we propose a stage structure model of single-species growth that assumes the species to be divided into immatures and matures. The mathematical expression of the model consists of two equations, one for the rate of change of growth of the immatures, the other for the matures. The model assumes a constant time τ required for a newly born individual to join the mature population from the immature population. The birth rate is a constant function of numbers of mature individuals; in that respect the number of immatures born depends only on the number of matures present. The death rate of immatures is a constant, while the death rate of matures is logistic. The only way a new mature individual can appear is for an immature individual who has survived for time τ to move from the immature to the mature population.

Thus we simplify the general Lotka-Von Foerster model into two retarded functional differential equations in two unknowns giving an expression modelling a single species population divided into two stages, immature and mature. A thorough analysis of this system is carried out in chapter two. In chapter three, we apply this model to two competitive populations, each divided into immatures and matures. In chapter four another four variable model is investigated that describes populations of predator and prey, each divided into matures and immatures. For this predator-prey model, we must use a system of integro-differential equations which is equivalent to a five varaiable system of retarded functional differential equations. In chapter five we consider a single-species model with a state-dependent time delay.

CHAPTER II

SINGLE SPECIES GROWTH WITH STAGE STRUCTURE

2.1. Introduction

It is the purpose of this chapter to develop and analyze a model of single-species growth where the individual members of the population have a life history that takes them through two stages, immature and mature. In particular, we have in mind mammalian or bird populations, which exhibit these two distinct stages.

There has been a fair amount of previous work on models of single-species population growth which consider various stages of life history. Stage structure has been introduced into population models in several different ways. For example, Bulmer (1977), Fisher and Goh (1984), and Desharnais and Lin (1987) approached the problem by utilizing discrete models. Continuous models (the approach taken in this thesis) were used by Anderson (1960), Landahl and Hanson (1975), Barclay and Van den Driessche (1980), Gurney, Nisbet and Lawton (1983), Koslesov (1983), Gurney and Nisbet (1985), and Wood, Blythe, Gurney, and Nisbet (1984). A stochastic model was even introduced by Tognetti in 1975.

In the present chapter we develop a continuous model which after time τ consists of two autonomous differential equations, one for each of the life-stages of the population, incorporating a discrete time delay τ representing the time from birth to maturity.

Single-species models consisting of one equation with discrete time delays have been studied extensively. In the earlier stages of the history of single-species models, the work usually involved some numerical analysis, as in Cunningham (1954), Wangersky and Cunningham (1956), and Mazanov (1973), or some simple mathematical analysis, as in Ross (1972) or Stirzaker (1975).

In 1975 Beddington and May gave conditions under which certain models would be stable for all values of the delay, and DeAngelis (1975) and Freedman and Gopalsamy (1986) gave conditions under which the models would remain globally asymptotically stable for all values of the delay. As well, in 1990 Aiello established sufficient conditions for a generalized nonlinear form of the delay logistic equation to have nonoscillatory solutions.

However, in most cases the models exhibit destabilization leading to oscillations as outlined in Kakutani and Markus's 1958 work on Hutchinson's logistic equation and in Caswell (1972), May, Conway, Hassell, and Southwood (1974), MacDonald (1978), Gurney, Blythe and Nisbet (1980), Rosen (1987), Kulenovic and Ladas (1987), and Hsieh (1988) as well.

For our model we will show that under appropriate conditions, there exists a globally asymptotically stable positive equilibrium. We also show that under suitable assumptions on the initial functions, the corresponding solutions are nonoscillatory.

In the next section we develop our model and establish several of its important properties. In section 3 we analyze the equilibria and their stability properties. Section 4 is devoted to the oscillation - nonoscillation question. In section 5 we ascertain how the total carrying capacity behaves as a function of the time delay. We give a brief discussion of our results in section 6.

2.2. Derivation of the Model

Let $x_i(t)$ and $x_m(t)$ denote the concentration of immature and mature populations of a given species respectively. We will assume that these populations are growing in a closed, homogeneous environment. We further assume that the number of mature individuals over a time interval equal to the length of time from birth to maturity is known (either from observation or assumption), and that the immature individuals entering the population during that period enter only as a result of the mature individuals already present giving birth. Let this time interval be $\tau > 0$ and assume that the interval where both populations are known is $-\tau \leq t \leq 0$. We then wish to follow the population dynamics for $t > 0$.

Let $\phi(t)$ be the observed or assumed number of matures present at time t, $-\tau \leq t \leq 0$. Let $x_i(0)$ be the observed value of $x_i(t)$ at time $t = 0$. At this point we note that for the values of t, $-\tau \leq t \leq 0$, we will sometimes write $\phi(t)$ as $x_m(t)$.

We now derive our model. Noting that for t, $-\tau \leq t \leq 0$, $x_m(t) = \phi(t)$ it takes the form,

$$\dot{x}_i(t) = \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau) \tag{2.1}$$

$$\dot{x}_m(t) = \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t), \qquad 0 \leq t \tag{2.2}$$

where "$\cdot$" $= \frac{d}{dt}$, $\alpha, \beta, \gamma > 0$ are constants. This model is derived as follows. We assume that at any time $t > -\tau$ birth into the immature population is proportional to the existing mature population with proportionality constant α. We then assume that the death rate of the immature population is proportional to the existing immature population with proportionality constant γ. We assume for the mature population that the death rate is of a logistic nature, i.e. proportional to the square of the population, with proportionality constant β. Finally we assume that those immatures born at time $t - \tau$, and which survive to time t, exit from the immature population and enter the mature population. This would be computed as follows. If $N(t)$ is a given population at time t, then assuming a constant death rate γ, the number from that group who survive from time t_1 to time t_2 is given by $N(t_2) = N(t_1)e^{-\gamma(t_2 - t_1)}$. Hence if $t_1 = t - \tau$ and $t_2 = t$ then $N(t) = N(t-\tau)e^{-\gamma\tau}$. So given our assumptions on the growth of the immature population, in the time interval $t - \tau$ to t the number of individuals born into the immature population and surviving until time t is given by, $\int_{t-\tau}^{t} \alpha x_m(s)e^{-\gamma(t-s)}ds = \alpha \int_{t}^{t+\tau} x_m(s-\tau)e^{-\gamma(t-s+\tau)}ds$ for $t \geq 0$. Note that when $t = 0$ our assumptions on the initial conditions give us that

$$x_i(0) = \alpha \int_{-\tau} x_m(s)e^{\gamma s}ds = \alpha \int_0^{\tau} x_m(s-\tau)e^{\gamma(s-\tau)}ds \qquad (2.3)$$

which is the total surviving immature population from the observed births on $-\tau \leq t \leq 0$.

Taking $x_i(0)$ from equation (2.3) and assuming $\phi(t)$ is continuous (for mathematical reasons) and nonnegative (for biological reasons), then solutions to systems (2.1)-(2.2) exist and are uniquely continuable for all positive time provided that all solutions are bounded (Driver, 1977).

2.3. Positivity and Boundedness

Now we must establish two important properties of this model, (i) that all solutions are indeed bounded; and for the model to make good biological sense, (ii) that all solutions are nonnegative. In fact we show that if $x_i(0) > 0$ and $x_m(t) > 0$, $-\tau \le t \le 0$, then all solutions are positive for $t > 0$.

Property (i) will follow as a consequence of the global asymptotic stability proved in the next section. Theorem 2.1 below establishes property (ii).

THEOREM 2.1. *Let $x_m(t) > 0$ on $-\tau \le t \le 0$. Then system (2.1)-(2.2) with initial conditions $x_m(t)$ and $x_i(0)$ as given by equation (2.3) has strictly positive solutions for $t > 0$.*

PROOF: We first show that $x_m(t) > 0$ for all $t > 0$. By our assumptions on initial conditions $x_m(0) > 0$, so that by continuity of solutions if $x_m(t) = 0$ for some value of t, then that $t > 0$. Let $t^* = \inf\{t > 0 : x_m(t) = 0\}$. Then

$$\dot{x}_m(t^*) = \alpha e^{-\gamma\tau} x_m(t^* - \tau)$$

so that $\dot{x}_m(t^*) > 0$. Hence for sufficiently small $\varepsilon > 0$, $\dot{x}_m(t^* - \varepsilon) > 0$. But by the definition of t^*, $\dot{x}_m(t^* - \varepsilon) \le 0$ must hold, so we have a contradiction. Hence $x_m(t) > 0$ for all $t > 0$.

Now suppose there exists a $t > 0$ such that $x_i(t) = 0$. Then let $t^* = \inf\{t > 0 : x_i(t^*) = 0\}$. Since $x_i(0) > 0$, by continuity of solutions $t^* > 0$ must be true. So by integrating equation (2.1) we get,

$$\begin{aligned} 0 = x_i(t^*) = e^{-\gamma t^*} x_i(0) + \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma s} x_m(s) ds \\ - \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma s} e^{-\gamma \tau} x_m(s-\tau) ds \end{aligned} \tag{2.4}$$

By substituting from equation (2.3) into equation (2.4) we get the equality,

$$\begin{aligned} \alpha e^{-\gamma t^*} \int_{-\tau}^{0} e^{\gamma s} x_m(s) ds + \alpha e^{\gamma t^*} \int_0^{t^*} e^{\gamma s} x_m(s) ds \\ = \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma (s-\tau)} x_m(s-\tau) ds. \end{aligned} \tag{2.5}$$

Combining the two integrals on the left hand side equation (2.5) becomes,

$$\alpha e^{-\gamma t^*} \int_{-\tau}^{t^*} e^{\gamma s} x_m(s) ds = \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma (s-\tau)} x_m(s-\tau) ds.$$

Then substituting $r = s - \tau$ in the right hand side and then resubstituting s for r we get,

$$\alpha e^{-\gamma t^*} \int_{-\tau}^{t^*} e^{\gamma s} x_m(s) ds = \int_{-\tau}^{t^* - \tau} e^{\gamma s} x_m(s) ds,$$

so that

$$\int_{-\tau}^{t^*} e^{\gamma s} x_m(s) ds = \int_{-\tau}^{t^* - \tau} e^{\gamma s} x_m(s) ds \tag{2.6}$$

must hold. Since $e^{\gamma t} x_m(t) > 0$ for all, equation (2.6) gives us a contradiction. Therefore such a t^* cannot exist and $x_i(t) > 0$ for all $t > 0$ must hold. The theorem is then proved.

Note here that the expression $x_i(t) = \int_{t-\tau}^{t} \alpha x_m(s) e^{-\gamma(t-s)} ds$ is an invariant integral of equation (2.1), with initial conditions $x_i(0) = \alpha \int_{-\tau}^{0} e^{\gamma s} \varphi(s) ds$. Biologically, this expresses the fact that at any time $t > 0$, $x_i(t)$ represents the accumulated survivors of all those immatures born between time $t - \tau$ and time t. This provides another, simpler proof that $x_i(t) > 0$ for $t > 0$.

We remark here that if the initial function $\phi_m(t) > 0$ on $-\tau \leq t \leq 0$, then $x_m(t)$ has a strictly positive lower bound depending on initial conditions. This can be seen as follows. Let $\delta_m = \frac{1}{2} \min\{\inf_{-\tau \leq t \leq 0} \phi_m(t),\ \alpha\beta^{-1}e^{-\gamma\tau}\}$. If we assume the existence of a t^* such that $t^* = \inf_{t>0}\{t : x_m(t) = \delta_m\}$, we see immediately that by continuity of solutions $t^* > 0$ must hold. Then at t^* we have,

$$
\begin{aligned}
\dot{x}_m(t^*) &= \alpha e^{-\gamma\tau} x_m(t^* - \tau) - \beta x_m^2(t^*) \\
&> \alpha e^{-\gamma\tau} \delta_m - \beta \delta_m^2 \\
&\geq \alpha e^{-\gamma\tau} \delta_m - \frac{1}{2} \alpha e^{-\gamma\tau} \delta_m = \frac{1}{2} \alpha e^{-\gamma\tau} \delta_m > 0.
\end{aligned}
$$

Thus $\dot{x}_m(t^*) > 0$, contradicting the definition of t^*. Therefore such a t^* does not exist, and we can conlude that $x_m(t)$ is bounded below by a strictly positive lower bound, depending on initial conditions.

As a final remark regarding our model, we note that the model is similar to the one discussed in Wood, Blythe, Gurney, and Nisbet (1989) in the case of two stages. The main thrust of the work in their paper however is to estimate the death rate (γ in our model).

2.4. Equilibria and their stability

The equilibria for our model are determined by setting $\dot{x}_i = \dot{x}_m = 0$ in system (2.1)-(2.2) and solving the resulting algebraic equations

$$\begin{aligned} &\alpha(1-e^{-\gamma\tau})x_m - \gamma x_i = 0 \\ &\alpha e^{-\gamma\tau}x_m - \beta x_m^2 = 0. \end{aligned} \tag{2.7}$$

There are two nonnegative solutions giving rise to two equilibria, $E_0(0,0)$ and $\hat{E}(\hat{x}_i, \hat{x}_m)$, where

$$\begin{aligned} &\hat{x}_i = \alpha^2\beta^{-1}\gamma^{-1}e^{-\gamma\tau}(1-e^{-\gamma\tau}), \\ &\hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau}. \end{aligned} \tag{2.8}$$

We first show that E_0 is a "saddle point", i.e. it has both positive and negative eigenvalues. To do this, we examine the variational system of system (2.1)-(2.2) about E_0, which takes the form

$$\begin{pmatrix} \dot{u}(t) \\ \dot{v}(t) \end{pmatrix} = \begin{pmatrix} -\gamma & \alpha \\ 0 & 0 \end{pmatrix} \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} + \begin{pmatrix} 0 & -\alpha e^{-\gamma\tau} \\ 0 & \alpha e^{-\gamma\tau} \end{pmatrix} \begin{pmatrix} u(t-\tau) \\ v(t-\tau) \end{pmatrix} \tag{2.9}$$

so that the eigenvalues for the system about E_0 must solve

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\gamma\tau}e^{-\tau\lambda} \\ 0 & \lambda-\alpha e^{-\gamma\tau}e^{-\tau\lambda} \end{vmatrix} = 0.$$

Thus the characteristic equation resulting from the matrix expression (2.9) is

$$(\lambda+\gamma)(\lambda-\alpha e^{-\tau(\lambda+\gamma)}) = 0. \tag{2.10}$$

We immediately see that $\lambda = -\gamma < 0$ is always a negative eigenvalue. To show that there exists a positive eigenvalue, we note that the graphs of $y = \lambda$ and $y = \alpha e^{-\tau(\lambda+\gamma)}$ must intersect at a positive value of λ.

In a similar manner, we could show that $\hat{E}$ is locally asymptotically stable. However, the following theorem gives us a much stronger result, namely that $\hat{E}$ is globally asymptotically stable.

THEOREM 2.2. *Suppose* $x_m(t) > 0$ *on* $-\tau \leq t \leq 0$. *Then* $\lim_{t\to\infty}(x_i(t), x_m(t)) = (\hat{x}_i, \hat{x}_m)$.

PROOF: We prove this result in three steps.

1. First we show that if $x_m(t)$ is eventually monotonic, then $\lim_{t\to\infty} x_m(t) = \hat{x}_m$. Hence, we suppose that there exists $T \geq \tau$ such that $\dot{x}_m(t) > 0$ for $t \geq T$. We can use that $\lim_{t\to\infty} x_m(t) \neq 0$, since $x_m(t)$ has a strictly positive lower bound if $x_m(t) > 0$ on $-\tau \leq t \leq 0$. Further, we can show that $\lim_{t\to\infty} x_m(t) \neq \infty$ since the second equation of system (2.2) can be written as

$$\dot{x}_m(t) = \beta\big[\hat{x}_m x_m(t-\tau) - x_m^2(t)\big], \tag{2.11}$$

and if $x_m(t) \to \infty$ monotonically, then for sufficiently large T, $t \geq T + \tau$, $\dot{x}_m(t) \geq 0$ must hold, but $x_m(t) > \hat{x}_m$ and $x_m(t) \geq x_m(t-\tau)$ implies by equation (2.11) that $\dot{x}_m(t) < 0$, a contradiction.

Thus $\lim_{t\to\infty} x_m(t) = \bar{x}_m$, where $0 < \bar{x}_m < \infty$ and $\lim_{t\to\infty} \dot{x}_m(t) = 0$. Hence from equation (2.11), taking $\lim_{t\to\infty}$, we get that $\bar{x}_m$ must satisfy $\hat{x}_m\bar{x}_m - \bar{x}_m^2 = 0$ and since $\bar{x}_m \neq 0$, then $\bar{x}_m = \hat{x}_m$.

2. Now suppose that $x_m(t)$ is not eventually monotonic. Then there must be either an infinite sequence of maxima greater than $\hat{x}_m$ or an infinite sequence of positive minima less than $\hat{x}_m$, or both. Assume without loss of generality that the former occurs, i.e. there exists a sequence of times $\{t_j\}$, $j = 1, 2, \dots$, such that $t_j \to \infty$ as $j \to \infty$, $t_1 \geq 2\tau$, $x_m(t_j) > \hat{x}_m$, $\dot{x}_m(t_j) = 0$,where $x_m(t_j)$ is a local maximum.

We first show that $\sup\limits_{t \geq t_1} x_m(t) = x_m(t_k)$ for some k. For if not, then there is a subsequence of $\{j\}$ (relabelled as $\{j\}$) such that $x_m(t_j) > x_m(t)$ for $2\tau < t < t_j$, $t_j \to \infty$ as $j \to \infty$. But then from equation (2.11) we get that $\dot{x}_m(t_j) < 0$ contradicting the definition of t_j.

Let $t_k = \sup_{t \geq t_1}(x_m(t))$. Let $s_1 = t_k$. By an analogous argument for the interval $t \geq t_k$, we can find a t_ℓ $(\ell > k)$ such that $\sup\limits_{t_k \leq t} x_m(t) = x_m(t_\ell)$. Let $s_2 = t_\ell$. Similarly we define $s_3, \dots$. The sequence $\{s_j\}$ has the properties that $s_j < s_{j+1}$, $s_j \to \infty$ as $j \to \infty$ and $x_m(s_j) \geq x_m(t)$ for $t > s_j$ (and of course $\dot{x}_m(s_j) = 0$).

Let $y_m(t) = x_m(t) - \hat{x}_m$. Then $\dot{y}_m(s_j) = 0$, and $y_m(s_j) \geq y_m(s_{j+1}) > 0$, $j = 2, 3, \dots$. Then by equation (2.11), we have that

$$0 = \dot{x}_m(s_j) = \beta[\hat{x}_m(y_m(s_j - \tau) + \hat{x}_m) - (y_m(s_j) + \hat{x}_m)^2]$$

so that,

$$\hat{x}_m y_m(s_j - \tau) + \hat{x}_m^2 - y_m^2(s_j) - 2\hat{x}_m y_m(s_j) - \hat{x}_m^2 = 0$$

giving us,

$$\hat{x}_m y_m(s_j - \tau) - y_m^2(s_j) - 2\hat{x}_m y_m(s_j) = 0$$

so that

$$y_m(s_j - \tau) = 2y_m(s_j) + \frac{y_m(s_j)^2}{\hat{x}_m}. \tag{2.12}$$

Hence, from equation (2.12), $y_m(s_j) < \frac{1}{2}y_m(s_j - \tau)$. Since $s_j \to \infty$ as $j \to \infty$, we choose a sub-sequence (again labelled $\{s_j\}$) so that $s_{j+1} - s_j \geq \tau$. Then $y_m(s_j - \tau) \leq y_m(s_{j-1})$, i.e. $y_m(s_j) < \frac{1}{2}y_m(s_{j-1})$. This shows that $y_m(s_j) \to 0$ as $j \to \infty$, proving that $\overline{\lim}_{t\to\infty} x_m(t) = \hat{x}_m$. Similarly $\lim_{t\to\infty} x_m(t) = \hat{x}_m$. Thus $\underline{\lim}_{t\to\infty} x_m(t) = \hat{x}_m$.

3. We now need to show that $\lim\limits_{t\to\infty} x_i(t) = \hat{x}_i$. Let $\varepsilon < \hat{x}_i$ be arbitrary. Choose $T > 2\tau$ so large that $x_m(t) = \hat{x}_m + \theta(t)$ where $|\theta(t)| < \frac{\varepsilon\gamma}{3\alpha(1-e^{-\gamma\tau})}$ when $t \geq T - \tau$. Corresponding to this choice of T, $x_i(T)$ will be determined from the initial condition $x_i(0)$. Choose $T_1 \geq T$ such that $e^{-\gamma t} < \frac{\varepsilon}{3x_i(T)}$ for $t \geq T_1$. Finally choose $T_2 \geq T_1$ such that for $t \geq T_2$, $e^{-\gamma(t-T)} < \frac{\varepsilon}{3\hat{x}_i - \varepsilon}$.

From (2.2) for $t \geq T$,and hence for $t \geq T_2$ we have

$$\begin{aligned}
x_i(t) &= x_i(T)e^{-\gamma(t-T)} + e^{-\gamma(t-T)}\int_T^t e^{\gamma(s-T)}[\alpha x_m(s) - \alpha e^{-\gamma\tau}x_m(s-\tau)]ds \\
&= x_i(T)e^{-\gamma(t-T)} + e^{-\gamma t}\int_T^t e^{\gamma s}[\alpha x_m(s) - \alpha e^{-\gamma\tau}x_m(s-\tau)]ds
\end{aligned}$$

so that for $t \geq T_2$,

$$|x_i(t) - \hat{x}_i| \leq x_i(T)e^{-\gamma(t-T)} + |e^{-\gamma t}\int_T^t e^{\gamma s}[\alpha x_m(s) - \alpha e^{-\gamma\tau}x_m(s-\tau)]ds - \hat{x}_i|.$$

Now $t \geq T_1$ so that $x_i(T)e^{-\gamma(t-\tau)} < \frac{\varepsilon}{3}$. Noting that $x_m(t) = \hat{x}_m + \theta(t)$ we get,

$$\begin{aligned}
|x_i(t) - \hat{x}_i| &\leq \frac{\varepsilon}{3} + |\alpha e^{-\gamma t}\int_T^t e^{\gamma s}[\hat{x}_m + \theta(s) - \hat{x}_m e^{-\gamma\tau} - e^{-\gamma\tau}\theta(s-\tau)]ds - \hat{x}_i| \\
&\leq \frac{\varepsilon}{3} + |\alpha\gamma^{-1}e^{-\gamma t}[(e^{\gamma t} - e^{\gamma T})(\hat{x}_m - \hat{x}_m e^{-\gamma\tau})] - \hat{x}_i| \\
&\quad + |\alpha e^{-\gamma t}\int_T^t e^{\gamma s}(\theta(s) - e^{-\gamma\tau}\theta(s-\tau))ds|.
\end{aligned}$$

Since $t > T$, $\theta(t) < \frac{\varepsilon\gamma}{3\alpha(1-e^{-\gamma\tau})}$ so that

$$\begin{aligned}
|x_i(t) - \hat{x}_i| &\le \frac{\varepsilon}{3} + |\alpha\gamma^{-1}\hat{x}_m(1 - e^{-\gamma(t-T)})(1 - e^{-\gamma\tau}) - \hat{x}_i| \\
&\qquad + |\alpha e^{-\gamma t}\int_T^t e^{\gamma s}\frac{\varepsilon\gamma}{3\alpha(1 - e^{-\gamma\tau})}(1 - e^{-\gamma\tau})ds| \\
&= \frac{\varepsilon}{3} + |\alpha\gamma^{-1}\hat{x}_m(1 - e^{-\gamma(t-T)})(1 - e^{-\gamma\tau}) - \hat{x}_i| \\
&\qquad + |\alpha\gamma^{-1}e^{-\gamma t}(e^{\gamma t} - e^{\gamma T})(\frac{\varepsilon\gamma}{3\alpha(1 - e^{-\gamma\tau})})(1 - e^{-\gamma\tau})|.
\end{aligned}$$

Now, by equations (2.7) we have that $\alpha\gamma^{-1}(1 - e^{-\gamma\tau})\hat{x}_m = \hat{x}_i$, so that

$$\begin{aligned}
|x_i(t) - \hat{x}_i(t)| &\le \frac{\varepsilon}{3} + |\hat{x}_i(1 - e^{-\gamma(t-T)} - \hat{x}_i| + |e^{-\gamma t}(e^{\gamma t} - e^{\gamma T})\frac{\varepsilon}{3}| \\
&= \frac{\varepsilon}{3} + e^{-\gamma(t-T)}\hat{x}_i + \frac{\varepsilon}{3}(1 - e^{-\gamma(t-T)}) \\
&= \frac{\varepsilon}{3} + e^{-\gamma(t-T)}(\hat{x}_i - \frac{\varepsilon}{3}) + \frac{\varepsilon}{3}
\end{aligned}$$

Again since $t > T_2$, $e^{-\gamma(t-T)} < \frac{\varepsilon}{3\hat{x}_i - \varepsilon}$ so that,

$$|x_i(t) - \hat{x}_i| \le \frac{\varepsilon}{3} + \frac{\varepsilon}{3\hat{x}_i - \varepsilon}\cdot\frac{3\hat{x}_i - \varepsilon}{3} + \frac{\varepsilon}{3} = \frac{\varepsilon}{3} + \frac{\varepsilon}{3} + \frac{\varepsilon}{3} = \varepsilon.$$

This proves the theorem.

2.5. Oscillation and nonoscillation of solutions

In this section we consider the question of whether or not solutions may oscillate about the carrying capacity. For our purposes, we say that a solution of system (2.1) - (2.2) *oscillates* or is *oscillatory*, if for any $T > 0$, there exists $t_i, t_m > T$ such that $x_i(t_i) = \hat{x}_i$, $\dot{x}_i(t_i) \neq 0$, and $x_m(t_m) = \hat{x}_m$, $\dot{x}_m(t_m) \neq 0$. If, however, there exists $T > 0$ such that $x_i(t) \neq \hat{x}_i$ and $x_m(t) \neq \hat{x}_m$ for all $t > T$, we say that the solution is *nonoscillatory*. Finally if the solution is such that $x_i(t)$ oscillates and $x_m(t)$ does not, or $x_m(t)$ oscillates and $x_i(t)$ does not, we say that the solution is ***mixed oscillatory - nonoscillatory*** (MON).

Note that as $\tau \to 0$, equations 2.1 and 2.2 tend to,

$$\dot{x}_i(t) = -\gamma x_i(t) \qquad\qquad x_i(0) = x_{i_0}$$

$$\dot{x}_m(t) = \alpha x_m(t) - \beta x_m^2(t), \quad x_m(0) = \phi(0).$$

As $\tau \to 0$, the system uncouples, reflecting the fact that with smaller time delays, the time spent in the immature state shortens, and if $\tau = 0$, the immature stage is skipped and new members of the species go directly into the adult stage. This point is further illustrated by observing what happens to the equilibria as $\tau \to 0$:

$$\lim_{\tau \to 0} \hat{x}_i = \lim_{\tau \to 0} \alpha^2 \beta^{-1} \gamma^{-1} e^{-\gamma\tau}(1 - e^{-\gamma\tau}) = 0$$

$$\lim_{\tau \to 0} \hat{x}_m = \alpha\beta^{-1}.$$

Thus with no time delay the system becomes the classical logistic equation

$$\dot{x}(t) = \alpha x(t) - \beta x^2(t), \quad x(0) = x_0,$$

with equilibrium at $x \equiv 0$ and at $x = \alpha\beta^{-1}$. It is well-known that all solutions of this equation are nonoscillatory.

Our first result for system (2.1) - (2.2) in this regard gives an upper bound on the distance between consecutive times at which $x_m(t)$ can cross $\hat{x}_m$. Let $t^* > \tau$ be such that $x_m(t^*) = \hat{x}_m$ and $\dot{x}_m(t^*) \neq 0$. Without loss of generality, assume $\dot{x}_m(t^*) > 0$ (the analysis for $\dot{x}_m(\tau^*) < 0$ follows analogously). Then, since $0 < \dot{x}_m(t^*) = \beta\hat{x}_m\big[x_m(t^* - \tau) - \hat{x}_m\big]$, we have that $x_m(t^* - \tau) > \hat{x}_m$. But clearly $x_m(t^* - \varepsilon) < \hat{x}_m$ for sufficiently small ε, since $\dot{x}_m(t^*) > 0$. Hence there exists t^{**} with $t^* - \tau < t^{**} < t^*$ such that $x_m(t^{**}) = \hat{x}_m$. Thus by continuity of solutions the following statement is clear.

THEOREM 2.3. *Let $t_1^* < t_2^*$ be such that $x_m(t_1^*) = x_m(t_2^*) = \hat{x}_m$ and $x_m(t) \neq \hat{x}_m$ for $t_1^* < t < t_2^*$. Then $t_2^* - t_1^* < \tau$.*

Note that the above theorem implies that if there were solutions with $x_m(t)$ oscillatory and τ small, then the oscillation would have to be rapid indeed.

Note also that if there is a value of t (say t^*) such that $x_m(t^*) = \hat{x}_m$, then there must also be such a value in every previous interval of time of length τ. From this fact, our next theorem follows directly.

THEOREM 2.4. *Let $\phi(t)$ be such that $\phi(t) \neq \hat{x}_m$ for $-\tau \leq t \leq 0$. Then $x_m(t) \neq \hat{x}_m$ for all $t \geq 0$ (and hence is nonoscillatory).*

This theorem further implies that there exist for system (2.1) - (2.2) either nonoscillatory or MON solutions. Unfortunately, this is as far as we are able to carry out the mathematical analysis at this time. However, Y.-L. Cao (personal communication) has a proof that oscillatory solutions exist, but that the manifolds containing the initial functions which lead to oscillatory solutions is so "thin" that they can never be found numerically.

We originally had a conjecture that all solutions are nonoscillatory.

The computer evidence for this conjecture is illustrated by considering system (2.1) - (2.2) with $\alpha = .5$, $\beta = .3$, $\gamma = .4$, $\tau = 1$, $\hat{x}_i = .460398$, $x_m(0) = \hat{x}_m = 1.1172$, $\phi_m(t) = \hat{x}_m(1 + .9\sin 10\pi t)$, giving $x_m(0) = \hat{x}_m$, (see Fig. 2.1). We see that on $0 \le t \le \tau$, the populations tend to fluctuate considerably. There are minor fluctuations on $\tau \le t \le 2\tau$, and solutions are monotonic for $t > 2\tau$. This is typical for the many computer solutions for a variety of parameter values and fluctuating initial functions. However, as mentioned, oscillatory solutions do exist, but, cannot be found numerically.

2.6. τ-Dependence of total carrying capacity

The x_i and x_m values for the interior equilibrium point $\hat{E}$, for the $\hat{x}_i$ and $\hat{x}_m$, may be thought of as functions of τ. We define the total carrying capacity $K(\tau)$ as

$$K(\tau) = \hat{x}_i(\tau) + \hat{x}_m(\tau). \tag{2.13}$$

We wish to determine how $K(\tau)$ changes with increasing τ. Hence we compute

$$K(\tau) = \frac{\alpha}{\beta\gamma} e^{-\gamma\tau}(\alpha + \gamma - \alpha e^{-\gamma\tau}). \tag{2.14}$$

Note that $K(0) = \alpha/\beta$ and $K(\infty) = 0$. From equation (2.14) we get that

$$\begin{aligned} \frac{d(K(\tau))}{d\tau} &= -\frac{\alpha}{\beta\gamma}\gamma e^{-\gamma\tau}(\alpha + \gamma - \alpha e^{-\gamma\tau}) + \frac{\alpha}{\beta\gamma} e^{-\gamma\tau}(\alpha\gamma e^{-\gamma\tau}) \\ &= \alpha\beta^{-1} e^{-\gamma\tau}(-\alpha - \gamma + \alpha e^{-\gamma\tau}) + \alpha\beta^{-1} e^{-\gamma\tau}(\alpha e^{-\gamma\tau}) \\ &= \alpha\beta^{-1} e^{-\gamma\tau}(2\alpha e^{-\gamma\tau} - \alpha - \gamma). \end{aligned} \tag{2.15}$$

Then, for any given value of τ, $\frac{d(K(\tau))}{d\tau} < 0$ if and only if $2\alpha e^{-\gamma\tau} - \alpha - \gamma < 0$, that is, if and only if $2\alpha e^{-\gamma\tau} < \alpha+\gamma$. This inequality will be true for all values of τ if $\alpha < \gamma$, since then, $2\alpha e^{-\gamma\tau} < 2\alpha < \alpha + \gamma$.

However, if $\alpha > \gamma$, the inequality will be true only for sufficiently large τ, and since $2\alpha e^{-\gamma\tau}$ is strictly monotone decreasing in τ, there will be one and only one value τ^* for which $2\alpha e^{-\gamma\tau^*} = \alpha + \gamma$.

Thus if $\alpha \leq \gamma$, then $\frac{dK}{d\tau} < 0$ and $K(\tau)$ is a strictly decreasing function for all $\tau > 0$. If $\alpha > \gamma$, then $K(\tau)$ is increasing on $0 \leq \tau < \tau^*$ and decreasing for $\tau > \tau^*$, where

$$\tau^* = -\gamma^{-1} \ln\left(\frac{\alpha+\gamma}{2\alpha}\right). \tag{2.16}$$

We compute $K(\tau^*)$ from substituting equation (2.16) into equation (2.14):

$$K(\tau^*) = \frac{(\alpha+\gamma)^2}{4\beta\gamma}. \tag{2.17}$$

Further

$$\frac{K(\tau^*)}{K(0)} = \frac{(\alpha+\gamma)^2}{4\alpha\gamma} > 1 \quad \text{if } \alpha > \gamma.$$

For example, if $\alpha = 2\gamma$, then $K(\tau^*) = \frac{9}{8}K(0)$. Thus if $\alpha > \gamma$, we have an optimal time delay τ^* that maximizes the total population.

One can get a second perspective as to the relevance of τ^* from the point of view of mutation and invasibility. Suppose that a genetic mutation occurs so that only the time delay is affected. Can the mutant strain successfully invade the already established strain?

To analyze this situation, let $x_i(t)$ and $x_m(t)$ represent the strain with time delay τ_1 and $y_i(t)$ and $y_m(t)$ represent the strain with time delay τ_2. Suppose the two strains compete for the same resources and hence satisfy the competitive system

$$\begin{aligned}
\dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau_1} x_m(t-\tau_1) - c_i x_i(t)(y_i(t) + y_m(t)) \\
\dot{x}_m(t) &= \alpha e^{-\gamma\tau_1} x_m(t-\tau_1) - \beta x_m^2(t) - c_m x_m(t)(y_i(t) + y_m(t)) \\
\dot{y}_i(t) &= \alpha y_m(t) - \gamma y_i(t) - \alpha e^{-\gamma\tau_2} y_m(t-\tau_2) - c_i y_i(t)(x_i(t) + x_m(t)) \qquad (2.18) \\
\dot{y}_m(t) &= \alpha e^{-\gamma\tau_2} y_m(t-\tau_2) - \beta y_m^2(t) - c_m y_m(t)(x_i(t) + x_m(t)) \\
& x_i(0) \geq 0, \quad x_m(0) \geq 0, \quad y_i(0) \geq 0, \quad y_m(0) \geq 0,
\end{aligned}$$

where c_i and c_m are the common competition constants.

The linearization of system (2.18) is, where x_i, x_m, y_1, and y_m are understood to be functions of t,

$$\begin{pmatrix} \dot{x}_i \\ \dot{x}_m \\ \dot{y}_i \\ \dot{y}_m \end{pmatrix}$$

$$= \begin{pmatrix} a_1 & \alpha & -c_i x_i & -c_i x_i \\ 0 & a_2 & -c_m x_m & -c_m x_m \\ -c_i y_i & -c_i y_i & a_3 & \alpha \\ -c_m y_m & -c_m y_m & 0 & a_4 \end{pmatrix}$$

$$\times \begin{pmatrix} x_i \\ x_m \\ y_i \\ y_m \end{pmatrix} +$$

$$\begin{pmatrix} 0 & -\alpha e^{-\gamma\tau_1} & 0 & 0 \\ 0 & \alpha e^{-\gamma\tau_1} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} x_i(t-\tau_1) \\ x_m(t-\tau_1) \\ y_i(t-\tau_1) \\ y_m(t-\tau_1) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\alpha e^{-\gamma\tau_2} \\ 0 & 0 & 0 & \alpha e^{-\gamma\tau_2} \end{pmatrix} \begin{pmatrix} x_i(t-\tau_2) \\ x_m(t-\tau_2) \\ y_i(t-\tau_2) \\ y_m(t-\tau_2) \end{pmatrix}.$$

where $a_1 = -\gamma - c_i(y_i + y_m)$, $a_2 = -2\beta x_m - c_m(y_i + y_m)$, $a_3 = -\gamma - c_i(x_i + x_m)$, $a_4 = -2\beta y_m - c_m(x_i + x_m)$.

To test the invasibility, we consider the characteristic matrix about the equilibrium $\widehat{F}_1 = (\hat{x}_i, \hat{x}_m, 0, 0)$, corresponding to (y_i, y_m) attempting to invade the (x_i, x_m) population which is at equilibrium.

At $\hat{F}_1 = (\hat{x}_i, \hat{x}_m, 0, 0)$ we observe that $\hat{x}_i + \hat{x}_m = K(\tau_1)$, and that $\hat{x}_i = \alpha\beta^{-1}e^{-\gamma\tau_1}$. At $\hat{F}_1$ the linearization becomes,

$$\begin{pmatrix} \dot{x}_i \\ \dot{x}_m \\ \dot{y}_i \\ \dot{y}_m \end{pmatrix} = \begin{pmatrix} -\gamma & \alpha & -c_i\hat{x}_i & -c_i\hat{x}_i \\ 0 & -2\beta\hat{x}_m & -c_m\hat{x}_m & -c_m\hat{x}_m \\ 0 & 0 & -\gamma - c_iK(\tau_1) & \alpha \\ 0 & 0 & 0 & -c_mK(\tau_1) \end{pmatrix} \begin{pmatrix} x_i \\ x_m \\ y_i \\ y_m \end{pmatrix} +$$

$$\begin{pmatrix} 0 & -\alpha e^{-\gamma\tau_1} & 0 & 0 \\ 0 & \alpha e^{-\gamma\tau_1} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} x_i(t-\tau_1) \\ x_m(t-\tau_1) \\ y_i(t-\tau_1) \\ y_m(t-\tau_1) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\alpha e^{-\gamma\tau_2} \\ 0 & 0 & 0 & \alpha e^{-\gamma\tau_2} \end{pmatrix} \begin{pmatrix} x_i(t-\tau_2) \\ x_m(t-\tau_2) \\ y_i(t-\tau_2) \\ y_m(t-\tau_2) \end{pmatrix}.$$

so that the characteristic matrix, denoted A_λ works out to be

$$A_\lambda = \begin{bmatrix} \lambda + \gamma & \alpha e^{-(\lambda+\gamma)\tau_1} - \alpha & c_i\hat{x}_i & c_i\hat{x}_i \\ 0 & \lambda + \alpha e^{-\gamma\tau_1}(2 - e^{-\lambda\tau_1}) & c_m\hat{x}_m & c_m\hat{x}_m \\ 0 & 0 & \lambda + \gamma + c_iK(\tau_1) & \alpha e^{-(\lambda+\gamma)\tau_2} - \alpha \\ 0 & 0 & 0 & \lambda - \alpha e^{-(\lambda+\gamma)\tau_2} + c_mK(\tau_1) \end{bmatrix}. \tag{2.19}$$

Since A_λ is diagonal, the eigenvalues of the variational matrix about $\widehat{F}_1$ are

$$\begin{aligned}
&\lambda_1 = -\gamma \\
&\lambda_2, \quad \text{where} \quad \lambda_2 = \alpha e^{-\gamma\tau_1}(e^{-\lambda_2\tau_1} - 2) \\
&\lambda_3 = -\gamma - c_i K(\tau_1) \\
&\lambda_4, \quad \text{where} \quad \lambda_4 = \alpha e^{-(\lambda_4+\gamma)\tau_2} - c_m K(\tau_1).
\end{aligned} \tag{2.20}$$

Now, λ_1 and λ_3 are easily seen to be negative. We then consider λ_2, the roots of the equation $\lambda_2 = \alpha e^{-\gamma\tau_1}(e^{-\lambda_2\tau_1} - 2)$.

Let $\lambda_2 = a + bi$. Then the equation becomes,

$$a + bi = \alpha e^{-\gamma\tau_1}(e^{-a\tau_1}\cos b\tau_1 - ie^{-a\tau_1}\sin b\tau_1 - 2).$$

Separating into real and imaginary parts we get.

$$2\alpha e^{-\tau_1\gamma} + a = ae^{-\gamma\tau_1}e^{-a\tau_1}\cos b\tau_1$$

$$b = -\alpha e^{-\gamma\tau_1}e^{-a\tau_1}\sin b\tau_1$$

squaring and adding,

$$(2\alpha e^{-\gamma\tau_1} + a)^2 + b^2 = (\alpha e^{-\gamma\tau_1}e^{-a\tau_1})^2 .$$

Now suppose $a > 0$. Then

$$(2\alpha e^{-\gamma\tau_1})^2 + b^2 < (2\alpha e^{-\gamma\tau_1} + a)^2 + b^2 = (\alpha e^{-\gamma\tau_1}e^{-a\tau_1})^2 < (\alpha e$$

giving us a contradiction. Therefore all λ_2 have negative real parts.

So the question of whether or not y can invade x is reduced to the question of whether or not there exists any λ_4 with positive real parts.

We now consider the roots of

$$\lambda_4 = \alpha e^{-(\lambda_4+\gamma)\tau_2} - c_m K(\tau_1) \tag{2.21}$$

If $c_m = 0$, we can see by comparing the graphs of $w - \lambda_4$ and $w(\lambda_4) = \alpha e^{(-\lambda_4+\gamma)\tau_2}$ that equation (2.21) has at least one positive real root.

For fixed $c_m > 0$, one could easily visualize cases where if τ_1 is close to τ^*, then $K(\tau_1)$ is close to $K(\tau^*)$ and all λ_4's have negative real parts, but if τ_1 is far from τ^* (higher or lower), then $K(\tau_1)$ is considerably smaller than $K(\tau^*)$ so that some λ_4's have positive real parts. In other words, if $K(\tau_1)$ is close to its maximum value (at $\tau_1 = \tau^*$), the y's could not invade the x's, but away from its maximum value invasion of mutated populations could occur.

2.7. Discussion

In this chapter we have considered a stage-structured population with two life stages, immature and mature, with the time from birth to maturity represented by a constant time delay.

We showed that there exists a globally asymptotically stable equilibrium for this model. That is, all populations with positive initial functions tend to a constant population level, either directly or through an oscillatory process. This extends a similar property for models with only one stage (and no time delay).

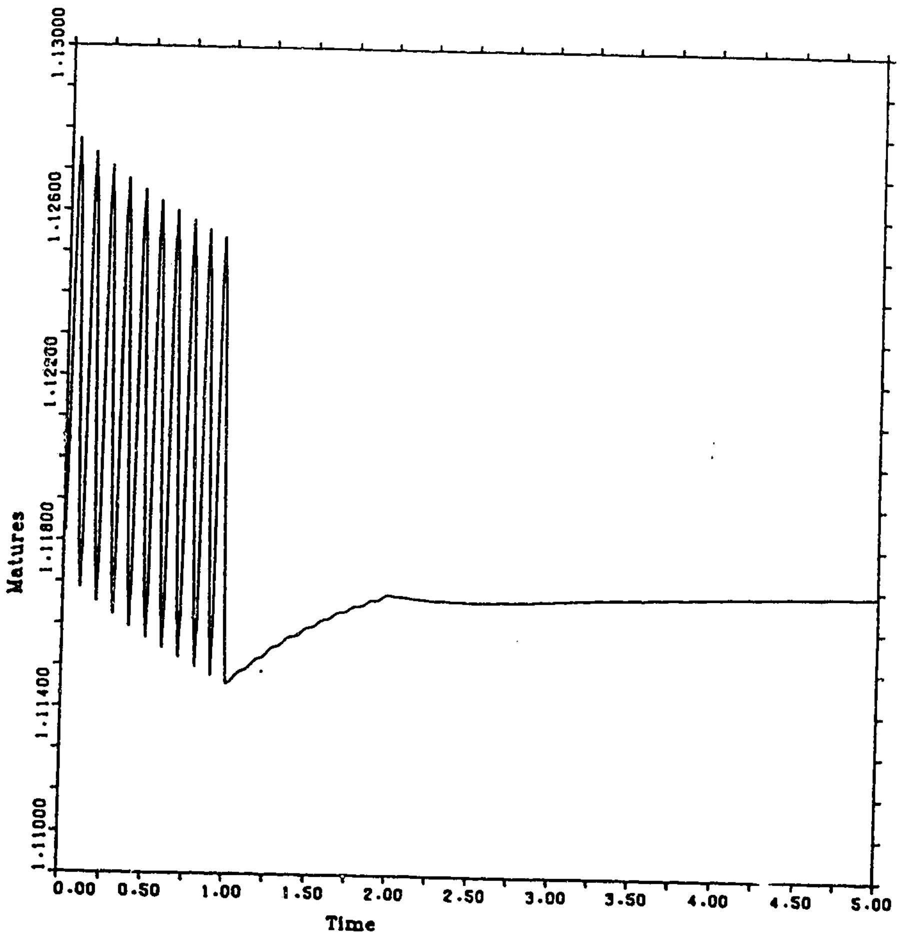
We have given criteria for the model to have nonoscillatory solutions.

We have also defined a total carrying capacity for the population. Under the biologically reasonable assumption that birth rate exceeds the death rate of immatures, we have shown that the carrying capacity reaches a maximum for a certain value of the time to maturity. This may be interpreted as an evolutionary strategy in changing the length of time to maturity so as to maximize the total stable equilibrium population values in a given environment.

In this chapter we have obtained results which both agree and disagree with results obtained in other papers. Our results agree with those authors (see for example the 1975 paper of Beddington and May) who claim that time delays are not necessarily destabilizing, and our results differ (see for example Barclay and Van den Driesshe (1980)) from those authors who observe an oscillation due to time delays.

Some questions which arise from our work need to be addressed. Can the model be extended to include varying times to maturity and will this affect the stability? What is the effect of a predator or a competition on the population? We leave these to future investigations.

Figure 2.1
Single Species Growth With
Oscillatory Initial Function



Single Species Growth Data Set #1

Immature Intrinsic Growth Rate: 0.5
Immature Intrinsic Death Rate: 0.4
Mature Logistic Death Rate: 0.3
Maturation Period: 1.0

Boundary Equilibrium: Xi = 0.4604
Xm = 1.1172

CHAPTER III

COMPETITION MODELS BETWEEN TWO STAGE-STRUCTURED SPECIES

3.1. Introduction

It is the purpose of this chapter to develop and analyse a model of competition between two species, each of whose members pass through an immature and a mature stage of their development.

The simplest competition models are of the Lotka-Volterra type, where species growth depends on the number of individuals present. An example of such a system with two carrying capacities is,

$$\dot{x}_1(t) = x_1(\alpha_1 - \beta_1 x_2 - \gamma_1 x_1)$$

$$\dot{x}_2(t) = x_2(\alpha_2 - \beta_2 x_1 - \gamma_2 x_2)$$

The behavior of this system is very simple. There are four possible equilibria. The origin $E_0 = (0,0)$ is an unstable equilibrium. On the axis there is $E_1 = (\alpha_1/\gamma_1, 0)$ and $E_2 = (0, \alpha_2/\gamma_2)$. As well an interior equilibrium will exist if and only if $\beta_1^{-1}\beta_2^{-1}\gamma_1\gamma_2 \neq 0$ holds. Now, if $\alpha_1\beta_1^{-1} > \alpha_2\gamma_2^{-1}$ and $\alpha_1\gamma_1 < \alpha_2\beta_2^{-1}$ both hold, E_1 and E_2 will repel in the x_2 and x_1 directions, respectively, and the interior equilibrium will be a stable attractor in the first quadrant. However, if $\alpha_1\beta_1^{-1} < \alpha_2\gamma_2^{-1}$ and $\alpha_1\gamma_1 > \alpha_2\beta_2^{-1}$ both hold, E_1 and E_2 will become asymptotically stable and the interior equilibrium will be an unstable saddle. If neither of these conditions hold there will be either a continuum of equilibria connecting E_1 and E_2 or there will be no interior equilibrium.

Much work has been done on this model and its variants, e.g. see Leung (1976), Pielou (1974), and Gopalsamy (1982). Gopalsamy (1982) for example analyzed the Lotka-Volterra competition model when the intrinsic growth rates of both species are periodic functions of time. As well, Lotka-Volterra models in a resource-based competition system have been considered by MacArthur (1970, 1972), by Hsu (1981), by Waltman (1983), and by Gopalsamy (1986).

Competition in a chemostat is another direction of development in this area, including investigations by Freedman, So and Waltman (1986, 1989) that consider chemostat competition with time delays. Keener (1983) is another example of investigation done in the chemostat competition area.

Another investigative area in the field of competitive systems is the more general Kolmogorov model. Some examples of work in this direction can be found in Farkas (1984) and in Farkas and Freedman (1989).

The model that we consider here can be looked upon as another variant of the basic Lotka-Volterra model with logistic growth. Our model is a two-stage structured system that divides each of the competing species into immatures and matures, giving us a four dimensional system of retarded functional differential equations.

In the next section we develop the model and establish that the resulting system is both dissipative and remains nonnegative for appropriate initial conditions. In section three we investigate the equilibria and their stability. Then in section four we analyse the global behavior of solutions. In section five we consider the results of computer simulations of some specific examples that illustrate the behavior of solutions in light of the analysis done in previous sections. We then give a brief discussion of the results in section six.

3.2. Derivation of the model

In chapter two we considered a model for single species growth with stage structure, given by

$$\begin{aligned} \dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau) \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t) \end{aligned}$$

where x_i and x_m represent the immature and mature population densities respectively. In this model we assumed a constant time τ to maturity, and α, β, and y were positive constants.

Here, we assume two competing species, each with stage structure. Hence we consider the system:

$$\begin{aligned} \dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau) \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t) - \delta x_m(t) y_m(t) \\ \dot{y}_i(t) &= \mu y_m(t) - \xi y_i(t) - \mu e^{-\xi\sigma} y_m(t-\sigma) \\ \dot{y}_m(t) &= \mu e^{-\xi\sigma} y_m(t-\sigma) - \eta y_m^2(t) - \rho y_m(t) x_m(t) \end{aligned} \tag{3.1}$$

where x_i and x_m represent population densities of the immature and mature members of the first species, and y_i and y_m represent population densities of immature and mature members of the second species. We assume that the pressure of competition is felt only by the adults of each species. This is rarely true but is valid in some special cases, for example, where the immatures are protected by the adults as is the case with some birds and their nestlings with breeding and feeding territories.

$\alpha > 0$ and $\mu > 0$ represent the intrinsic growth rates of the competing species, $\gamma > 0$ and $\xi > 0$ represent the intrinsic death rates of the immature populations, and $\beta > 0$ and $\eta > 0$ represent the logistic death rates of the mature populations. Each of the two species has a different maturation period, represented by $\tau > 0$ for the first species and by $\sigma > 0$ for the second. The competition between the two species is represented by $\delta > 0$ and $\rho > 0$, where $\delta > 0$ is the intrinsic competition rate that a unit population density of the second species adults imposes on the first species adults, and $\rho > 0$ is the intrinsic competition rate that a unit population density of first species adults imposes on the second species adults.

As was noted in chapter 2, $x_i(t)$ and $y_i(t)$ can be expressed in integral form, $x_i(t) = \alpha \int_{t-\tau}^{t} e^{-\gamma(t-s)} x_m(s)ds$ and $y_i(t) = \mu \int_{t-\sigma}^{t} e^{-\xi(\sigma-s)} y_m(s)ds$.

We shall say that a set of initial conditions $\varphi_i(0), \varphi_m(t), \phi_i(0), \phi_m(t))$, where φ_m and ϕ_m are defined on the interval $[-\tau, 0]$ and on $[-\sigma, 0]$ respectively, is admissible if $\varphi_i(0) > 0$ and $\phi_i(0) > 0$, if $\varphi_m(t) > 0$ and $\phi_m(t) > 0$ on $[-\tau, 0]$ and on $[-\sigma, 0]$ respectively, and if $\varphi_m(t)$ and $\phi_m(t)$ are continuous on the closed interval $[-\tau, 0]$ and $[-\sigma, 0]$ respectively. The derivatives at the left and right endpoints are taken from the right and left, respectively.

For a set of initial conditions to be admissible we further require that $\varphi_i(0)$ and $\phi_i(0)$ also satisfy,

$$\varphi_i(0) = \int_{-\tau}^{0} \alpha\varphi_m(s)e^{\gamma s}ds \text{ and } \phi_i(0) = \int_{-\sigma}^{0} \mu\phi_m(s)e^{-\xi s}ds$$

so that at any given time $t \geq 0$, $x_i(t)$ and $y_i(t)$ will represent the accumulated survivors of those born into the immature population in the time intervals $[t-\tau, t]$ and $[t-\sigma, t]$, respectively.

Now given an admissible set of initial conditions for system (3.1), let there exist a point t_0, where $t_0 = \inf_{t>0}\{t : x_m(t) = 0\}$. Then we have

$$\dot{x}_m(t_0) = \alpha e^{-\gamma\tau}x_m(t_0 - \tau) > 0$$

by definition of t_0. This gives us a contradiction, thus $x_m(t) > 0$ for $t > 0$. One can similarly conclude that $y_m(t) > 0$ for $t > 0$ also holds.

Then using the same arguments we used in the previous chapter for the single species case, we can conclude that $x_i(t) > 0$ and $y_i(t) > 0$ for $t > 0$. We have proved the following

THEOREM 3.1. *Given an admissible set of initial conditions, solutions to system (3.1) will always remain positive.*

Next we note that $\dot{x}_m(t) \leq \alpha e^{-\gamma\tau}x_m(t-\tau) - \beta x_m^2(t)$, and since we showed in Chapter 2 that solutions to the equation $\dot{w}(t) = \alpha e^{-\gamma\tau}w(t-\tau) - \beta w^2(t)$ are bounded above, we can apply a comparison theorem (Birkhoff and Rota (1969)) to conclude that $x_m(t)$ and $y_m(t)$ are both bounded above. Again, the proof that $x_i(t)$ and $y_i(t)$ are bounded above is virtually the same as for the single species case. Thus we have proved the following

THEOREM 3.2. *Given an admissible set of initial conditions, solutions to system (3.1) are bounded above.*

In fact, we can say more about the boundedness of solutions to system (3.1) in that we can set bounds to the system that are independent of the initial function:

THEOREM 3.3. *Given an admissible set of initial conditions, system (3.1) is dissipative.*

PROOF: Set $z(t) = x_i(t) + x_m(t)$. Then

$$\dot{z}(t) = \alpha x_m(t) - \gamma x_i(t) - \beta x_m^2(t) - \delta x_m(t) y_m(t).$$

Since $\delta > 0$, and by Theorem 3.1, $x_m(t) > 0$ and $y_m(t) > 0$ it follows that

$$\begin{aligned}\dot{z}(t) &< \alpha x_m(t) - \gamma x_i(t) - \beta x_m^2(t) \\ &= -\gamma z(t) + (\alpha + \gamma) x_m(t) - \beta x_m^2(t)\end{aligned}$$

The last two terms of this expression satisfy the inequality,

$$(\alpha + \gamma) x_m - \beta x_m^2 \leq \frac{(\alpha + \gamma)^2}{4\beta}$$

the maximum value being attained when $x_m = \frac{\alpha+\gamma}{2\beta}$. Thus we have the relation,

$$\dot{z}(t) < -\gamma z(t) + (\alpha + \gamma)^2 / 4\beta$$

and applying a comparison theorem (Birkhoff and Rota (1969)) and integrating we get

$$z(t) \leq z(0)e^{-\gamma t} + (\alpha+\gamma)^2/4\beta\gamma.$$

Using exactly the same procedure for $w(t) = y_i(t) + y_m(t)$ we get,

$$w(t) \leq w(0)e^{-\xi t} + \frac{(\mu+\xi)^2}{4\eta\xi}.$$

So, as t tends toward infinity, there is a bounded attracting region in the positive cone, towards which all solutions tend, which is independent of initial conditions. Therefore system (3.1) is dissipative, proving the theorem.

3.3. Stability and Existence of Equilibria

There are three types of equilibria, one at the origin denoted $E_0(0,0,0,0)$, two boundary equilibria, denoted $\hat{E}_x(\hat{x}_i, \hat{x}_m, 0, 0)$ and $\hat{E}_y(0,0,\hat{y}_i,\hat{y}_m)$, and finally at most one interior equilibrium denoted by $\tilde{E}(\tilde{x}_i, \tilde{x}_m, \tilde{y}_i, \tilde{y}_m)$.

The boundary equilibria represent the states when one of the competitors exists without the other. As we have seen in the previous section each of the two species represented has a globally asymptotically stable equilibrium point in its plane. Thus

$$\hat{x}_i = \alpha^2\beta^{-1}\gamma^{-1}e^{-\gamma\tau}(1-e^{-\gamma\tau}),\ \hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau}$$

and

$$\hat{y}_i = \mu^2\eta^{-1}\xi^{-1}e^{-\xi\sigma}(1-e^{-\xi\sigma}),\ \hat{y}_m = \mu\eta^{-1}e^{-\xi\sigma}$$

for the boundary equilibria $\hat{E}_x(\hat{x}_i, \hat{x}_m, 0, 0)$ and $\hat{E}_y(0,0,\hat{y}_i,\hat{y}_m)$.

If an interior equilibrium did exist, it would have to satisfy the following system:

$$0 = \alpha x_m - \gamma x_i - \alpha e^{-\gamma\tau} x_m \tag{3.2a}$$

$$x_m = \alpha\beta^{-1} e^{-\gamma\tau} - \beta^{-1}\delta y_m \tag{3.2b}$$

$$0 = \mu y_m - \xi y_i - \mu e^{-\xi\sigma} y_m \tag{3.2c}$$

$$y_m = \mu\eta^{-1} e^{-\xi\sigma} - \eta^{-1}\rho x_m \tag{3.2d}$$

so that

$$\begin{aligned} x_i &= \alpha\gamma^{-1} x_m (1 - e^{-\gamma\tau}) \\ y_i &= \mu\xi^{-1} y_m (1 - e^{-\xi\sigma}) \end{aligned} \tag{3.3}$$

is true. This tells us that if we have positive solutions of (3.2b) and (3.2d) at points $\tilde{x}_m$ and $\tilde{y}_m$, then $\tilde{x}_i$ and $\tilde{y}_i$ can be found from (3.2a) and (3.2c). They will also be positive, and $(\tilde{x}_i, \tilde{x}_m, \tilde{y}_i, \tilde{y}_m)$ will be an interior equilibrium.

We can solve (3.2) and (3.3) explicitly to get expressions for $\tilde{x}_i, \tilde{x}_m, \tilde{y}_i$ and $\tilde{y}_m$ in terms of the parameters:

$$\begin{aligned} \tilde{x}_i &= \alpha\gamma^{-1}\left(\frac{\alpha\beta^{-1}e^{-\gamma\tau} - \beta^{-1}\delta\mu\eta^{-1}e^{-\xi\sigma}}{1 - \beta^{-1}\delta\eta^{-1}\rho}\right)(1 - e^{-\gamma\tau}) \\ \tilde{x}_m &= \frac{\alpha\beta^{-1}e^{-\gamma\tau} - \beta^{-1}\delta\mu\eta^{-1}e^{-\xi\sigma}}{1 - \beta^{-1}\delta\eta^{-1}\rho} \\ \tilde{y}_i &= \mu\xi^{-1}\left(\frac{\mu\eta^{-1}e^{-\xi\sigma} - \alpha\beta^{-1}\eta^{-1}\rho e^{-\gamma\tau}}{1 - \beta^{-1}\delta\eta^{-1}\rho}\right)(1 - e^{-\xi\sigma}) \\ \tilde{y}_m &= \frac{\mu\eta^{-1}e^{-\xi\sigma} - \alpha\beta^{-1}\eta^{-1}\rho e^{-\gamma\tau}}{1 - \beta^{-1}\delta\eta^{-1}\rho} \end{aligned}$$

if $1 - \beta^{-1}\delta\eta^{-1}\rho \neq 0$. Note that there is no guarantee that these solutions are positive.

Now, to get positive solutions of (3.2), system (3.3) allows that we need only consider solutions of the system

$$\begin{aligned} x_m &= \alpha\beta^{-1}e^{-\gamma\tau} - \beta^{-1}\delta y_m \\ y_m &= \mu\eta^{-1}e^{-\xi\sigma} - \eta^{-1}\rho x_m \,. \end{aligned} \tag{3.4}$$

It is readily apparent by looking at the graphs of these linear equations that positive solutions of (3.4) can exist if and only if one of the following pair of two part conditions holds:

Condition A: $\alpha\beta^{-1}e^{-\gamma\tau} > \mu\rho^{-1}e^{-\xi\sigma}$ and $\alpha\delta^{-1}e^{-\gamma\tau} < \mu\eta^{-1}e^{-\xi\sigma}$

Condition B: $\alpha\beta^{-1}e^{-\gamma\tau} < \mu\rho^{-1}e^{-\xi\sigma}$ and $\alpha\delta^{-1}e^{-\gamma\tau} > \mu\eta^{-1}e^{-\xi\sigma}$.

Further, any such solution will be unique due to the linear nature of (3.4). In addition, we observe that if either of conditions A or B is true, then $1 - \beta^{-1}\delta\eta^{-1}\rho \neq 0$. We see this in the following manner: first assume condition A is true. Then

$$\beta^{-1}\delta = \frac{\alpha\beta^{-1}e^{-\gamma\tau}}{\alpha\delta^{-1}e^{-\gamma\tau}} > \frac{\mu\rho^{-1}e^{\xi\sigma}}{\mu\eta^{-1}e^{-\xi\sigma}} = \eta\rho^{-1}$$

so that $\beta^{-1}\delta\eta^{-1}\rho > 1$ giving us that $1 - \beta^{-1}\delta\eta^{-1}\rho < 0$. Similarly if condition B holds then $1 - \beta^{-1}\delta\eta^{-1}\rho > 0$ holds. Finally, noting that since condition A or condition B implies a positive solution of (3.4) exists then (3.3) would indicate that a positive solution to (3.2) exists as well. Thus we have the following

THEOREM 3.3. *If either condition A or condition B is true, then there exists a unique interior equilibrium, for system (3.1).*

Next, we would like to investigate the stability of system (3.1) about each of these equilibria. Linearizing the system we get,

$$\begin{pmatrix} \dot{x}_i(t) \\ \dot{x}_m(t) \\ \dot{y}_i(t) \\ \dot{y}_m(t) \end{pmatrix} = \begin{pmatrix} -\gamma & \alpha & 0 & 0 \\ 0 & -2\beta x_m - \delta y_m & 0 & -\delta x_m \\ 0 & 0 & -\xi & \mu \\ 0 & -\rho y_m & 0 & -2\eta y_m - \rho x_m \end{pmatrix} \begin{pmatrix} x_i(t) \\ x_m(t) \\ y_i(t) \\ y_m(t) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & -\alpha e^{-\gamma\tau} & 0 & 0 \\ 0 & \alpha e^{-\gamma\tau} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} x_i(t-\tau) \\ x_m(t-\tau) \\ y_i(t-\tau) \\ y_m(t-\tau) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\mu e^{-\xi\sigma} \\ 0 & 0 & 0 & \mu e^{-\xi\sigma} \end{pmatrix} \begin{pmatrix} x_i(t-\sigma) \\ x_m(t-\sigma) \\ y_i(t-\sigma) \\ y_m(t-\sigma) \end{pmatrix}.$$

Then the characteristic equation becomes,

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\gamma\tau}e^{-\lambda\tau} & 0 & 0 \\ 0 & \lambda+2\beta x_m+\delta y_m-\alpha e^{-\gamma\tau}e^{-\lambda\tau} & 0 & \delta x_m \\ 0 & 0 & \lambda+\xi & -\mu+\mu e^{-\xi\sigma}e^{-\lambda\sigma} \\ 0 & \rho y_m & 0 & \lambda+2\eta y_m+\rho x_m-\mu e^{-\xi\sigma}e^{-\lambda\sigma} \end{vmatrix} = 0.$$

At E_0 (0,0,0,0) this becomes,

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\tau(\gamma+\lambda)} & 0 & 0 \\ 0 & \lambda-\alpha e^{-\tau(\gamma+\lambda)} & 0 & 0 \\ 0 & 0 & \lambda+\xi & -\mu+\mu e^{-\sigma(\xi+\lambda)} \\ 0 & 0 & 0 & \lambda-\mu e^{-\sigma(\xi+\lambda)} \end{vmatrix} = 0.$$

Thus $\lambda = -\gamma$ and $\lambda = -\xi$ are eigenvalues at the origin. In addition to these two negative eigenvalues, solutions to the equations

$$\lambda = \alpha e^{-\tau(\gamma+\lambda)} \quad \text{and}$$

$$\lambda = \mu e^{-\sigma(\xi+\lambda)}$$

give further eigenvalues at E_0. Both of these equations will have a real, positive solution, making E_0 a saddle point. Complex solutions to these equations exist, but as we have seen, solutions to (3.1) that arise out of admissible initial conditions do not have components in the eigenspace of complex eigenvalues, since such components would necessarily be oscillatory about E_0. We have seen that solutions arising out of admissible initial conditions remain positive hence such oscillations could not occur.

Next we consider the equilibria on the boundary, namely $\hat{E}_x$, and $\hat{E}_y$. At the equilibrium point $\hat{E}_x$ the characteristic equation becomes

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\tau(\gamma+\lambda)} & 0 & 0 \\ 0 & \lambda+2\beta\hat{x}_m-\alpha e^{-\gamma\tau}e^{-\lambda\tau} & 0 & \delta\hat{x}_m \\ 0 & 0 & \lambda+\xi & -\mu+\mu e^{-\sigma(\xi+\lambda)} \\ 0 & 0 & 0 & \lambda+\rho\hat{x}_m-\mu e^{-\sigma(\xi+\lambda)} \end{vmatrix} = 0.$$

Again, $\lambda = -\gamma$ and $\lambda = -\xi$ are two negative, real eigenvalues. The other eigenvalues are given by the roots of

$$(\lambda+2\beta\hat{x}_m-\alpha e^{-\tau(\gamma+\lambda)})(\lambda+\rho\hat{x}_m-\mu e^{-\sigma(\xi+\lambda)}) = 0.$$

First consider roots of $\lambda+2\beta\hat{x}_m-\alpha e^{-\tau(\gamma+\lambda)} = 0$. Since $2\beta\hat{x}_m = 2\alpha e^{-\gamma\tau}$ this is equivalent to

$$\lambda+\alpha e^{-\gamma\tau}(2-e^{-\lambda\tau}) = 0. \tag{3.5}$$

Now let $\lambda = a+ib$ be a root of equation (3.5), where $a > 0$. Then equation (3.5) becomes,

$$a+ib+\alpha e^{-\gamma\tau}(2-(e^{-a\tau}\cos b\tau - ie^{-a\tau}\sin b\tau)) = 0$$

so that,

$$a + 2\alpha e^{-\gamma\tau} = \alpha e^{-\gamma\tau} e^{-a\tau} \cos b\tau$$

$$b \qquad = -\alpha e^{-\gamma\tau} e^{-a\tau} \sin b\tau$$

Squaring and adding,

$$(a + 2\alpha e^{-\gamma\tau})^2 + b^2 = (\alpha e^{-\gamma\tau} e^{-a\tau})^2.$$

Since we are assuming a to be positive, we have

$$4\alpha^2 e^{-2\gamma\tau} + b^2 < \alpha^2 e^{-2\gamma\tau},$$

giving us a contradiction. Thus all roots of (3.5) give us eigenvalues with negative real part.

Next we consider roots of the equation

$$\lambda + \rho \hat{x}_m - \mu e^{-\sigma(\xi+\lambda)} = 0. \tag{3.6}$$

Again let $\lambda = a + ib$. Then, noting that

$$\hat{x}_m = \alpha\beta^{-1} e^{-\gamma\tau}$$

we have

$$a + ib + \alpha\beta^{-1}\rho e^{-\gamma\tau} - \mu e^{-\xi\sigma}(e^{-a\sigma}\cos b\sigma - ie^{-a\sigma}\sin b\sigma) = 0.$$

Expressing this in terms of its real and imaginary parts we get,

$$a + \alpha\beta^{-1}\rho e^{-\gamma\tau} = \mu e^{-\sigma(a+\xi)} \cos b\sigma$$

$$b \qquad = -\mu e^{-\sigma(a+\xi)} \sin b\sigma$$

Squaring and adding,

$$(a + \alpha\beta^{-1}\rho e^{-\gamma\tau})^2 + b^2 = \mu^2 e^{-2\sigma(a+\xi)}.$$

Now let condition A hold, which implies that

$$\alpha\beta^{-1}e^{-\gamma\tau} > \mu\rho^{-1}e^{-\xi\sigma}$$

is true. Then

$$\alpha\beta^{-1}\rho e^{-\gamma\tau} > \mu e^{-\xi\sigma}$$

will hold. Now let us assume $a > 0$. Then,

$$(a + \alpha\beta^{-1}\rho e^{-\gamma\tau})^2 + b^2 = \mu^2 e^{-2\sigma\xi}e^{-2a\sigma} <$$

$$(\alpha\beta^{-1}\rho e^{-\gamma\tau})^2 e^{-2a\sigma} < (\alpha\beta^{-1}\rho e^{-\gamma\tau})^2$$

giving us a contradiction. Thus if condition A holds, all eigenvalues have negative real parts, and $\hat{E}_x$ is asymptotically stable.

If condition A does not hold yet $\alpha\beta^{-1}e^{-\gamma\tau} > \mu\rho^{-1}e^{-\xi\sigma}$ still does hold, we will, of course, have no interior equilibrium (since neither conditions A nor B can hold), yet $\hat{E}_x$ is asymptotically stable.

If $\alpha\beta^{-1}e^{-\gamma\tau} < \mu\rho^{-1}e^{-\xi\sigma}$ were true (which would be the case if condition B were to hold) then since this is equivalent to $\rho\hat{x}_m < \mu e^{-\xi\sigma}$, the equation

$$\lambda + \rho\hat{x}_m = \mu e^{-\sigma(\xi+\lambda)}$$

would have at least one real positive root making $\hat{E}_x$ a saddle point.

The analysis for the equilibrium $\hat{E}_y(0,0,\hat{y}_i,\hat{y}_m)$ is similar. The eigenvalues are again $\lambda = -y$ and $\lambda = -\xi$, plus the roots of the expression

$$(\lambda + 2\eta\hat{y}_m - \mu e^{-\sigma(\xi+\lambda)})(\lambda + \delta\hat{y}_m - \alpha e^{-\tau(\gamma+\lambda)}) = 0$$

Using the fact that $\hat{y}_m = \mu\eta^{-1}e^{-\xi\sigma}$ we see that

$$\lambda + 2\eta\hat{y}_m - \alpha e^{-\sigma(\xi+\lambda)} = \lambda + \mu e^{-\xi\sigma}(2 - e^{-\lambda\sigma}).$$

First we consider the roots of $\lambda + \mu e^{-\xi\sigma}(2 - e^{-\lambda\sigma}) = 0$. Again, letting $\lambda = a + ib$ and separating into real and complex parts, we obtain

$$\begin{aligned} a + 2\mu e^{-\xi\sigma} &= \mu e^{-\xi\sigma}e^{-a\sigma}\cos b\sigma \\ b &= \mu e^{-\xi\sigma}e^{-a\sigma}\sin b\sigma. \end{aligned}$$

Then making the assumptions that $a > 0$, and squaring and adding we get, similar to the analysis for $\hat{E}_x$,

$$(a + 2\mu e^{-\xi\sigma})^2 + b^2 = (\mu e^{-\xi\sigma}e^{-a\sigma})^2$$

and the assumed positivity of a gives us a contradiction. Thus all roots of the expression

$$(\lambda + 2\eta\hat{y}_m - \alpha e^{-\sigma(\xi+\lambda)}) = 0$$

give us negative real, or complex roots with negative real parts.

We now consider the roots of the expression

$$\lambda + \delta\hat{y}_m - \alpha e^{-\tau(\gamma+\lambda)} = 0 \tag{3.7}$$

Let $\lambda = a + ib$, and again assume condition A to be true, so that $\alpha\delta^{-1}e^{-\gamma\tau} < \mu\eta^{-1}e^{-\xi\sigma}$ holds, or $\alpha e^{-\gamma\tau} < \delta\mu\eta^{-1}e^{-\xi\sigma}$. Then (3.7) becomes,

$$a + bi + \delta\mu\eta^{-1}e^{-\xi\sigma} - \alpha e^{-\gamma\tau}(e^{-a\tau}\cos b\tau - ie^{-a\tau}\sin b\tau) = 0,$$

or, separating into real and complex parts,

$$\begin{aligned} a + \delta\mu\eta^{-1}e^{-\xi\sigma} &= \alpha e^{-\gamma\tau}e^{-a\tau}\cos b\tau \\ b &= \alpha e^{-\gamma\tau}e^{-a\tau}\sin b\tau. \end{aligned}$$

Squaring and adding, we obtain

$$(a + \delta\mu\eta^{-1}e^{-\xi\sigma})^2 + b^2 = (\alpha e^{-\gamma\tau}e^{-a\tau})^2$$

Now with our assumption that condition A holds, we further assume that $a > 0$. Then

$$\begin{aligned} (a + \delta\mu\eta^{-1}e^{-\xi\sigma})^2 + b^2 = (\alpha e^{-\gamma\tau}e^{-a\tau})^2 < \\ (\delta\mu\eta^{-1}e^{-\xi\sigma})^2 e^{-2a\tau} < (\delta\mu\eta^{-1}e^{-\xi\sigma})^2 \end{aligned}$$

would have to hold, contradicting our assumption that $a > 0$. Thus if condition A holds $\hat{E}_y$ is asymptotically stable as is $\hat{E}_x$. If condition A does not hold yet

$$\alpha\delta^{-1}e^{-\gamma\tau} < \mu\eta^{-1}e^{-\xi\sigma}$$

still does hold, $\hat{E}_y$ is still asymptotically stable but there is no interior equilibrium.

On the other hand, if

$$\alpha\delta^{-1}e^{-\gamma\tau} > \mu\eta^{-1}e^{-\xi\sigma}$$

were true (which would be the case if condition B were to hold), then since this is equivalent to

$$\delta\hat{y}_m < \alpha e^{-\gamma\tau}$$

the expression

$$\lambda + \delta\hat{y}_m - \alpha e^{-\gamma\tau}e^{-\tau\lambda} = 0$$

would have at least one positive, real root and $\hat{E}_y$ would be a saddle point.

We can summarize what we have done in the following theorem:

THEOREM 3.5. *Given system (3.1) with an admissible set of initial conditions:*

1) *If condition A is true, then*
    - a) *An interior equilibrium exists,*
    - b) $\hat{E}_x(\hat{x}_i, \hat{x}_m, 0, 0)$ *and* $\hat{E}_y(0, 0, \hat{y}_i, \hat{y}_m)$ *are both asymptotically stable.*
2) *If condition A does not hold, yet* $\alpha\beta^{-1}e^{-\gamma\tau} > \mu\rho^{-1}e^{-\xi\sigma}$,
    - a) *there is no interior equilibrium,*
    - b) $\hat{E}_x(\hat{x}_i, \hat{x}_m, 0, 0)$ *is asymptotically stable,*
    - c) $\hat{E}_y(0, 0, \hat{y}_i, \hat{y}_m)$ *is saddle point.*
3) *If condition A does not hold yet* $\alpha\delta^{-1}e^{-\gamma\tau} < \mu\eta^{-1}e^{-\xi\sigma}$,
    - a) *There is no interior equilibrium*
    - b) $\hat{E}_x(\hat{x}_i, \hat{x}_m, 0, 0)$ *is a saddle*
    - c) $\hat{E}_y(0, 0, \hat{y}_i, \hat{y}_m)$ *is asymptotically stable.*

4) If condition B holds,

a) An interior equilibrium exists,

b) $\hat{E}_x(\hat{x}_i, \hat{x}_m, 0, 0)$ and $\hat{E}_y(0, 0, \hat{y}_i, \hat{y}_m)$ are both saddles.

There remains the critical case where $1 - \beta^{-1}\delta\eta^{-1}\rho = 0$. There would then exist a continuum of equilibria, and at least one of the eigenvalues for both $\hat{E}_x$ and $\hat{E}_y$ would be zero.

Finally we consider the stability about the interior equilibrium under the conditions when it exists. The characteristic equation about $\tilde{E}(\tilde{x}_i, \tilde{x}_m, \tilde{y}_i, \tilde{y}_m)$ is given by,

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\tau(\gamma+\lambda)} & 0 & 0 \\ 0 & \lambda+2\beta\tilde{x}_m+\delta\tilde{y}_m-\alpha e^{-\tau(\gamma+\lambda)} & 0 & \delta\tilde{x}_m \\ 0 & 0 & \lambda+\xi & -\mu+\mu e^{-\sigma(\xi+\lambda)} \\ 0 & \rho\tilde{y}_m & 0 & \lambda+2\eta\tilde{y}_m+\rho\tilde{x}_m-\mu e^{-\sigma(\xi+\lambda)} \end{vmatrix} = 0.$$

Clearly $\lambda = -\gamma$ and $\lambda = -\xi$ are negative, real eigenvalues. We are then left with,

$$\begin{vmatrix} \lambda+2\beta\tilde{x}_m+\delta\tilde{y}_m+\alpha e^{-\tau(\gamma+\lambda)} & \delta\tilde{x}_m \\ \rho\tilde{y}_m & \lambda+2\eta\tilde{y}_m+\rho\tilde{x}_m-\mu e^{-\sigma(\xi+\lambda)} \end{vmatrix} = 0.$$

We therefore need to examine roots of the equation

$$\lambda^2 + [2\beta\tilde{x}_m + \delta\tilde{y}_m - \alpha e^{-\tau(\gamma+\lambda)}) + (2\eta\tilde{y}_m + \rho\tilde{x}_m - \mu e^{-\sigma(\xi+\lambda)})]\lambda$$
$$+ (2\beta\tilde{x}_m + \delta\tilde{y}_m - \alpha e^{-\tau(\gamma+\lambda)})(2\eta\tilde{y}_m + \rho\tilde{x}_m - \mu e^{-\sigma(\xi+\lambda)}) - \delta\rho\tilde{x}_m\tilde{y}_m = 0,$$

i.e.

$$\begin{aligned}
&\lambda^2 + [(2\beta\tilde{x}_m + \delta\tilde{y}_m - \alpha e^{-\tau(\gamma+\lambda)}) + (2\eta\tilde{y}_m + \rho\tilde{x}_m - \mu e^{-\sigma(\xi+\lambda)})]\lambda \\
&\quad + (2\beta\tilde{x}_m - \alpha e^{-\tau(\gamma+\lambda)})(2\eta\tilde{y}_m - \mu e^{-\sigma(\xi+\lambda)}) \\
&\quad + (2\eta\tilde{y}_m - \mu e^{-\sigma(\xi+\lambda)})\delta\tilde{y}_m + (2\beta\tilde{x}_m - \alpha e^{-\tau(\gamma+\lambda)})\rho\tilde{x}_m = 0
\end{aligned}$$

or

$$\begin{aligned}
&\lambda^2 + (2\beta\tilde{x}_m + \delta y_m + 2\eta\tilde{y}_m + \rho\tilde{x}_m)\lambda + 4\beta\eta\tilde{x}_m\tilde{y}_m + 2\eta\delta\tilde{y}_m^2 \\
&\quad + 2\beta\rho\tilde{x}_m^2 - (ae^{-\gamma\tau}e^{-\tau\lambda} + \mu e^{-\xi\sigma}e^{-\sigma\lambda})\lambda - \quad \delta\tilde{y}_m e^{-\xi\sigma}e^{-\sigma\lambda} \\
&\quad - \alpha\rho\tilde{x}_m e^{-\gamma\tau}e^{-\tau\lambda} - 2\beta\mu\tilde{x}_m e^{-\xi\sigma}e^{-\sigma\lambda} - 2\alpha\eta\tilde{y}_m e^{-\gamma\tau}e^{-\tau\lambda} \\
&\quad + \alpha\mu e^{-\gamma\tau}e^{-\xi\sigma}e^{-\lambda(\tau+\sigma)} = 0.
\end{aligned}$$

This is equivalent to

$$\begin{aligned}
&\lambda^2 + (2\beta\tilde{x}_m + \delta\tilde{y}_m + 2\eta\tilde{y}_m + \rho\tilde{x}_m)\lambda + (4\beta\eta\tilde{x}_m\tilde{y}_m + 2\eta\delta\tilde{y}_m^2 + 2\beta\rho\tilde{x}_m^2) \\
&= (\alpha e^{-\tau(\gamma+\lambda)} + \mu e^{-\sigma(\xi+\lambda)})\lambda + \alpha e^{-\tau(\gamma+\lambda)}(2\eta\tilde{y}_m + \rho\tilde{x}_m) \qquad (3.8) \\
&\quad + \mu e^{-\sigma(\xi+\lambda)}(2\beta\tilde{x}_m + \delta\tilde{y}_m) - (\alpha e^{-\tau(\gamma+\lambda)})(\mu e^{-\sigma(\xi+\lambda)}).
\end{aligned}$$

The left hand side of equation (3.8) is a quadratic equation in λ with a vertex at a negative value of λ and concave up. Thus the left hand side of equation (3.8) is positive at $\lambda = 0$ and monotone increasing from $\lambda > 0$, with its limit going to infinity as t approaches plus infinity.

The right hand side of (3.8) is an expression that tends to zero as t tends to plus infinity. Thus if

$$\begin{aligned}
&(4\beta\eta\tilde{x}_m\tilde{y}_m + 2\eta\delta\tilde{y}_m^2 + 2\beta\rho\tilde{x}_m^2) < \\
&\alpha e^{-\gamma\tau}(2\eta\tilde{y}_m + \rho\tilde{x}_m) + \mu e^{-\xi\sigma}(2\beta\tilde{x}_m + \delta\tilde{y}_m) - (\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})
\end{aligned} \qquad (3.9)$$

then we have at least one positive, real root and the interior equilibrium becomes an unstable saddle point.

Since we have explicit expressions for $\tilde{x}_m$ and $\tilde{y}_m$ in terms of the parameters, we can substitute these into equation (3.9) to get sufficient conditions for the interior equilibrium to be unstable in terms of the parameters. Inequality (3.9) becomes

$$\begin{aligned}
&4\frac{(\alpha e^{-\gamma\tau}-\delta\mu\eta^{-1}e^{-\xi\sigma})(\mu e^{-\xi\sigma}-\alpha\beta^{-1}\rho e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2} \\
&\quad+\frac{2(\mu e^{-\xi\sigma}-\alpha\beta^{-1}\rho e^{-\gamma\tau})(\mu\eta^{-1}\delta e^{-\xi\sigma}-\alpha\beta^{-1}\eta^{-1}\rho\delta e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2} \\
&\quad+\frac{2(\alpha e^{-\gamma\tau}-\delta\mu\eta^{-1}e^{-\xi\sigma})(\alpha\beta^{-1}\rho e^{-\gamma\tau}-\beta^{-1}\delta\mu\eta^{-1}\delta e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}< \\
&\alpha e^{-\gamma\tau}\left(\frac{2\mu e^{-\xi\sigma}-2\alpha\beta^{-1}\rho e^{-\gamma\tau}+\alpha\beta^{-1}\rho e^{-\gamma\tau}-\beta^{-1}\delta\mu\eta^{-1}\rho e^{-\xi\sigma}}{(1-\beta^{-1}\delta\eta^{-1}\rho)}\right) \\
&\quad+\mu e^{-\xi\sigma}\left(\frac{2\alpha e^{-\gamma\tau}-2\delta\mu\eta^{-1}e^{-\xi\sigma}+\mu\eta^{-1}\delta e^{-\xi\sigma}-\alpha\beta^{-1}\eta^{-1}\rho\delta e^{-\gamma\tau}}{(1-\beta^{-1}\delta\eta^{-1}\rho)}\right) \\
&\quad-(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})
\end{aligned} \tag{3.10}$$

We will consider the left hand side and the right hand side of equation (3.10) separately.

The left hand side of equation (3.10) becomes,

$$\frac{4(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 4(\alpha e^{-\gamma\tau})(\alpha\beta^{-1}\rho e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$- \frac{4(\delta\mu\eta^{-1}e^{-\xi\sigma})(\mu e^{-\xi\sigma}) + 4(\delta\mu\eta^{-1}e^{-\xi\sigma})(\alpha\beta^{-1}\rho e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$+ \frac{2(\mu e^{-\xi\sigma})(\mu\eta^{-1}\delta e^{-\xi\sigma}) - 2(\mu e^{-\xi\sigma})(\alpha\beta^{-1}\eta^{-1}\rho\delta e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$- \frac{2(\alpha\beta^{-1}\rho e^{-\gamma\tau})(\mu\eta^{-1}\delta e^{-\xi\sigma}) + 2(\alpha\beta^{-1}\rho e^{-\gamma\tau})(\alpha\beta^{-1}\eta^{-1}\rho\delta e^{-\gamma\tau})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$+ \frac{2(\alpha e^{-\gamma\tau})(\alpha\beta^{-1}\rho e^{\xi\sigma}) - 2(\alpha e^{-\gamma\tau})(\beta^{-1}\delta\mu\eta^{-1}\rho e^{-\xi\sigma})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$- \frac{2(\delta\mu\eta^{-1}e^{-\xi\sigma})(\alpha\beta^{-1}\rho e^{-\gamma\tau}) + 2(\delta\mu\eta^{-1}e^{-\xi\sigma})(\beta^{-1}\delta\mu\eta^{-1}\rho e^{-\xi\sigma})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$= \frac{4(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 2(\alpha e^{-\gamma\tau})(\alpha\beta^{-1}\rho e^{-\gamma\tau}) - 2(\mu e^{-\xi\sigma})(\delta\mu\eta^{-1}e^{-\xi\sigma})}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$+ \frac{-4\alpha\beta^{-1}\delta\mu\eta^{-1}\rho e^{-(\gamma\tau+\xi\sigma)} + 2(\alpha^2\beta^{-1}\rho e^{-2\gamma\tau})(\beta^{-1}\delta\eta^{-1}\rho)}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$+ \frac{2(\mu^2\eta^{-1}\delta e^{-2\xi\sigma})(\beta^{-1}\delta\eta^{-1}\rho)}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$= \frac{4(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 2\alpha^2\beta^{-1}\rho e^{-2\gamma\tau}(1-\beta^{-1}\delta\eta^{-1}\rho) - 2\mu^2\eta^{-1}\delta e^{-2\xi\sigma}(1-\beta^{-1}\delta\eta^{-1}\rho)}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$- \frac{4(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})(\beta^{-1}\delta\eta^{-1}\rho)}{(1-\beta^{-1}\delta\eta^{-1}\rho)^2}$$

$$= \frac{4(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 2\alpha^2\beta^{-1}\rho e^{-2\gamma\tau} - 2\mu^2\eta^{-1}\delta e^{-2\xi\sigma}}{(1-\beta^{-1}\delta\eta^{-1}\rho)}.$$

The right hand side of equation (3.10) becomes,

$$\frac{2(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 2\alpha^2\beta^{-1}\rho e^{-2\gamma\tau} + \alpha^2\beta^{-1}\rho e^{-2\gamma\tau} - (\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})(\beta^{-1}\delta\eta^{-1}\rho)}{1-\beta^{-1}\delta\eta^{-1}\rho}$$
$$+\frac{2(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 2\mu^2\eta^{-1}\delta e^{-2\xi\sigma} + \mu^2\eta^{-1}\delta e^{-2\xi\sigma} - (\alpha e^{-\gamma\tau})(u e^{-\xi\sigma})(\beta^{-1}\delta\eta^{-1}\rho)}{1-\beta^{-1}\delta\eta^{-1}\rho}$$
$$-(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})$$
$$=\frac{2(\alpha e^{-\gamma\tau})(\mu e^{\xi\sigma}) + 2(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})(1-\beta^{-1}\delta\eta^{-1}\rho)}{1-\beta^{-1}\delta\eta^{-1}\rho} - (\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})$$
$$-\frac{\alpha^2\beta^{-1}\rho e^{-2\gamma\tau} + \mu^2\eta^{-1}\delta e^{-2\xi\sigma}}{1-\beta^{-1}\delta\eta^{-1}\rho}$$
$$=(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})\left(1+\frac{2}{1-\beta^{-1}\delta\eta^{-1}\rho}\right) - \frac{\alpha^2\beta^{-1}\rho e^{-2\gamma\tau} + \mu^2\eta^{-1}\delta e^{-2\xi\sigma}}{1-\beta^{-1}\delta\eta^{-1}\rho}.$$

Thus a real, positive eigenvalue at the interior equilibrium will exist if

$$\frac{4(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - 2\alpha^2\beta^{-1}\rho e^{-2\gamma\tau} - 2\mu^2\eta^{-1}\delta e^{-2\xi\sigma}}{(1-\beta^{-1}\delta\eta^{-1}\rho)}$$
$$<(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})\left(1+\frac{2}{1-\beta^{-1}\delta\eta^{-1}\rho}\right) - \frac{\alpha^2\beta^{-1}\rho e^{-2\gamma\tau} + \mu^2\eta^{-1}\delta e^{-2\xi\sigma}}{1-\beta^{-1}\delta\eta^{-1}\rho}$$

which is equivalent to,

$$\frac{2(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) - \alpha^2\beta^{-1}\rho e^{-2\gamma\tau} - \mu^2\eta^{-1}\delta e^{-2\xi\sigma}}{1-\beta^{-1}\delta\eta^{-1}\rho} < (\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma}) \qquad (3.11)$$

Unfortunately, one cannot apply either condition A or condition B to this in order to conclude that the presence of either of these conditions would indicate the presence of a positive eigenvalue for the interior equilibrium.

3.4. Global Behavior of Solutions

As we have seen, the presence of either condition A or condition B will tell us something about the stability of the boundary equilibria, and about the presence of an interior equilibrium. However, as we have observed, we cannot draw any conclusions about the stability of the interior equilibrium from the presence of either condition A or of condition B. The only thing we can say about the stability of the interior equilibrium is that if equation (3.11) is true, the interior equilibrium will be a saddle point. Equation (3.11) being true is equivalent to

$$\frac{(\alpha e^{-\gamma\tau})(\mu e^{-\xi\sigma})(1+\beta^{-1}\delta\eta^{-1}\rho)-(\alpha e^{-\gamma\tau})^2\beta^{-1}\rho-(\mu e^{-\xi\sigma})^2\eta^{-1}\delta}{1-\beta^{-1}\delta\eta^{-1}\rho} < 0.$$

We call the left side of this inequality the characteristic equation factor, or CEF. If the behavior of this time delay system has any parallel to that of the non-time-delay Lotka-Volterra case, we would expect a negative CEF to be associated with condition A and a positive CEF to be associated with condition B. In the next section we will consider an example where this behavior is indeed the case.

3.5. Computer Simulations and Examples

We consider here a series of examples where all parameters remain constant except for the maturation time σ of the second species. Specifically we have the system,

$$\begin{aligned}
\dot{x}_i &= 0.5x_m - 0.4x_i - 0.5e^{-.4\times 0.7}x_m(t-0.7) \\
\dot{x}_m &= 0.5e^{-0.4\times 0.7}x_m(t-0.7) - 0.3x_m^2 - 0.2x_m y_m \\
\dot{y}_i &= 0.5y_m - 0.4y_i - 0.5e^{-0.4\sigma}y_m(t-\sigma) \\
\dot{y}_m &= 0.5e^{-0.4\sigma}y_m(t-\sigma) - 0.3y_m^2 - 0.2y_m x_m
\end{aligned} \tag{3.12}$$

where the variables are functions of time unless otherwise noted.

If the quantity σ is set to the value 0.7, which makes it equal to τ, we have an interior equilibrium whose (x_i, x_m) and (y_i, y_m) values are equal. Condition B is true, the CEF is positive and the interior equilibrium appears to be globally asymptotically stable judging by the numerical evidence.

The series of phase-plane graphs we have done for system (3.12) have the second species maturation period σ range from 0.7 to 2.0. (see figures 1-5). The stable interior equilibrium moves toward the first species boundary equilibrium, and the CEF decreases as σ increases. At approximately the value $\sigma = 1.7136$, the interior equilibrium merges with the boundary equilibrium, the CEF becomes zero, and the positive eigenvalue at the boundary also becomes zero. As σ is increased further the CEF continues to decrease, no interior equilibrium exists, the first species boundary equilibrium $\tilde{E}_x$ stabilizes, while the second species boundary equilibrium $\tilde{E}_y$ remains unstable. Thus we see that by changing the time delay, a stable interior equilibrium can disappear, and an unstable boundary equilibrium may be made to become stable.

The second series of examples we present concerns the system

$$\begin{aligned}
\dot{x}_i &= 0.5x_m - 0.4x_i - 0.5e^{-.4\times 0.7}x_m(t-0.7) \\
\dot{x}_m &= 0.5e^{-0.4\times 0.7}x_m(t-0.7) - 0.2x_m^2 - 0.3x_m y_m \\
\dot{y}_i &= 0.5y_m - 0.4y_i - 0.5e^{-0.4\sigma}y_m(t-\sigma) \\
\dot{y}_m &= 0.5e^{-0.4\sigma}y_m(t-\sigma) - 0.2y_m^2 - 0.3y_m x_m
\end{aligned} \tag{3.13}$$

With $\sigma = \tau = 0.7$ we have an interior equilibrium whose (x_i, x_m) and (y_i, y_m) components are again equal. Condition A is true, the CEF is negative and the numerical evidence indicates an unstable interior equilibrium, while the boundary equilibria are stable. The basins of attraction of the boundary equilibria are divided by a separatrix Γ, which is also a stable manifold for the interior equilibrium.

Increasing σ from 0.7 to 2.0 results in the unstable interior equilibrium moving toward the $\hat{E}_y(0,0,\hat{y}_i,\hat{y}_m)$ boundary equilibrium, merging with $\hat{E}_y$, and vanishing. $\hat{E}_y$ becomes unstable, while $\hat{E}_x$ becomes globally asymptotically stable. See figures 6-10.

The third series of examples, covered in figure 3.11 through figure 3.13, is of the system

$$\begin{aligned}
\dot{x}_i &= 0.5x_m - 0.4x_i - 0.5e^{-0.4\times 0.7}x_m(t-0.7)\\
\dot{x}_m &= 0.5e^{-0.4\times 0.7}x_m(t-0.7) - 0.3x_m^2 - 0.2x_m y_m\\
\dot{y}_i &= 0.5y_m - 0.2y_i - 0.5e^{-0.2\times\sigma}y_m(t-\sigma)\\
\dot{y}_m &= 0.5e^{-0.2\times\sigma}y_m(t-\sigma) - 0.2y_m^2 - 0.3y_m x_m.
\end{aligned}$$

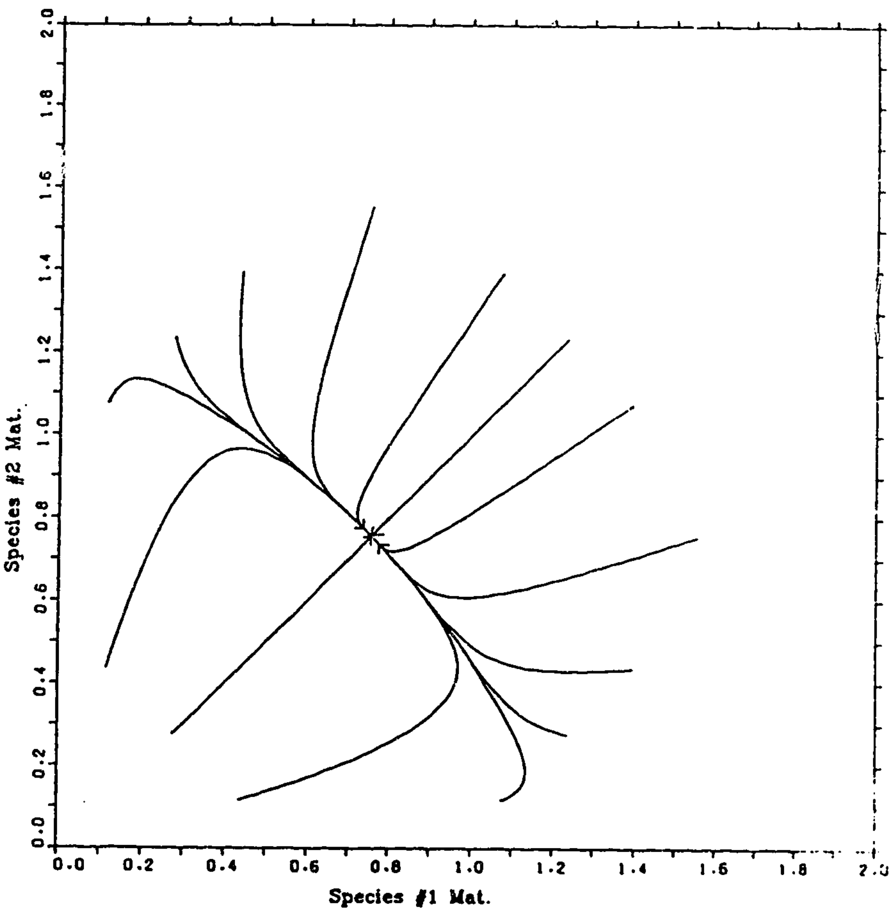
With $\sigma = 0.7$ there exists a continuum of interior equilibria, if $\sigma = 1.2$ the x-species boundary equilibrium becomes globally asymptotically stable, and when $\sigma = 0.4$ the y-species boundary equilibrium becomes globally asymptoptically stable. In none of these cases is either condition A or condition B true, indicating that, in the nongeneric case at least, either condition A or condition B being true is not necessary for the existence of interior equilibria.

3.6 Concluding Remarks

The results of the analysis of system (3.1) indicates that system (3.1) does not deviate radically in its behavior from the two dimensional case with no time delays. In the generic delay case the presence of either condition A or condition B is necessary and sufficient for the existence of an interior equilibrium. Condition A and condition B are similar to those necessary conditions for the existence of an interior equilibrium in the case where the system has no time delays. Setting the delays to zero gives those conditions; the presence of either one being sufficient, and the presence of one or the other being necessary, for the existence of an interior equilibrium in the case with no time delays, and the presence of one or the other conditions determining the stability of the interior equilibrium.

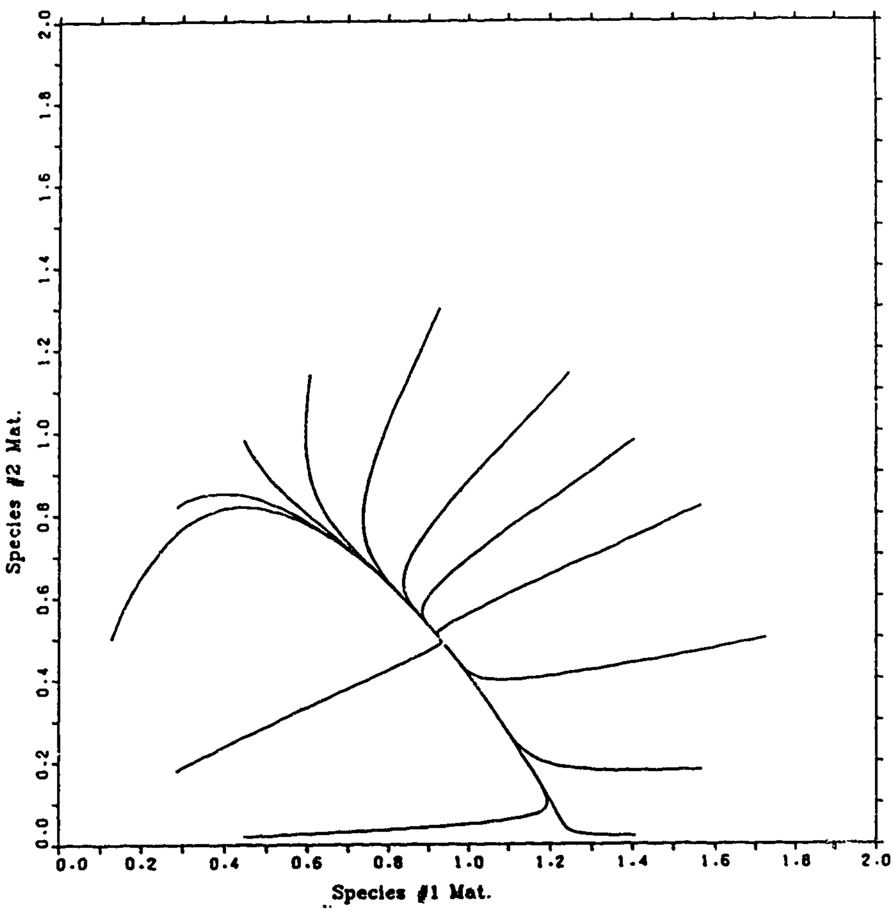
By varying the time delay we can make an interior equilibrium disappear, and either destabilize a stable boundary equilibrium or stabilize an unstable boundry equilibrium. In the time delay case we have sufficient conditions for an interior equilibrium to be stable, but unlike the case with no time delays we cannot draw any conclusions about the stability of the interior equilibrium from the presence of either condition A or of condition B.

Figure 3.1 Competition Set #5



```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.3000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.2000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.3000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.2000000
Species2 Maturation Period:  0.7000000

Interior Equilibrium: Xi = 0.23072   Xm =  0.75578
                      Yi = 0.23072   Ym =  0.75578

Characteristic equation factor:    0.02856

Condition B is true

X-boundary equilibrium: Xi =  0.57680   Xm =  1.88946
Y-boundary equilibrium: Yi =  0.38453   Ym =  1.25964
```

Figure 3.2 Competition Set #6



Species1 Intrinsic Growth Rate: 0.5000000
Species1 Mature Death Rate: 0.3000000
Species1 Immature Death Rate: 0.4000000
Species1 - Species2 Competition Constant: 0.2000000
Species1 Maturation Period: 0.7000000
Species2 Intrinsic Growth Rate: 0.5000000
Species2 Mature Death Rate: 0.3000000
Species2 Immature Death Rate: 0.4000000
Species2 - Species1 Competition Constant: 0.2000000
Species2 Maturation Period: 1.0000000

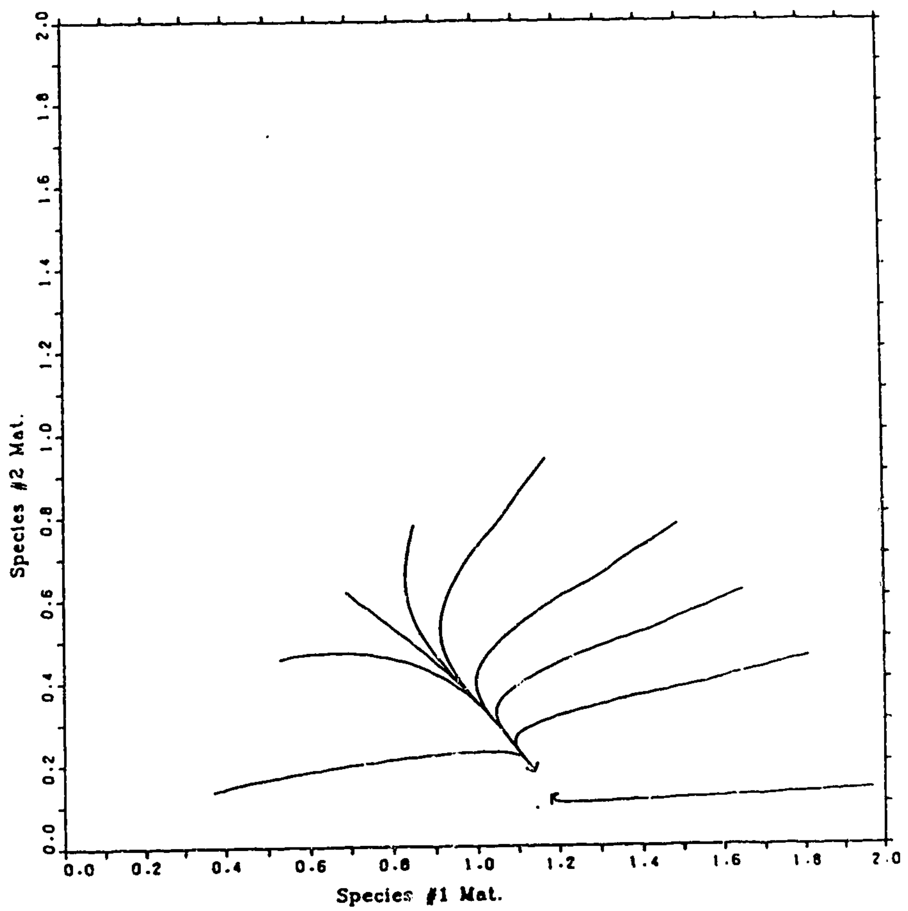
Interior Equilibrium: Xi = 0.28290 Xm = 0.92671
Yi = 0.20580 Ym = 0.49939

Characteristic equation factor: 0.02314

Condition B is true

X-boundary equilibrium: Xi = 0.51157 Xm = 1.67580
Y-boundary equilibrium: Yi = 0.46040 Ym = 1.11720

Figure 3.3 Competition Set #7



Species1 Intrinsic Growth Rate: 0.5000000
Species1 Mature Death Rate: 0.3000000
Species1 Immature Death Rate: 0.4000000
Species1 - Species2 Competition Constant: 0.2000000
Species1 Maturation Period: 0.7000000
Species2 Intrinsic Growth Rate: 0.5000000
Species2 Mature Death Rate: 0.3000000
Species2 Immature Death Rate: 0.4000000
Species2 - Species1 Competition Constant: 0.2000000
Species2 Maturation Period: 1.5000000

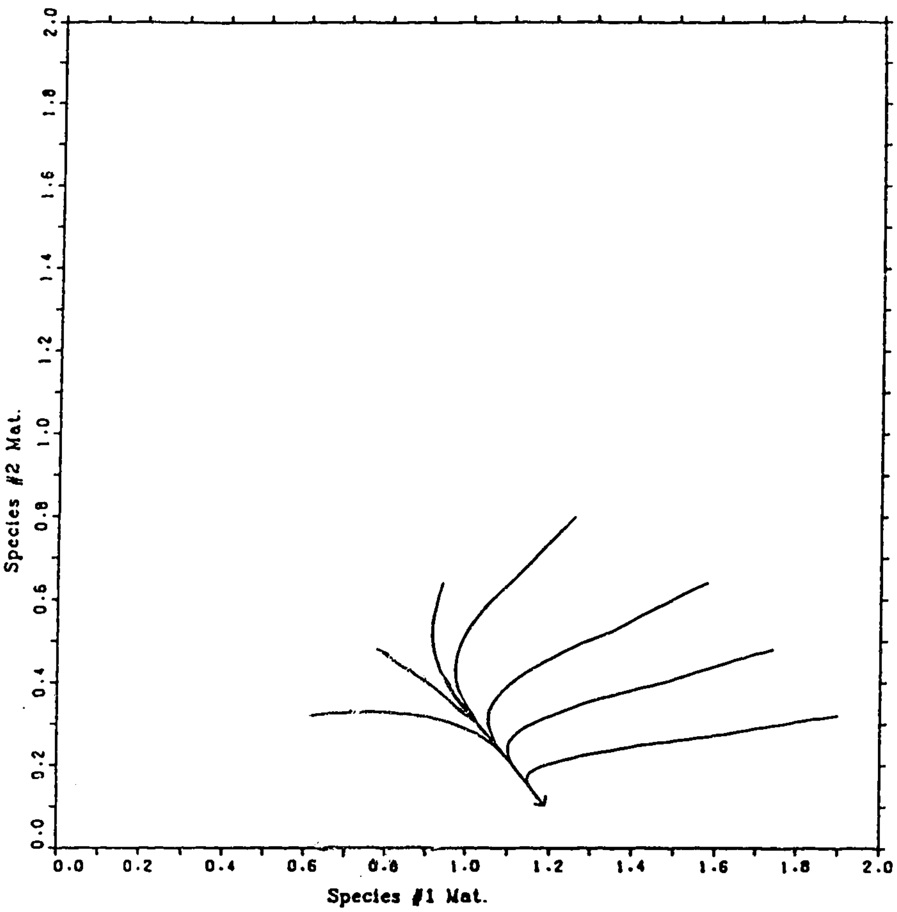
Interior Equilibrium: Xi = 0.35708 Xm = 1.16973
Yi = 0.07606 Ym = 0.13487

Characteristic equation factor: 0.00789

Condition B is true

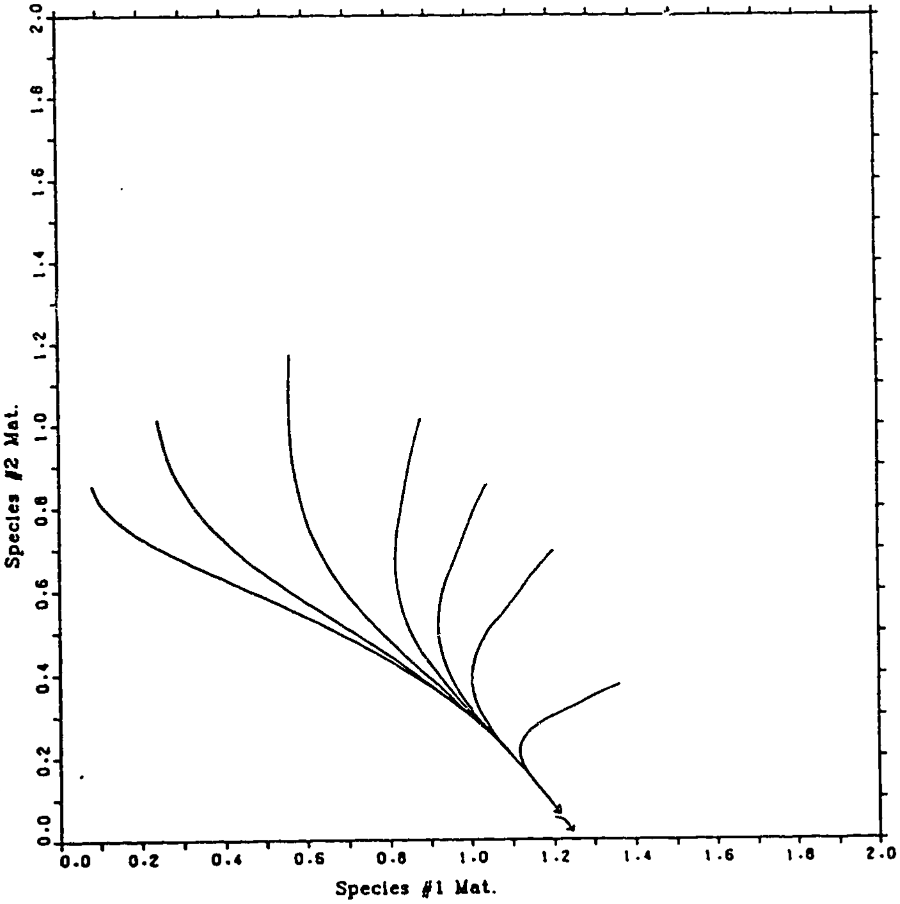
X-boundary equilibrium: Xi = 0.41884 Xm = 1.37203
Y-boundary equilibrium: Yi = 0.51587 Ym = 0.91469

Figure 3.4   Competition Set #8



```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.3000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.2000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.3000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.2000000
Species2 Maturation Period:  1.7136000

Interior Equilibrium: Xi = 0.38452    Xm =  1.25961
                      Yi = 0.00002    Ym =  0.00004

Characteristic equation factor:    0.00000

Condition B is true

X-boundary equilibrium: Xi =  0.38454   Xm =  1.25967
Y-boundary equilibrium: Yi =  0.52080   Ym =  0.83978
```

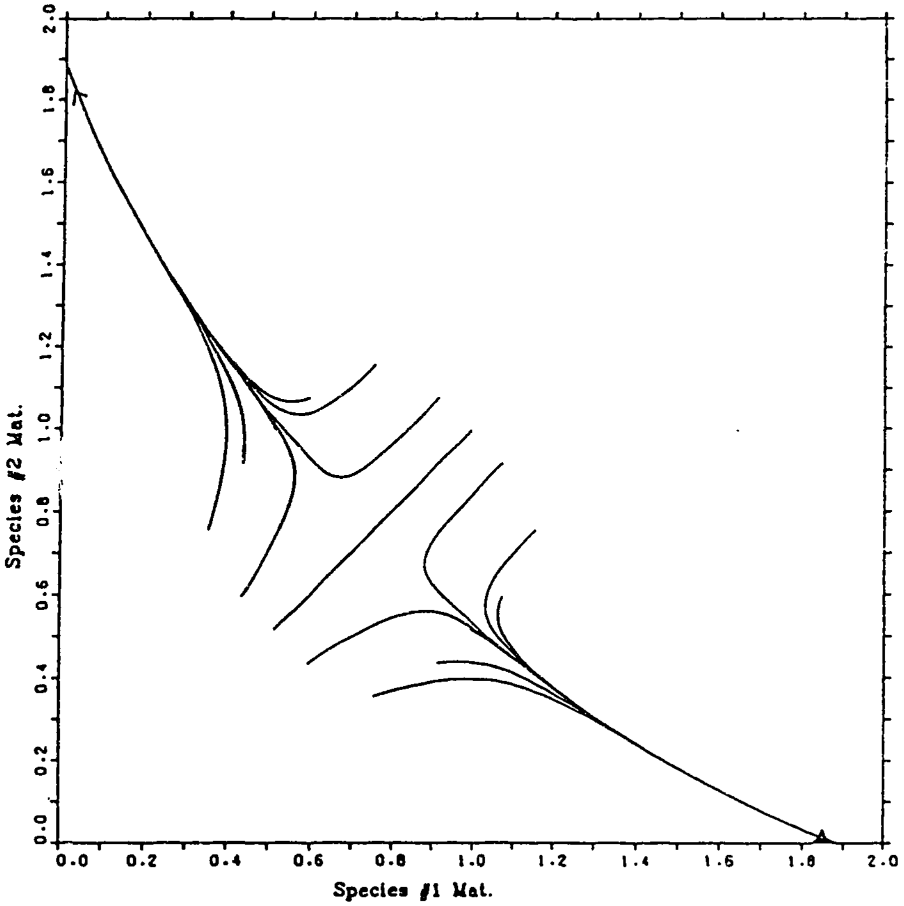
Figure 3.5 Competition Set #9



Species1 Intrinsic Growth Rate: 0.5000000
Species1 Mature Death Rate: 0.3000000
Species1 Immature Death Rate: 0.4000000
Species1 - Species2 Competition Constant: 0.2000000
Species1 Maturation Period: 0.7000000
Species2 Intrinsic Growth Rate: 0.5000000
Species2 Mature Death Rate: 0.3000000
Species2 Immature Death Rate: 0.4000000
Species2 - Species1 Competition Constant: 0.2000000
Species2 Maturation Period: 2.0000000

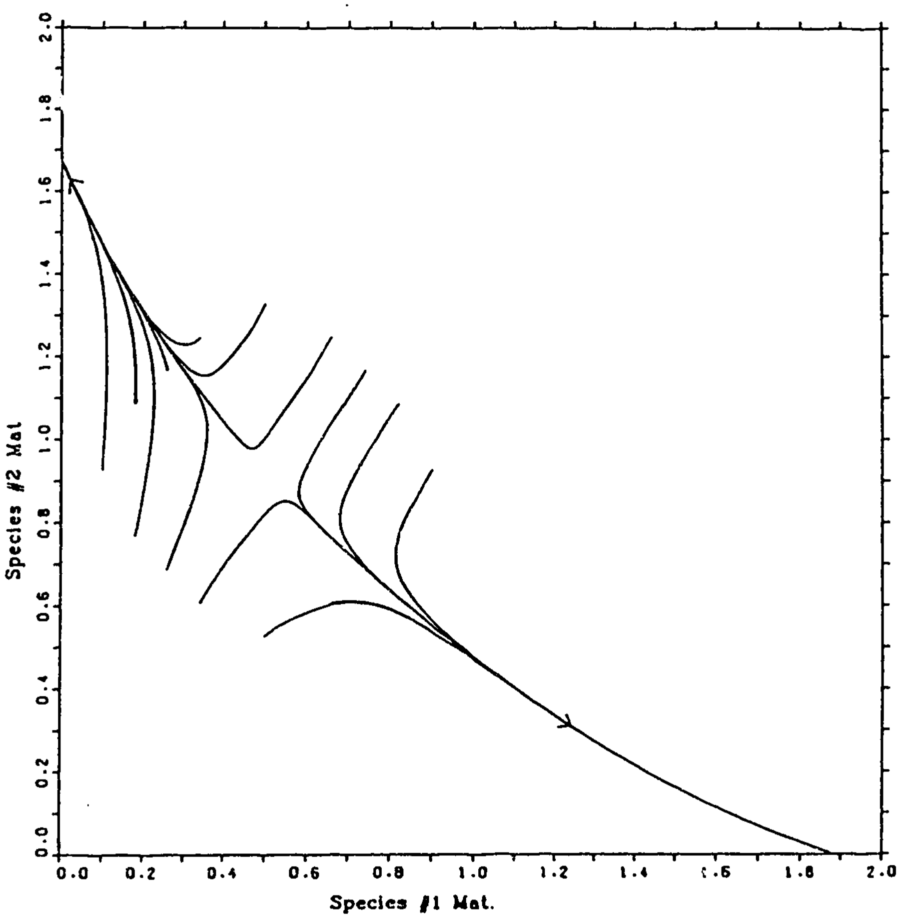
X-boundary equilibrium: Xi = 0.34292 Xm = 1.12332
Y-boundary equilibrium: Yi = 0.51548 Ym = 0.74888

Figure 3.6 Competition Set #10



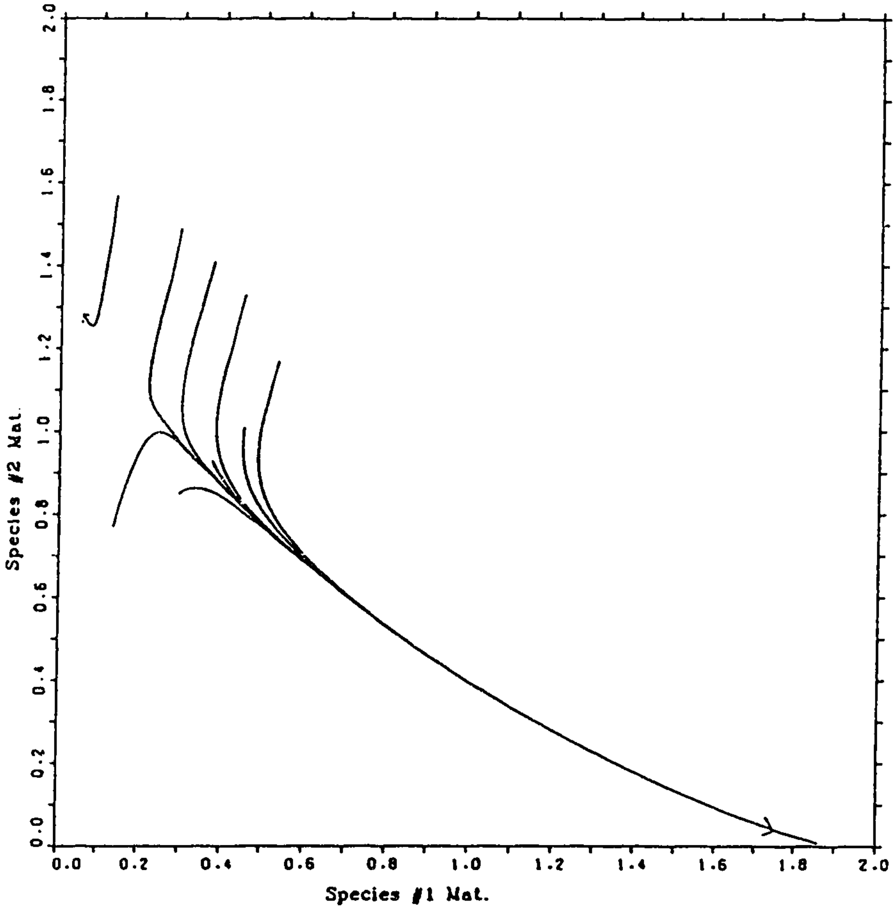
```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.2000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.3000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.2000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.3000000
Species2 Maturation Period:  0.7000000

Interior Equilibrium: Xi = 0.23072    Xm =  0.75578
                      Yi = 0.23072    Ym =  0.75578

Characteristic equation factor:   -0.02856

Condition A is true

X-boundary equilibrium: Xi =  0.38453   Xm =  1.25964
Y-boundary equilibrium: Yi =  0.57680   Ym =  1.88946
```

Figure 3.7 Competition Set #11



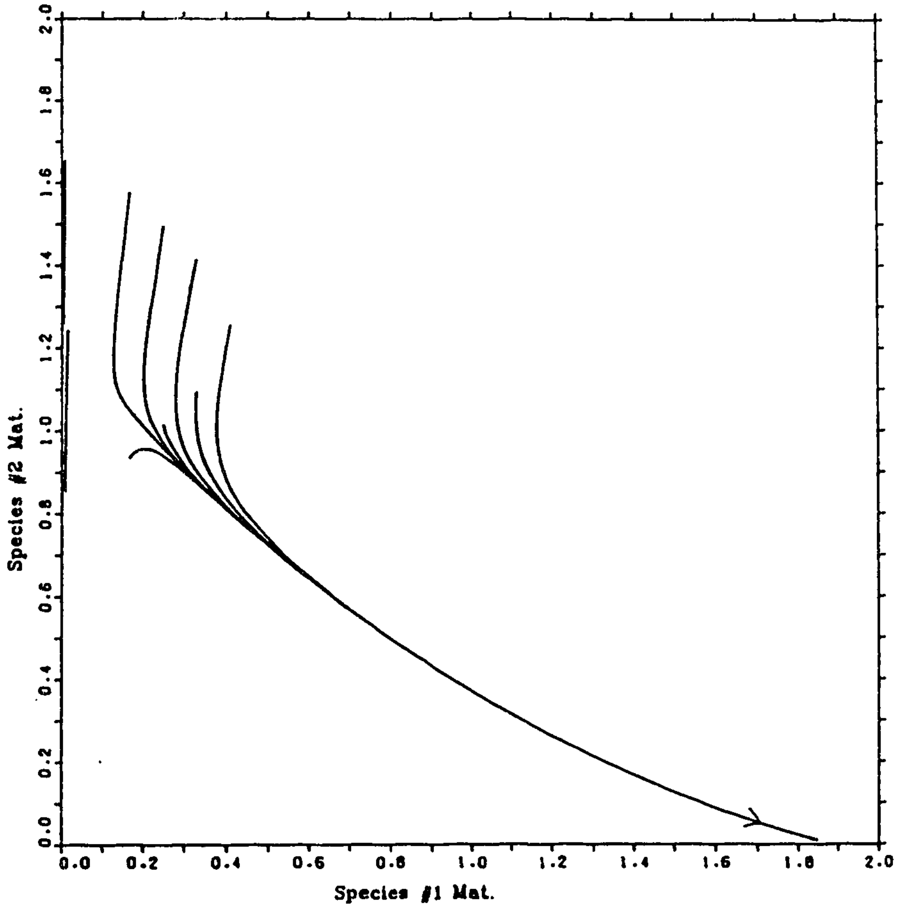
```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.2000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.3000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.2000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.3000000
Species2 Maturation Period:  1.0000000

Interior Equilibrium: Xi = 0.15245    Xm =  0.49939
                      Yi = 0.38190    Ym =  0.92671

Characteristic equation factor:   -0.02314

Condition A is true

X-boundary equilibrium: Xi =  0.34105   Xm =  1.11720
Y-boundary equilibrium: Yi =  0.69060   Ym =  1.67580
```

Figure 3.8   Competition Set #13



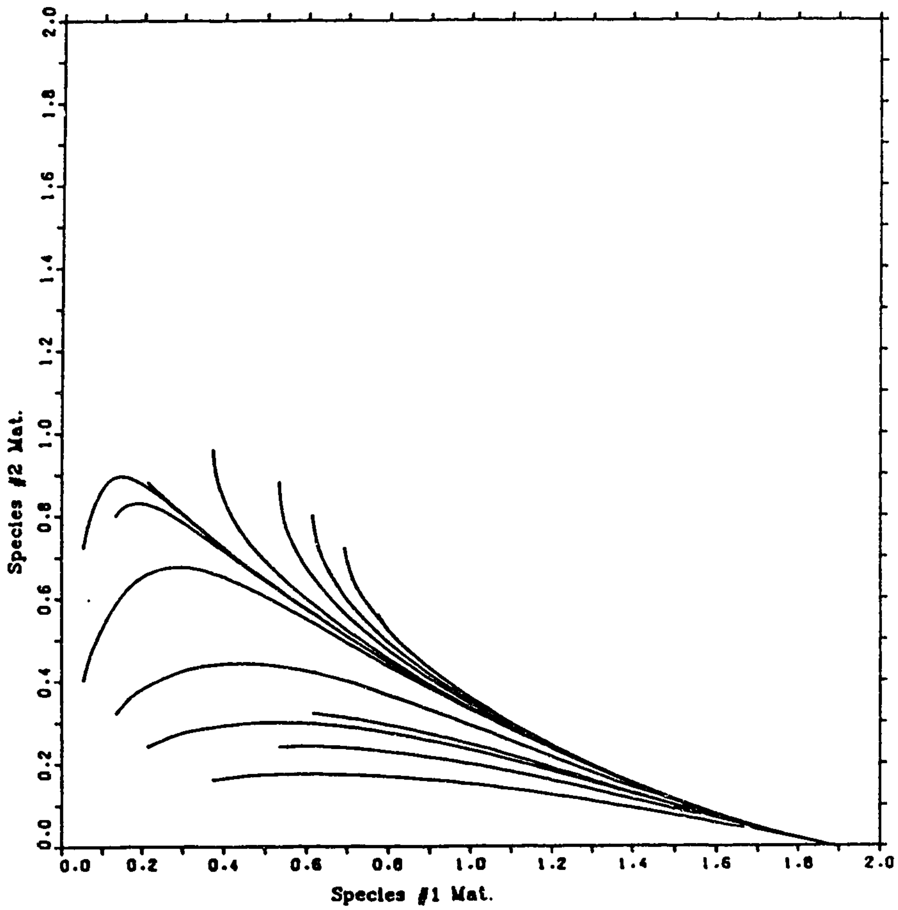
```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.2000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.3000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.2000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.3000000
Species2 Maturation Period:  1.5000000

Interior Equilibrium: Xi = 0.04117    Xm =  0.13487
                      Yi = 0.65971    Ym =  1.16973

Characteristic equation factor:   -0.00789

Condition A is true

X-boundary equilibrium: Xi =  0.27923   Xm =  0.91469
Y-boundary equilibrium: Yi =  0.77380   Ym =  1.37203
```

Figure 3.9 Competition Set #14



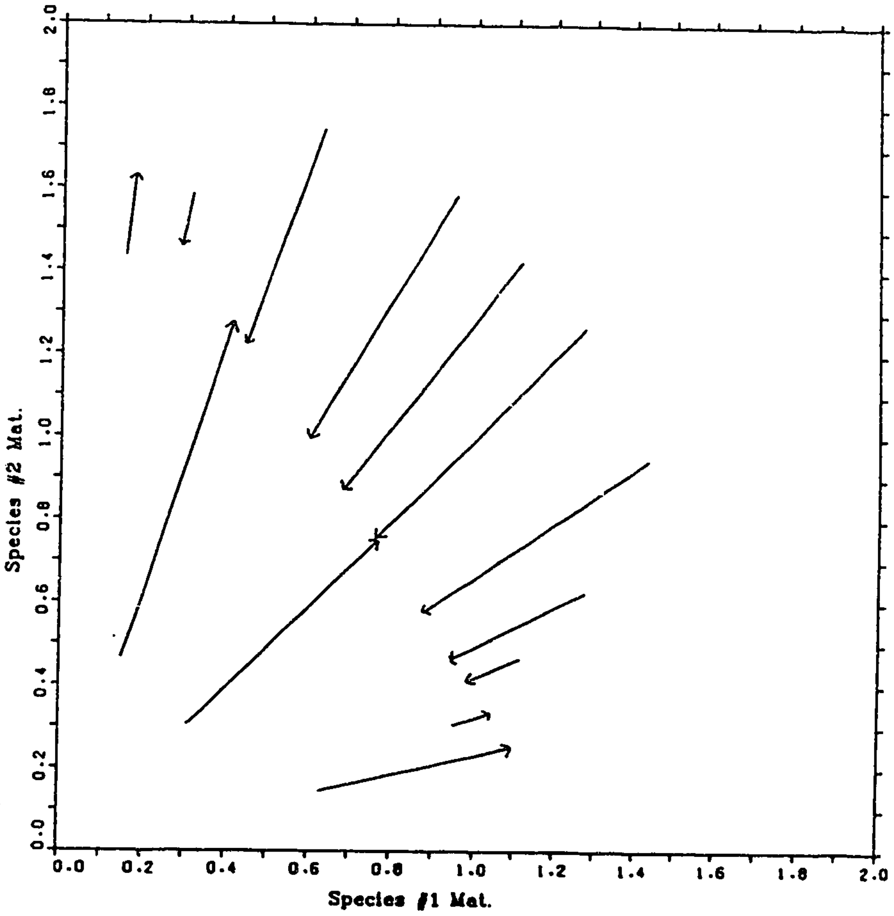
```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.2000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.3000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.2000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.3000000
Species2 Maturation Period:  1.7000000

Interior Equilibrium: Xi = 0.00253    Xm =  0.00828
                      Yi = 0.77345    Ym =  1.25412

Characteristic equation factor:   -0.00052

Condition A is true

X-boundary equilibrium: Xi =  0.25776   Xm =  0.84436
Y-boundary equilibrium: Yi =  0.78111   Ym =  1.26654
```

Figure 3.10 Competition Set #15



```
Species1 Intrinsic Growth Rate:  0.5000000
Species1 Mature Death Rate:  0.2000000
Species1 Immature Death Rate:  0.4000000
Species1 - Species2 Competition Constant:  0.3000000
Species1 Maturation Period:  0.7000000
Species2 Intrinsic Growth Rate:  0.5000000
Species2 Mature Death Rate:  0.2000000
Species2 Immature Death Rate:  0.4000000
Species2 - Species1 Competition Constant:  0.3000000
Species2 Maturation Period:  2.0000000

X-boundary equilibrium: Xi =  0.22861   Xm =  0.74888
Y-boundary equilibrium: Yi =  0.77323   Ym =  1.12332
```

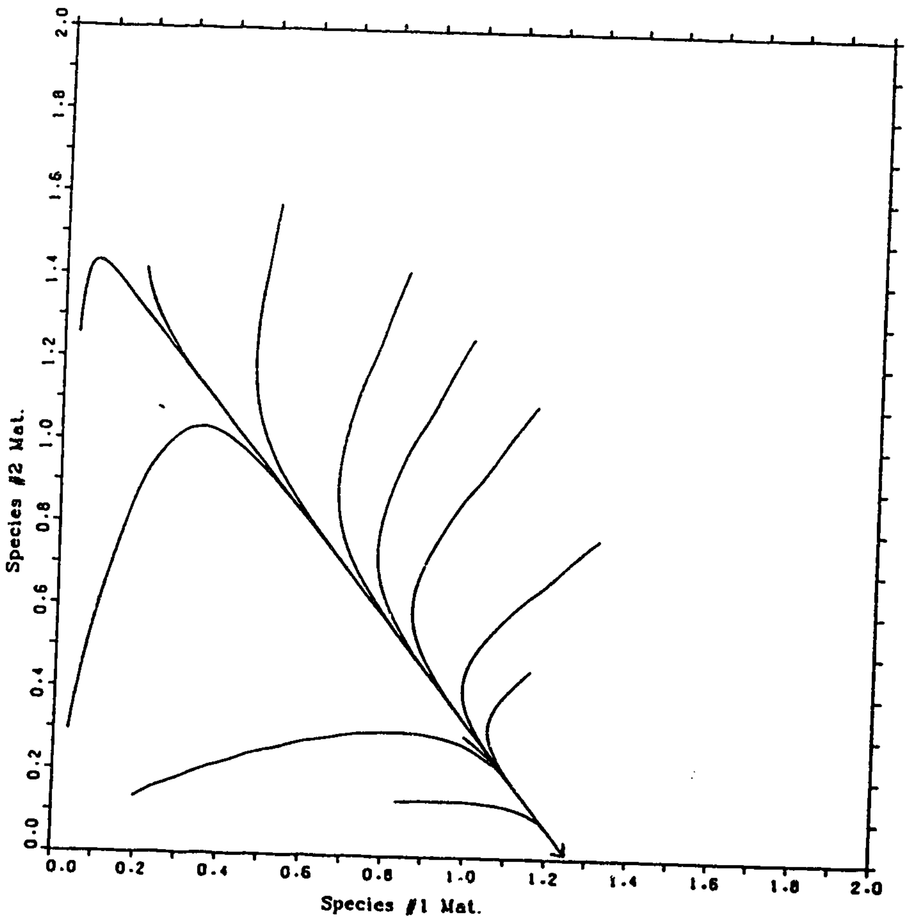
Figure 3.11 Competition Set #20



Species1 Intrinsic Growth Rate: 0.5000000
Species1 Mature Death Rate: 0.3000000
Species1 Immature Death Rate: 0.4000000
Species1 - Species2 Competition Constant: 0.2000000
Species1 Maturation Period: 0.7000000
Species2 Intrinsic Growth Rate: 0.5000000
Species2 Mature Death Rate: 0.2000000
Species2 Immature Death Rate: 0.4000000
Species2 - Species1 Competition Constant: 0.3000000
Species2 Maturation Period: 0.7000000

X-boundary equilibrium:	Xi = 0.38453	Xm = 1.25964
Y-boundary equilibrium:	Yi = 0.57680	Ym = 1.88946

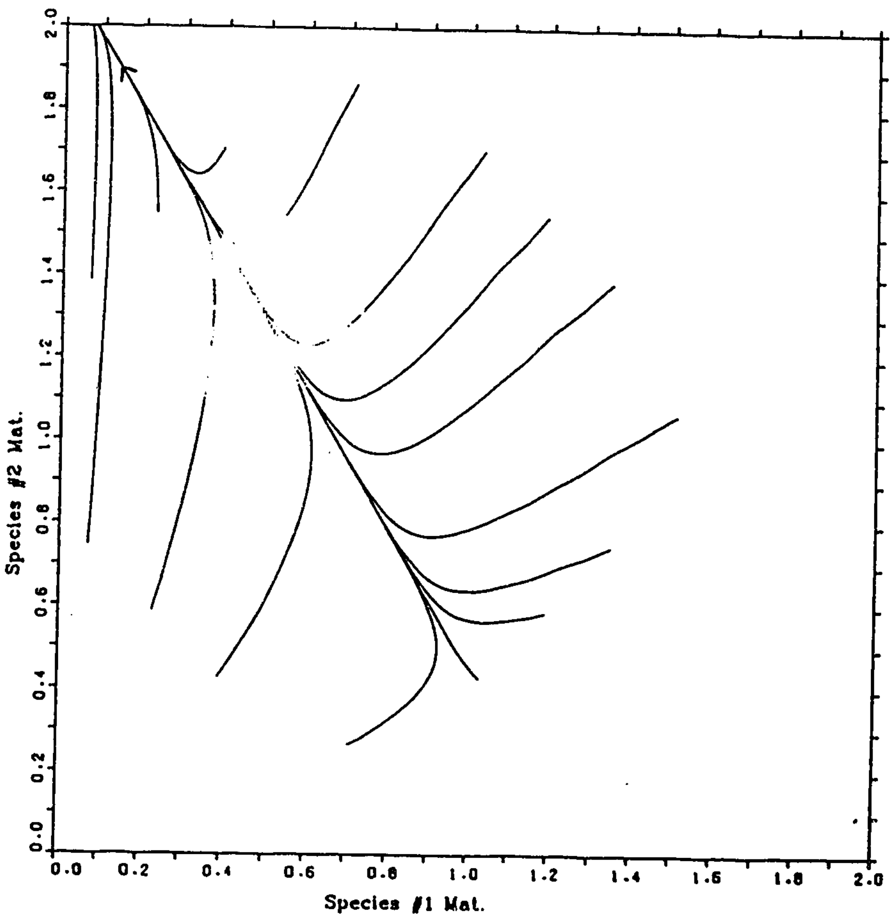
Figure 3.12 Competition Set #21



Species1 Intrinsic Growth Rate: 0.5000000
Species1 Mature Death Rate: 0.3000000
Species1 Immature Death Rate: 0.4000000
Species1 - Species2 Competition Constant: 0.2000000
Species1 Maturation Period: 0.7000000
Species2 Intrinsic Growth Rate: 0.5000000
Species2 Mature Death Rate: 0.2000000
Species2 Immature Death Rate: 0.4000000
Species2 - Species1 Competition Constant: 0.3000000
Species2 Maturation Period: 1.2000000

X-boundary equilibrium: Xi = 0.31483 Xm = 1.03131
Y-boundary equilibrium: Yi = 0.73716 Ym = 1.54696

Figure 3.13 Competition Set #22



Species1 Intrinsic Growth Rate: 0.5000000
Species1 Mature Death Rate: 0.3000000
Species1 Immature Death Rate: 0.4000000
Species1 - Species2 Competition Constant: 0.2000000
Species1 Maturation Period: 0.7000000
Species2 Intrinsic Growth Rate: 0.5000000
Species2 Mature Death Rate: 0.2000000
Species2 Immature Death Rate: 0.4000000
Species2 - Species1 Competition Constant: 0.3000000
Species2 Maturation Period: 0.4000000

X-boundary equilibrium: Xi = 0.43356 Xm = 1.42024
Y-boundary equilibrium: Yi = 0.39373 Ym = 2.13036

CHAPTER FOUR

A STAGE-STRUCTURED PREDATOR-PREY MODEL

4.1. Introduction

In this chapter we will consider a model of predator and prey populations that incorporates time delays into the system in order to take into account an immature stage of growth for both predator and prey. As we saw in the introduction, chapter one, much work has been done in the area of modelling predator-prey systems, and we discussed some work by several investigators who modified simple Lotka-Volterra systems that had the property of having all solutions periodic into systems that gave more realistic dynamics.

As well, we can also use more general models such as the Gause intermediate model (Freedman, 1987) to get results that better correspond with reality. Much work has also been done using these models, see for example Kuang and Freedman (1988) for a discussion on the uniqueness of limit cycles in Gause intermediate systems, or Hofbauer and So (1990) who give an example of a Gause type predator-prey model with concave prey isocline and at least two limit cycles. As well, Freedman and Wolkowicz (1986) and Wolkowicz (1988) investigate generalized Gause type models involving group defense.

An even more general model is the Kolmogorov model (Kolmogorov, 1936) which is expressed in the form

$$\dot{x}(t) = x(t)f(x,y)$$

$$\dot{y}(t) = y(t)g(x,y)$$

where conditions are imposed on f and g that makes x a prey and y a predator. This model was further modified and investigated by Rescigno and Richardson (1965), May (1972), Albrecht, Gatzke, and Wax (1973), and Albrecht, Gatzke Haddad and Wax (1974).

These more general models have been utilized by investigators to better understand some phenomena found in nature. The work done on group defense is an example. The paper by Freedman and Wolkowicz (1986) proposed a model of a predator-prey system where the prey exhibits group defense against the predator and where an enrichment of the prey food source could lead to extinction of that predator. Freedman and Quan (1988) then showed that, given such a system, it is possible to introduce a third population which will stabilize the system to allow all three populations to coexist without extinction.

The effect of parasites on a predator-prey system has also been investigated. Hadeler and Freedman (1989) proposed a model where a predator population could not survive on uninfected prey, but could avoid extinction if enough prey became infected by a parasite. Freedman (1990) also gave results in this area.

Another example of work done to account for conditions found in nature is the investigation by Hainzl (1988) on a predator-prey model that allows for satiation effects on the predator. As well, predator-prey models where the prey is dispersed in a patchy environment were given by Freedman and Takeuchi (1989). Mukherijee and Roy (1990) considered a model of a pair of predator-prey systems where the two prey species compete. Finally, Dunbar, Rybakowski,and Schmitt (1986) and Freedman and Shukla (1989) investigated models of diffusive predator-prey systems using partial differential equations.

The development of predator-prey models incorporating a time lag have not been ignored. May (1973) investigated models of vegetation-herbivore and vegetation-herbivore-carnivore populations where resource limitations have delayed effects. Freedman and Rao (1986) applied some results concerning a system of two autonomous ordinary differential equations with two discrete time delays to draw conclusions regarding a Kolmogorov predator-prey system.

In the next section we develop our time delay model. In section 4.3 we establish positivity and boundedness of the system. In section 4.4 we establish the existence of boundary equilibria and analyse their stability, and in section 4.5 we show when interior equilibria exist. In section 4.6 we discuss the stability of the interior equilibrium, indicating that the possibilitiy of a Hopf bifurcation exists. Then in section 4.7 we discuss the results of numerical simulations, and in the final section we discuss the conclusions that we can draw from the investigation.

4.2. Derivation of the Model

Let $x_i(t)$ and $x_m(t)$ denote the concentration of immature and mature prey populations, and let $y_i(t)$ and $y_m(t)$ denote the concentration of immature and mature predator populations, respectively. We will assume that the populations are growing in a closed, homogeneous environment. Let the time interval from birth to maturity of the prey and predator be τ and σ respectively, and denote the larger of these intervals by Δ, so that $\Delta = \max(\tau, \sigma)$ throughout this chapter.

We further assume that in the initial time interval, no immatures of either the prey or the predator are introduced except through birth from the existing respective mature populations. The model does not account for any immatures introduced into the system except through the birth process.

We also assume that in the initial time interval $[-\Delta, 0]$, no prey are introduced before time $t = -\tau$ and no predators are introduced before time $t = -\sigma$. Thus the system is started up by introducing mature prey between time $-\tau$ and 0, and by introducing mature predators into the system between time $-\sigma$ and 0.

In addition we assume that, once introduced, a prey individual does not drop out of the population through any means other than dying at the normal death rate, or being eaten by the predator under the predation conditions laid down by the model. Likewise, a predator does not drop out by any means other than normal death process.

The model we develop also assumes that the immature predators do not themselves hunt prey, but that they thrive on prey that are normally caught by the mature predators. We further simplify the model by assuming Lotka-Volterra dynamics on the parameters.

So we have strictly positive initial functions $\phi_i(t), \phi_m(t)$, and $\theta_m(t)$ which represent the immature prey, mature prey, and predator populations, respectively, in the initial time interval $-\Delta \leq t \leq 0$. We further require that $\phi_i(t), \phi_m(t)$, and $\theta_m(t)$ be continuous for $-\Delta \leq t \leq 0$. Of course, $\phi_m(t) = 0$ on $[-\Delta, -\tau]$ if $\Delta > \tau$, and $\theta_m(t) = 0$ on $[-\Delta, -\sigma)$ if $\Delta > \sigma$. As well, $\phi_i(t) \equiv 0$ on $[-\Delta, -\tau]$ since no prey matures are introduced into the system before $t = -\tau$. With these initial functions the model becomes,

$$\begin{aligned}
\dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \kappa y_m(t) x_i(t) - \alpha x_m(t-\tau) e^{-\gamma\tau} e^{-\kappa \int_{t-\tau}^{t} y_m(s) ds} \\
\dot{x}_m(t) &= \alpha x_m(t-\tau) e^{-\gamma\tau} e^{-\kappa \int_{t-\tau}^{t} y_m(s) ds} - \beta x_m^2(t) - y_m(t) \rho x_m(t) \\
\dot{y}_i(t) &= c y_m(t)[\kappa x_i(t) + \rho x_m(t)] - \varepsilon y_i(t) \\
&\qquad - c e^{-\varepsilon\sigma} y_m(t-\sigma)[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma)] \\
\dot{y}_m(t) &= c e^{-\varepsilon\sigma} y_m(t-\sigma)[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma)] - \xi y_m(t).
\end{aligned} \tag{4.1}$$

Note that $x_i(t)$ and $y_i(t)$ both satisfy on invariant integral conditions. The initial conditions gie us that at $t = 0$,

$$\begin{aligned}
x_i(t) &= \int_{-\tau}^{0} \alpha e^{-\gamma s} \phi_m(s) e^{-\kappa \int_s^0 \theta_m(r) dr} ds \\
y_i(0) &= \int_{-\sigma}^{0} c \theta_m(s)[\kappa \phi_i(s) + \rho \phi_m(s)] e^{\varepsilon s} ds.
\end{aligned}$$

For valued or $t > 0$, these initial conditions give us solutions of the form

$$\begin{aligned}
x_i(t) &= \int_{t-\tau}^{t} \alpha e^{-\gamma(t-s)} e^{-\gamma(t-s)} e^{-\kappa \int_s^t y_m(r) dr} x_m(s) ds \\
y_i(t) &= \int_{t-\sigma}^{t} e^{-\varepsilon(t-s)} y_m(s)[\kappa x_i(s) + \rho x_m(s)] ds.
\end{aligned}$$

In this manner the admissible initial conditions give us solutions that remain in the manifold defined by this condition, so that at any given time $t = 0$, the matures of either species are the accumulated survivors of those born between $t - \tau$ and t (or $t - \sigma$ and t).

Here, we assume all functions, in particular the initial functions, to be sufficiently smooth to ensure existence and uniqueness of the initial function problem (Driver, 1977). The parameters of system (4.1) are as follows:

α - birth rate of immature prey in terms of the concentration of mature prey,

β - logistic death rate of mature prey,

γ - intrinsic death rate of immature prey,

κ - intrinsic predation constant on immature prey,

ρ - intrinsic predation constant on mature prey,

τ - maturation time for prey species,

c - efficiency of conversion of prey biomass into predator biomass when prey is eaten by predator,

ε - intrinsic death rate of immature predator species,

ξ - intrinsic death rate of mature predator species,

σ - maturation time for predator species.

All constants are strictly greater than zero. The expression $\alpha x_m(t-\tau)e^{-\gamma\tau}e^{-\kappa\int_{t-\tau}^{t} y_m(s)ds}$ gives the number of prey individuals leaving the immature population and entering the mature population at time t. It is obtained by observing that at any time s, the number of immature prey who die from natural causes is $\gamma x_i(s)$, and the number of who are eaten by predators is $x_i(s)(\kappa y_m(s))$. Solving the expression

$$\dot{x}_i(s) = -x_i(s)(\gamma + \kappa y_m(s)), \text{ when } x_i(t_0) = \alpha x_m(t-\tau),$$

we get the number of immature prey who survive until they mature at time t as being $\alpha x_m(t-\tau)e^{-\gamma\tau}e^{-\kappa\int_{t-\tau}^{t} y_m(s)ds}$.

As well, for a set of initial conditions to be admissible as described above, $(\phi_i(t), \phi_m(t), \theta_i(t), \theta_m(t))$ must satisfy

$$\begin{aligned} \phi_i(t) &= \int_{-\tau}^{t} \alpha e^{\gamma s}\phi_m(s)e^{-\kappa\int_s^0 \theta_m(r)dr}ds \quad -\tau \leq t \leq 0, \\ \theta_i(t) &= \int_{-\sigma}^{t} c\theta_m(s)[\kappa\phi_i(s) + \rho\phi_m(s)]e^{\epsilon s}ds \quad -\sigma \leq t \leq 0. \end{aligned}$$

In the sequel we assume

$$\begin{aligned} x_i(t) &= \phi_i(t), \\ x_m(t) &= \phi_m(t), \\ y_i(t) &= \theta_i(t), \\ y_m(t) &= \theta_m(t), \end{aligned}$$

on the interval $-\Delta \leq t \leq 0$.

4.3. Positivity and Boundedness

We must now establish that the model (4.1) makes good biological sense, that is, given an admissible set of initial conditions, we must prove that solutions to system (4.1) do not become negative and that those solutions do not increase without bound.

First we show that the mature prey population remains positive:

THEOREM 4.1. *Given system (4.1) with an admissible set of initial conditions, the mature prey component $x_m(t)$ of a solution to system (4.1) remains positive.*

PROOF: Let $x_m(t)$ be the mature prey component of a solution of system (4.1) with an admissible set of initial conditions. Suppose $x_m(t) = 0$ for some value of t. Then let $t_0 = \inf_{t>0}\{t : x_m(t) = 0\}$. From the admissibility of initial conditions we know that $x_m(0) > 0$, so by continuity of solutions we can conclude that $t_0 > 0$. Since $y_m(t_0)\rho x_m(t_0) = 0$ we have,

$$\dot{x}_m(t_0) = \alpha x_m(t_0 - \tau)e^{-\gamma\tau}e^{-\kappa\int_{t_0-\tau}^{t_0} y_m(s)ds}.$$

Now since, α, $e^{-\gamma\tau}$, and $e^{-\kappa\int_{t_0-\tau}^{t_0} y_m(s)ds}$ are all positive, and by definition of t_0, $x_m(t_0 - \tau)$ is positive, we must have that $\dot{x}(t_0) > 0$, contradicting our definition of t_0. Therefore $x_m(t) > 0$ for all $t > 0$, and the theorem is proved.

Now we can prove that the immature prey population remains positive as well.

THEOREM 4.2. *Given system (4.1) with an admissible set of initial conditions, the immature prey component $x_i(t)$ of a solution to system (4.1) remains positive.*

Proof: Integrating the expression

$$\dot{x}_i(t) = \alpha x_m(t) - \gamma x_i(t) - \kappa y_m(t)x_i(t) - \alpha x_m(t-\tau)e^{-\gamma\tau}e^{-\kappa\int_{t-\tau}^{t} y_m(s)ds} \tag{4.2}$$

with the initial condition

$$x_i(0) = \int_{-\tau}^{0} \alpha e^{\gamma s}\phi_m(s)e^{-k\int_s^0 \theta_m(r)dr}ds, \text{ we get, for } t > 0,$$

$$\begin{aligned} x_i(t) = e^{-\gamma t}e^{-\kappa\int_0^t y_m(s)ds}[x_i(0) + \int_0^t e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds \\ - \int_0^t e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s-\tau)e^{-\gamma\tau}e^{-\kappa\int_{s-\tau}^{s} y_m(r)dr}ds] \end{aligned} \tag{4.3}$$

Assume that there exists some value of t such that $x_i(t) = 0$. Let t^* be the infimum of all such values of t. Then at t^* equation (4.3) gives,

$$\begin{aligned} x_i(0) + \int_0^{t^*} e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds \\ = \int_0^{t^*} e^{\gamma(s-\tau)}e^{\kappa\int_0^{s-\tau} y_m(r)dr}\alpha x_m(s-\tau)ds. \end{aligned} \tag{4.4}$$

With a change of variables $q = s - \tau$ in the right hand side of equation (4.4) and substituting s back for q, we get by combining the initial condition with equation (4.4),

$$\begin{aligned} \int_{-\tau}^{0} e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds + \int_0^{t^*} e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds \\ = \int_{-\tau}^{t^*-\tau} e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds \end{aligned}$$

or

$$\int_{-\tau}^{t^*} e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds = \int_{-\tau}^{t^*-\tau} e^{\gamma s}e^{\kappa\int_0^s y_m(r)dr}\alpha x_m(s)ds$$

which is clearly impossible. Therefore no such t^* exists and $x_i(t) > 0$ for all $t > 0$.

An alternate proof to theorem 4.2 results from the previously mentioned invariant integral condition satisfied by $x_i(t)$, where for $t > 0$, $x_i(t) = \alpha \int_{t-\tau}^{t} e^{-\gamma(t-s)} e^{-\kappa \int_s^t y_m(s)ds} x_m(s)ds$.

Now we are in a position to prove that the mature predator population remains positive.

THEOREM 4.3. *Given system (4.1) with an admissible set of initial conditions, the mature predator component $y_m(t)$ of a solution to system (4.1) remains positive.*

PROOF: Assume $y_m(t) = 0$ for some value of t. Then let $t_0 = \inf_{t>0}\{t : y_m(t) = 0\}$. t_0 must be positive by the admissibility of initial conditions and by continuity of solutions. Then at t_0,

$$\dot{y}_m(t_0) = ce^{-\epsilon\sigma} y_m(t-\sigma)[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma)].$$

But we have already proved that $x_i(t)$ and $x_m(t)$ are strictly positive. By definition of t_0, $y_m(t-\sigma) > 0$ so that $\dot{y}_m(t_0) > 0$, contradicting our definition of t_0. Therefore $y_m(t) > 0$ for all $t \geq 0$ and the theorem is proved.

Finally, we can prove that the immature predator population remains positive.

THEOREM 4.4. *Given system (4.1) with an admissible set of initial conditions, the immature predator component $y_i(t)$ of a solution to system (4.1) remains positive.*

PROOF: Integrating the expression

$$\begin{aligned}\dot{y}_i(t) = cy_m(t)[\kappa x_i(t) + \rho x_m(t)] - \varepsilon y_i(t)\\ - ce^{-\varepsilon\sigma} y_m(t-\sigma)[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma)]\end{aligned}$$

we get for $t > 0$,

$$\begin{aligned}y_i(t) = e^{-\varepsilon t}(y_i(0) + \int_0^t e^{\varepsilon s} c y_m(s)[\kappa x_i(s) + \rho x_m(s)]ds\\ - \int_0^t e^{\varepsilon s} ce^{-\varepsilon\sigma} y_m(s-\sigma)[\kappa x_i(s-\sigma) + \rho x_m(s-\sigma)]ds)\end{aligned} \tag{4.5}$$

Now we hypothesize the existence of a $t^* > 0$ such that $y_i(t^*) = 0$. Let t^* be the infimum of all such t^*. Then we get at t^*,

$$\begin{aligned}y_i(0) + \int_0^{t^*} ce^{\varepsilon s} y_m(s)[\kappa x_i(s) + \rho y_m(s)]ds\\ = \int_0^{t^*} ce^{\varepsilon(s-\sigma)} y_m(s-\sigma)[\kappa x_i(s-\sigma) + \rho x_m(s-\sigma)]ds\end{aligned} \tag{4.6}$$

Now we know that $y_i(t)$ satisfies the initial condition,

$$y_i(0) = \int_{-\sigma}^{0} ce^{\varepsilon s} y_m(s)[\kappa x_i(s) + \rho x_m(s)]ds \tag{4.7}$$

by admissibility of initial conditions.

Combining equation (4.6) and equation (4.7) we get,

$$\begin{aligned}\int_{-\sigma}^{0} ce^{\varepsilon s} y_m(s)[\kappa x_i(s) + \rho x_m(s)]ds + \int_0^{t^*} ce^{\varepsilon s} y_m(s)[\kappa x_i(s) + \rho x_m(s)]ds\\ = \int_0^{t^*} ce^{\varepsilon(s-\sigma)} y_m(s-\sigma)[\kappa x_i(s-\sigma) + \rho x_m(s-\sigma)]ds.\end{aligned} \tag{4.8}$$

By a change of variable $q = s - \sigma$ in the right hand side of equation (4.8) and then substituting s back for q and by combining the two expressions in the left hand side of equation (4.8), the equation becomes,

$$\int_{-\sigma}^{t^*} ce^{\varepsilon s} y_m(s)[\kappa x_i(s) + \rho x_m(s)]ds = \int_{-\sigma}^{t^*-\sigma} ce^{\varepsilon s} y_m(s)[\kappa x_i(s) + \rho x_m(s)]ds \tag{4.9}$$

Equation (4.9) is clearly impossible, so no such t^* can exist and $y_i(t) > 0$ for all $t > 0$. This proves the theorem.

Again, the invariant integral condition met by $y_i(t)$ gives us an alternate proof of the positivity of $y_i(t)$ for $t > 0$.

Note that theorem 4.3 and theorem 4.4 do not rule out the possibility of the predator going extinct; the values of $y_i(t)$ and $y_m(t)$ are not necessarily bounded away from zero. All we can conclude is that mathematically solving the system gives us values for $y_i(t)$ and $y_m(t)$ that do not go to zero in finite time. That is not to say that, in finite time, those values cannot get small enough to become biologically indistinguishable from zero, however.

In the single species case that we covered in chapter two, we saw that solutions to the prey system without the predator tended towards a globally asymptotically stable equilibrium point which was independent of initial conditions. Since in the presence of predators one might expect the numbers of prey to be even smaller, and since a finite number of prey can support only a finite number of predators, one might come to the conclusion that the system is dissipative, that is, that there would exist a bounded attracting region in the positive cone. We shall see that such a conclusion is correct.

THEOREM 4.5. *System (4.1) is dissipative.*

Proof: Let $z(t) = cx_i(t) + cx_m(t) + y_i(t) + y_m(t)$. Then

$$\begin{aligned}\dot{z}(t) &= c\dot{x}_i(t) + c\dot{x}_m(t) + \dot{y}_i(t) + \dot{y}_m(t) \\ &= c\alpha x_m(t) - c\gamma x_i(t) - c\beta x_m^2(t) - \varepsilon y_i(t) - \xi y_m(t).\end{aligned}$$

Let $\delta = \min(\gamma, \varepsilon, \xi)$, and we have

$$\begin{aligned}\dot{z}(t) &\leq c\alpha x_m(t) - \delta(cx_i(t) + y_i(t) + y_m(t)) - c\beta x_m^2(t) \\ &= -\delta z(t) + c(\alpha + \delta)x_m(t) - c\beta x_m^2(t)\end{aligned}$$

Now, the expression $c(\alpha+\delta)x_m(t) - c\beta x_m^2(t)$ has a maximum value of $c(\alpha+\delta)^2/4\beta$ when $x_m(t) = (\alpha + \delta)/2\beta$. So,

$$\dot{z}(t) \leq -\delta z + c(\alpha + \delta)^2/4\beta.$$

Now if $w(t)$ is a function satisfying the ordinary differential equation $\dot{w}(t) = -\delta w(t) + c(\alpha + \delta)^2/4\beta$ with the initial condition $w(0) = z(0)$, integrating would give us

$$w(t) = e^{-\delta t}z(0) + (c(\alpha + \delta)^2/4\beta\delta)(1 - e^{-\delta t})$$

Thus $\lim_{t\to\infty} w(t) = c(\alpha+\delta)^2/4\beta\delta$, and applying a comparison theorem (Birkhoff and Rota, 1969) we conclude that $\overline{\lim}_{t\to\infty} z(t) \leq c(\alpha+\delta)^2/4\beta\delta$. Now if $\overline{\lim}_{t\to\infty}(cx_i(t) + cx_m(t) + y_i(t) + y_m(t)) \leq c(\alpha + \delta)^2/4\beta\delta$, we can conclude that $\overline{\lim}_{t\to\infty}(x_i(t) + x_m(t) + y_i(t) + y_m(t)) \leq \overline{\lim}_{t\to\infty}(x_i(t) + x_m(t) + \frac{1}{c}y_i(t) + \frac{1}{c}y_m(t)) = \overline{\lim}_{t\to\infty} \frac{1}{c}z(t) \leq (\alpha + \delta)^2/4\beta\delta$ since $c < 1$. This value is independent of initial conditions, so system (4.1) is dissipative, and the theorem is proved.

We have shown that system (4.1) makes some biological sense in that solutions do not become negative and solutions are eventually bounded above by some value that is independent of initial conditions. We are now able to discuss the local and global behavior of solutions.

4.4. Existence and Local Stability of Boundary Equilibria

System (4.1) has three types of equilibria, namely the equilibrium point $E_0(0,0,0,0)$ at the origin, one equilibrium on the boundary, $E_1 = (\hat{x}_i, \hat{x}_m, 0, 0)$, and interior equilibria, possibly unique, $E^*(x_i^*, x_m^*, y_i^* y_m^*)$. The prey values at the boundary equilibrium E_1 are,

$$\hat{x}_i = \alpha^2\beta^{-1}\gamma^{-1}e^{-\gamma\tau}(1-e^{-\gamma\tau}) = \hat{x}_m\alpha\gamma^{-1}(1-e^{-\gamma\tau}),$$

$$\hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau}.$$

In order to analyse the local stability at the boundary equilibrium, we must linearize the system. To do this with the integro-differential system (4.1), we first make a substitution of a new variable into the system in order to transform the distributed delay $\int_{t-\tau}^{t} y_m(s)ds$ into a fixed delay which will simplify the linearization process. Thus we let $Y_m(t) = \int_{t-\tau}^{t} y_m(s)ds$ and add the equation $\dot{Y}_m(t) = y_m(t) - y_m(t-\tau)$ with the initial condition $Y_m(0) = \int_{-\tau}^{0} y_m(s)ds$ to the system. Here $y_m(s) = \theta_m(s)$ on the interval $[-\tau, 0]$. Thus we get the augmented system,

$$\begin{aligned}
\dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \kappa y_m(t) x_i(t) - \alpha x_m(t-\tau) e^{-\gamma\tau} e^{-kY_m(t)} \\
\dot{x}_m(t) &= \alpha x_m(t-\tau) e^{-\gamma\tau} e^{-\kappa Y_m(t)} - \beta x_m^2(t) - y_m(t) \rho x_m(t) \\
\dot{y}_i(t) &= c y_m(t)[\kappa x_i(t) + \rho x_m(t)] - \varepsilon y_i(t) - c e^{-\epsilon\sigma} y_m(t-\sigma)[\kappa x_i(t-\sigma) + \rho x_m(t \\
\dot{y}_m(t) &= c e^{-\epsilon\sigma} y_m(t-\sigma)[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma) - \xi y_m(t) \\
\dot{Y}_m(t) &= y_m(t) - y_m(t-\tau)
\end{aligned} \tag{4.10}$$

with the initial conditions as above.

Note that system (4.10), the augmented system, will have an equilibrium $F_0(0,0,0,0,0)$ at the origin, a boundary equilibrium $F_1(\hat{x}_i, \hat{x}_m, 0, 0, 0)$ and possible interior equilibria $F^*(x_i^*, x_m^*, y_i^*, y_m^*, \tau y_m^*)$. The values $\hat{x}_i, \hat{x}_m, x_i^*, x_m^*, y_i^*, y_m^*$ do not change from those given for the four dimensional system (4.1), since $Y_m(t)$ does not appear in the first four equations.

As well, we observe that there is a one-to-one correspondence between solutions to system (4.1) and a subset of solutions to the augmented system (4.10) by the relation,

$$(x_i(t), x_m(t), y_i(t), y_m(t)) \Leftrightarrow (x_i(t), x_m(t), y_i(t), y_m(t), \int_{t-\tau}^{t} y_m(s)ds). \tag{4.11}$$

The linearization of the augmented system (4.10) becomes,

$$\begin{pmatrix} \dot{u}_i(s) \\ \dot{u}_m(s) \\ \dot{v}_i(s) \\ \dot{v}_m(s) \\ \dot{V}_m(s) \end{pmatrix} = \begin{pmatrix} -\gamma + \kappa y_m(t) & \alpha & 0 & -\kappa x_i(t) & J_{15} \\ 0 & J_{22} & 0 & -\rho x_m(t) & J_{25} \\ c\kappa y_m(t) & J_{32} & -\varepsilon & J_{34} & 0 \\ 0 & 0 & 0 & -\xi & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} u_i(s) \\ u_m(s) \\ v_i(s) \\ v_m(s) \\ V_m(s) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & J^\tau_{12} & 0 & 0 & 0 \\ 0 & J^\tau_{22} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 \end{pmatrix} \begin{pmatrix} u_i(s-\tau) \\ u_m(s-\tau) \\ v_i(s-\tau) \\ v_m(s-\tau) \\ V_m(s-\tau) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ J^\sigma_{31} & J^\sigma_{32} & 0 & J^\sigma_{34} & 0 \\ J^\sigma_{41} & J^\sigma_{42} & 0 & J^\sigma_{44} & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} u_i(s-\sigma) \\ u_m(s-\sigma) \\ v_i(s-\sigma) \\ v_m(s-\sigma) \\ V_m(s-\sigma) \end{pmatrix}. \tag{4.12}$$

where

$$J_{15} = \kappa\alpha x_m(t-\tau)e^{-\gamma\tau}e^{-\kappa Y_m(t)}$$

$$J_{22} = -2\beta x_m(t) - \rho y_m(t)$$

$$J_{25} = -\kappa\alpha x_m(t-\tau)e^{-\gamma\tau}e^{-\kappa Y_m(t)}$$

$$J_{32} = c\rho y_m(t)$$

$$J_{34} = c[\kappa x_i(t) + \rho x_m(t)]$$

$$J^\tau_{12} = -\alpha e^{-\gamma\tau}e^{-\kappa Y_m(t)}$$

$$J^\tau_{22} = \alpha e^{-\gamma\tau}e^{-\kappa Y_m(t)}$$

$$J^\sigma_{31} = -c\kappa e^{-\epsilon\sigma}y_m(t-\sigma)$$

$$J^\sigma_{32} = -c\rho e^{-\epsilon\sigma}y_m(t-\sigma)$$

$$J^\sigma_{34} = -ce^{-\epsilon\sigma}[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma)]$$

$$J^\sigma_{41} = c\kappa e^{-\epsilon\sigma}y_m(t-\sigma)$$

$$J^\sigma_{42} = c\rho e^{-\epsilon\sigma}y_m(t-\sigma)$$

$$J_{44} = ce^{-\epsilon\sigma}[\kappa x_i(t-\sigma) + \rho x_m(t-\sigma)]$$

Then, at the equilibrium point F_0 at the origin all the J_{ij} values are zero except for $J^{\tau}_{12} = -J^{\tau}_{22} = -\alpha e^{-\gamma\tau}$.

Thus at E_0 the linearization becomes

$$\begin{pmatrix} \dot{u}_i(t) \\ \dot{u}_m(t) \\ \dot{v}_i(t) \\ \dot{v}_m(t) \\ \dot{V}_m(t) \end{pmatrix} = \begin{pmatrix} -\gamma & \alpha & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\varepsilon & 0 & 0 \\ 0 & 0 & 0 & -\xi & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} u_i(t) \\ u_m(t) \\ v_i(t) \\ v_m(t) \\ V_m(t) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & -\alpha e^{-\gamma\tau} & 0 & 0 & 0 \\ 0 & \alpha e^{-\gamma\tau} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 \end{pmatrix} \begin{pmatrix} u_i(s-\tau) \\ u_m(s-\tau) \\ v_i(s-\tau) \\ v_m(s-\tau) \\ V_m(s-\tau) \end{pmatrix} \tag{4.13}$$

with there being no nonzero terms in any variables in $(t-\sigma)$. The characteristic equation then becomes,

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\gamma\tau}e^{-\lambda\tau} & 0 & 0 & 0 \\ 0 & \lambda-\alpha e^{-\gamma\tau}e^{-\lambda\tau} & 0 & 0 & 0 \\ 0 & 0 & \lambda+\varepsilon & 0 & 0 \\ 0 & 0 & 0 & \lambda+\xi & 0 \\ 0 & 0 & 0 & -1+e^{-\lambda\tau} & \lambda \end{vmatrix} = 0$$

As we note later, the eigenvalue $\lambda = 0$ in the augmented system is not an eigenvalue that corresponds with any admissible initial function of the original system. The agumented system then has three negative eigenvalues; $\lambda = -\gamma$, $\lambda = -\varepsilon$, and $\lambda = -\xi$. As well, we have eigenvalues resulting from roots of the expression $\lambda = \alpha e^{-\tau(\gamma+\lambda)}$. We can readily see that this expression has a real, positive root by observing that when $\lambda = 0$, the right hand side of the expression is strictly positive, and that as λ increases, the right hand side decreases to zero.

Therefore, F_0 is a "saddle" point, and by our previous discussion we can conclude that E_0 is also a "saddle" point equilibrium.

Next, we observe that any solution about E_0 that has a component that is in the eigenspace of an eigenvalue that has a nonzero imaginary part will oscillate about E_0. This would necessitate some component or components of the solution going from positive to negative values. But we have shown that given a set of admissible initial conditions, this does not happen. Thus no set of initial conditions can have a component in the eigenspace of a complex eigenvalue.

As a further remark, we will note that the eigenspace of the zero eigenvalue consists of functions $\omega(t)$ for which,

$$0 = \gamma\omega_1 - (\alpha + \alpha e^{-\gamma\tau})\omega_2$$

$$0 = -\alpha e^{-\gamma\tau}\omega_2$$

$$0 = \varepsilon\omega_3$$

$$0 = \xi\omega_4$$

$$0 = (-1+1)\omega_5.$$

So $\omega_5(t)$ is arbitrary, and all the rest of the components of $\omega(t)$ are zero. Such a function does not correspond with any nonzero admissible initial function of system (4.1).

Next, we investigate the behavior of system (4.1) near the boundary equilibrium point E_1. To do this we look at the behavior of the augmented system

(4.10) near the equilibrium point F_1, noting the correspondence (4.11) between solutions of system (4.1) and the augmented system (4.10). At F_1 the linearized system of the augmented system becomes,

$$L(F_1) = \begin{pmatrix} \dot{u}_i(t) \\ \dot{u}_m(t) \\ \dot{v}_i(t) \\ \dot{v}_m(y) \\ \dot{V}_m(t) \end{pmatrix} = \begin{pmatrix} -\gamma & \alpha & 0 & -\kappa\hat{x}_i & \kappa\alpha\hat{x}_m e^{-\gamma\tau} \\ 0 & -2\beta\hat{x}_m & 0 & -\rho\hat{x}_m & -\kappa\alpha\hat{x}_m e^{-\gamma\tau} \\ 0 & 0 & -\varepsilon & c[\kappa\hat{x}_i + \rho\hat{x}_m)] & 0 \\ 0 & 0 & 0 & -\xi & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix} \begin{pmatrix} u_i(t) \\ u_m(t) \\ v_i(t) \\ v_m(y) \\ V_m(t) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & -\alpha e^{-\gamma\tau} & 0 & 0 & 0 \\ 0 & \alpha e^{-\gamma\tau} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 \end{pmatrix} \begin{pmatrix} u_i(t-\tau) \\ u_m(t-\tau) \\ v_i(t-\tau) \\ v_m(t-\tau) \\ V_m(t-\tau) \end{pmatrix} +$$

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -ce^{\varepsilon\sigma}[\kappa\hat{x}_i + \rho\hat{x}_m] & 0 \\ 0 & 0 & 0 & +ce^{\varepsilon\sigma}[\kappa\hat{x}_i + \rho\hat{x}_m] & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} u_i(t-\sigma) \\ u_m(t-\sigma) \\ v_i(t-\sigma) \\ v_m(t-\sigma) \\ V_m(t-\sigma) \end{pmatrix}.$$

Then the characteristic equation of the augmented system is,

$$\begin{vmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\gamma\tau}e^{-\tau\lambda} & 0 & \kappa\hat{x}_i & -\kappa\alpha\hat{x}_m e^{-\gamma\tau} \\ 0 & \lambda+2\beta\hat{x}_m - \alpha e^{-\gamma\tau}e^{-\tau\lambda} & 0 & \rho\hat{x}_m & \kappa\alpha\hat{x}_m e^{-\gamma\tau} \\ 0 & 0 & \lambda+\varepsilon & a_1 & 0 \\ 0 & 0 & 0 & a_2 & 0 \\ 0 & 0 & 0 & -1+e^{-\tau\lambda} & \lambda \end{vmatrix} = 0$$

where here $a_1 = -c[\kappa\hat{x}_i+\rho\hat{x}_m](1-e^{-\sigma(\varepsilon+\lambda)})$ and $a_2 = \lambda-c[\kappa\hat{x}_i+\rho\hat{x}_m]e^{-\sigma(\varepsilon+\lambda)}+\xi$.

We see immediately that the augmented system has two negative eigenvalues, $\lambda = -\gamma$ and $\lambda = -\varepsilon$. We then observe that we get more eigenvalues from the expressions,

$$\lambda = -2\beta\hat{x}_m + \alpha e^{-\gamma\tau}e^{-\tau\lambda} \tag{4.14}$$

$$\lambda = c[\kappa\hat{x}_i + \rho\hat{x}_m]e^{-\sigma(\varepsilon+\lambda)} - \xi \tag{4.15}$$

Finally we observe that $\lambda = 0$ is also an eigenvalue of the augmented system.

Let us first consider equation (4.14). Since $\hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau}$, we can rewrite equation (4.14) as,

$$\lambda = \alpha e^{-\gamma\tau}e^{-\tau\lambda} - 2\alpha e^{-\gamma\tau} = \alpha e^{-\gamma\tau}(e^{-\tau\lambda} - 2).$$

when $\lambda = 0$ the right hand side is negative,and as λ decreases, the right hand side increases, becoming positive when λ decreases below $-\frac{1}{\tau}\ell n2$. Thus equation (4.14) has a negative, real solution.

We can say more; all solutions of equation (4.14) have a negative real part. To see this, let $\lambda = a + ib$. Then equation (4.14) becomes

$$a + ib = \alpha e^{-\gamma\tau}e^{-a\tau}(\cos\tau b - i\sin\tau b) - 2\alpha e^{-\gamma\tau}$$

or,

$$a + 2\alpha e^{-\gamma\tau} = \alpha e^{-\gamma\tau}e^{-a\tau}\cos\tau b$$

$$b = -\alpha e^{-\gamma\tau}e^{-a\tau}\sin\tau b.$$

Squaring and adding we get,

$$(a + 2\alpha e^{-\gamma\tau})^2 + b^2 = (\alpha e^{-\gamma\tau}e^{-a\tau})^2.$$

Now suppose $a \geq 0$. We would then have, since $\lambda = 0$ is not a solution,

$$(2\alpha e^{-\gamma\tau})^2 < (a + 2\alpha e^{-\gamma\tau})^2 + b^2 = (\alpha e^{-\gamma\tau}e^{-a\tau})^2 \leq (\alpha e^{-\gamma\tau})^2$$

contradicting our assumption that $a \geq 0$. Therefore equation (4.14) has at least one negative root, and any other roots of equation (4.14) will have a strictly negative real part.

We now consider equation (4.15).

$$\lambda = ce^{-\sigma(e+\lambda)}(\kappa\hat{x}_i + \rho\hat{x}_m) - \xi.$$

This expression will have a positive, real solution if $H = ce^{-\sigma e}[\kappa\hat{x}_i + \rho\hat{x}_m] > \xi$.

Now suppose $ce^{-\sigma e}[\kappa\hat{x}_i + \rho\hat{x}_m] < \xi$. We shall see that under these conditions, equation (4.15) has no solution with positive real part. To see this, let $H = ce^{-\sigma e}[\kappa\hat{x}_i + \rho\hat{x}_m]$, and let $\lambda = a + ib$. Then equation (4.15) becomes

$$\lambda = He^{-\sigma\lambda} - \xi = a + ib = He^{-\sigma a}(\cos\sigma b - i\sin\sigma b) - \xi.$$

or

$$a + \xi = He^{-\sigma a}\cos\sigma b$$

$$b = -He^{-\sigma a}\sin\sigma b.$$

Squaring and adding, we get

$$(a+\xi)^2 + b^2 = (He^{-\sigma a})^2$$

But we are assuming that $H < \xi$ and $a > 0$, so we have

$$\xi^2 < (a+\xi)^2 + b^2 = (He^{-\sigma a})^2 < H^2$$

contradicting our hypothesis. Therefore if $H < \xi$ then equation (4.15) has no solution with zero or positive real part.

Thus we see that if $ce^{-\sigma\epsilon}[\kappa\hat{x}_i + \rho\hat{x}_m] < \xi$ then the boundary equilibrium E_1 is stable, and if $ce^{-\sigma\epsilon}[\kappa\hat{x}_i + \rho\hat{x}_m] > \xi$, the equilibrium E_1 is an unstable saddle.

Now we consider the eigenvalue $\lambda = 0$. We will look at the eigenvectors corresponding to this eigenvalue. Let us denote the linearized system of the augmented system (4.10) at the equilibrium point F_1 by $L(F_1)$. Let $\omega(t)$ be a function satifying $L(F_1)\omega(t) = \lambda\omega(t)$. Then,

$$\lambda\omega_1(t) = -\gamma\omega_1 + (\alpha e^{-\tau(\gamma+\lambda)})\omega_2 - \kappa\hat{x}_i\omega_4 + \kappa\alpha\hat{x}_m e^{-\gamma\tau}\omega_5 \tag{4.16a}$$

$$\lambda\omega_2(t) = (-2\beta\hat{x}_m + \alpha e^{-\tau(\lambda+\gamma)})\omega_2 - \rho\hat{x}_m\omega_4 - \kappa\alpha\hat{x}_m e^{-\gamma\tau} w_5 \tag{4.16b}$$

$$\lambda\omega_3(t) = -\varepsilon w_3 - c[\kappa\hat{x}_i + \rho\hat{x}_m](1 - e^{-\sigma(\epsilon+\lambda)})\omega_4 \tag{4.16c}$$

$$\lambda\omega_4(t) = \{c[\kappa\hat{x}_i + \rho\hat{x}_m]e^{-\sigma(\epsilon+\lambda)} - \xi\}\omega_4 \tag{4.16d}$$

$$\lambda\omega_5(t) = (1 - e^{-\tau\lambda})\omega_4 \tag{4.16e}$$

If λ is an eigenvalue such that $\lambda = 0$, $\omega_4(t) = 0$ by equation (4.16e), making $\omega_5(t)$ arbitrary. $0 = -\varepsilon\omega_3(t)$ by equation (4.16c) implying that $\omega_3 = 0$. Thus no admissible initial function starting in the interior can be in the eigenspace corresponding to the eigenvalue $\lambda = 0$.

Thus, we have shown that if $H < \xi$, all eigenvalues except $\lambda = 0$ have negative real part, and that the eigenspace corresponding to the zero eigenvalue contains no admissible initial functions or solutions. We can conclude then, that given system (4.10) with admissible initial functions, if $H < \xi$, the boundary equilibrium F_1 will act as an asymptotically stable equilibrium. If $H > \xi$, F_1 will be unstable, since at least one positive, real eigenvalue will exist.

Thus our analysis indicates that given system (4.1) with admissible initial functions, the boundary point E_1 will be asymptotically stable if $H < \xi$, but will be unstable if $H > \xi$. This is intuitive, since H represents the growth rate of the predator when the prey population is at its carrying capacity, and ξ is the death rate of the predator. Clearly, if the growth rate of the predator is less than its death rate when its food supply is at its carrying capacity, the predator cannot survive. If $H > \xi$, some predator population will be supported by the prey population, its numbers being dependent on how large $H - \xi$ is. Indeed, computer evidence indicates that when $H > \xi$, system (4.1) exhibits persistence.

4.5. Existence of an Interior Equilibrium

In this section we consider the existence of an interior equilibrium E^* for system (4.1). Such an equilibrium must result from a solution of

$$\begin{aligned}
0 &= -x_i^*(\gamma + \kappa y_m^*) + (\alpha x_m^* - \alpha e^{-\gamma\tau} e^{-\kappa y_m^* \tau} x_m^*) \\
0 &= -y_m^* \rho x_m^* + x_m^*(\alpha e^{-\gamma\tau} e^{-\kappa y_m^* \tau} - \beta x_m^*) \\
0 &= c y_m^*(\kappa x_i^* + \rho x_m^*)(1 - e^{-\varepsilon\sigma}) - \varepsilon y_i^* \\
0 &= c y_m^* e^{-\varepsilon\sigma}(\kappa x_i^* + \rho x_m^*) - \xi y_m^*
\end{aligned} \tag{4.17}$$

with each of x_i^*, x_m^*, y_i^*, and y_m^* being strictly greater than zero. Rewriting the equations (4.17) we get,

$$x_i^* = \frac{\alpha x_m^*(1 - e^{-\tau(\gamma+\kappa y_m^*)}}{\gamma + \kappa y_m^*} \tag{4.18a}$$

$$y_m^* = \rho^{-1}(\alpha e^{-\tau(\gamma+\kappa y_m^*)} - \beta x_m^*) \tag{4.18b}$$

$$y_i^* = c\varepsilon^{-1} y_m^*(\kappa x_i^* + \rho x_m^*)(1 - e^{-\varepsilon\sigma}) \tag{4.18c}$$

$$\xi = ce^{-\varepsilon\sigma}(\kappa x_i^* + \rho x_m^*) \tag{4.18d}$$

Now, equation (4.18d) reflects the fact that at any interior equilibrium, the rate at which new mature predators are being brought into the system must equal the mature predator death rate.

Equation (4.18b) gives a relation between x_m^* and y_m^*. It will have a solution for any nonzero value of x_m^* such that $\alpha e^{-\gamma\tau} - \beta x_m^* > 0$. This can be easily seen since if $y_m^* = 0$ such a value of x_m^* would give the right hand side of equation (4.18b) a positive value, and increasing y_m^* would cause the right side of equation (4.18b) to decrease monotonically to zero. Thus for every $x_m^* > 0$ such that $\alpha e^{-\gamma\tau} - \beta x_m^* > 0$ one and only one $y_m^* > 0$ can be found to solve equation (4.18b).

Then for any solution (x_m^*, y_m^*) of equation (4.18b), equation (4.18a) gives us a value for x_i^* and equation (4.18c) gives us a value for y_i^*. Note that if x_m^* is a very small value, then equation (4.18a) will give a small value for x_i^*. And as x_m^* increases toward $\hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau}$, equation (4.18b) will give values of y_m^*

that decrease toward zero. Then values of x_i^* obtained by equation (4.18a) will increase toward $\hat{x}_i = \hat{x}_m \alpha \gamma^{-1}(1 - e^{-\gamma\tau})$.

We see then, that as x_m^* increases from zero to $\hat{x}_m$, x_i^* will increase from zero to $\hat{x}_i$. Thus if $ce^{-\epsilon\sigma}(\kappa\hat{x}_i + \rho\hat{x}_m) > \xi$, there will be at least one value (x_i^*, x_m^*) such that equation (4.18d) is satisfied, giving us an interior equilibrium $(x_i^*, x_m^*, y_i^*, y_m^*)$.

We can then summarize the preceeding discussion in the form of a theorem:

THEOREM 4.6. *Given system(4.1), if* $ce^{-\epsilon\sigma}(\kappa\hat{x}_i + \rho\hat{x}_m) > \xi$ *then at least one interior equilibrium exists.*

Conditions for uniqueness of the interior equilibrium seem difficult to obtain at this time but numerical evidence indicates that uniqueness of interior equilibria is easy to achieve.

Observe that an interior equilibrium for system (4.1) will also be an interior equilibrium for the augmented system (4.10),and that an interior equilibrium for the augmented system will be an interior equilibrium for system (4.1).

4.6. Hopf Bifurcation at Interior Equilibria

Now, given the existence of an interior equilibrium, we would like to investigate its stability. Specifically, we consider the existence of a Hopf bifurcation at E^*.

We first calculate the characteristic equation about E^*. Referring to equation (4.12) we compute the characteristic equation to be,

$$\begin{vmatrix} \lambda + a_{11} & a_{12} & 0 & a_{14} & a_{15} \\ 0 & \lambda + a_{22} & 0 & a_{24} & a_{25} \\ a_{31} & a_{32} & \lambda + \varepsilon & a_{34} & 0 \\ a_{41} & a_{42} & 0 & \lambda + a_{44} & 0 \\ 0 & 0 & 0 & a_{54} & \lambda \end{vmatrix} = 0.$$

Since $(\lambda + \varepsilon)$ factors out, this is equivalent to,

$$(\lambda + \varepsilon) \begin{vmatrix} \lambda + a_{11} & a_{12} & a_{14} & a_{15} \\ 0 & \lambda + a_{22} & a_{24} & a_{25} \\ a_{41} & a_{42} & \lambda + a_{44} & 0 \\ 0 & 0 & a_{54} & \lambda \end{vmatrix} = 0.$$

where

$$a_{11} = \gamma + \kappa y_m^*$$

$$a_{12} = -\alpha + \alpha e^{-\tau(\gamma + \kappa y_m^* + \lambda)}$$

$$a_{14} = \kappa x_i^*$$

$$a_{15} = -\kappa \alpha x_m^* e^{-\tau(\gamma + \kappa y_m^*)}$$

$$a_{22} = 2\beta x_m^* + \rho y_m^* - \alpha e^{-\tau(\gamma + \kappa y_m^* + \lambda)}$$

$$a_{24} = \rho x_m^*$$

$$a_{25} = \kappa \alpha x_m^* e^{-\tau(\gamma + \kappa y_m^*)}$$

$$a_{41} = -c\kappa y_m^* e^{-\sigma(\varepsilon + \lambda)}$$

$$a_{42} = -c\rho y_m^* e^{-\sigma(\varepsilon + \lambda)}$$

$$a_{44} = -c[\kappa x_i^* + \rho x_m^*] e^{-\sigma(\varepsilon + \lambda)} + \xi$$

$$a_{54} = e^{-\tau\lambda} - 1$$

Thus the characteristic equation becomes

$$\begin{aligned}(\lambda+\varepsilon)[\lambda\{(\lambda+a_{11})[(\lambda+a_{22})(\lambda+a_{44})-a_{24}a_{42}]\\ +a_{41}(a_{12}a_{24}-a_{14}(\lambda+a_{22}))\}\\ -a_{54}\{(\lambda+a_{11})(-a_{25}a_{42})+a_{41}(a_{12}a_{25}-a_{15}(\lambda+a_{22})\}]=0\end{aligned}$$

or,

$$\begin{aligned}(\lambda+\varepsilon)[\lambda^4+(a_{11}+a_{22}+a_{44})\lambda^3+(a_{11}a_{22}+a_{11}a_{44}+a_{22}a_{44})\lambda^2\\ +(a_{11}a_{22}a_{44})\lambda-a_{24}a_{42}\lambda^2-a_{11}a_{24}a_{42}\lambda+a_{12}a_{24}a_{41}\lambda\\ -a_{14}a_{41}\lambda^2-a_{14}a_{22}a_{41}\lambda+a_{25}a_{42}a_{54}\lambda+a_{11}a_{25}a_{42}a_{54}\\ -a_{12}a_{25}a_{41}a_{54}+a_{15}a_{41}a_{54}\lambda+a_{15}a_{22}a_{41}a_{54}]=0\end{aligned}$$

so that the characteristic equation equals,

$$\begin{aligned}(\lambda+\varepsilon)[\lambda^4+(a_{11}+a_{22}+a_{44})\lambda^3+(a_{11}a_{22}+a_{11}a_{44}+a_{22}a_{44}-a_{24}a_{42}-a_{14}a_{41})\lambda^2\\ +(a_{11}a_{22}a_{44}-a_{11}a_{24}a_{42}+a_{12}a_{24}a_{41}-a_{14}a_{22}a_{41}\\ +a_{25}a_{42}a_{54}+a_{15}a_{41}a_{54})\lambda\\ +(a_{11}a_{25}a_{42}a_{54}-a_{12}a_{25}a_{41}a_{54}+a_{15}a_{22}a_{41}a_{54})]=0\end{aligned}$$

Clearly $\lambda=-\varepsilon$ is an eigenvalue. For the rest of the characteristic equation we substitute the original algebraic expressions back in for the a_{ij} components, at the same time observing that since the equilibrium point $(x_i^*, x_m^*, y_i^*, y_m^*)$ solves equations (4.18) we have that

$$ce^{-\varepsilon\sigma}(\kappa x_i^*+\rho x_m^*)=\xi$$

so that

$$a_{44} = -\xi e^{-\sigma\lambda} + \xi = \xi(1 - e^{-\sigma\lambda}).$$

In this manner the characteristic equation becomes,

$$\begin{aligned}
&\lambda^4 + [(\gamma + \kappa y_m^*) + (2\beta x_m^* + \rho y_m^*) - (\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)}) + \xi(1 - e^{-\sigma\lambda})]\lambda^3 \\
&\quad + [(\gamma + \kappa y_m^*)(2\beta x_m^* + \rho y_m^*) - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)}) \\
&\quad + (\gamma + \kappa y_m^*)(\xi(1 - e^{-\sigma\lambda})) + (2\beta x_m^* + \rho y_m^* - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})\xi(1 - e^{-\sigma\lambda}) \\
&\quad + (\rho_m(x_m^*))(cy^*\rho e^{-\sigma(\varepsilon+\lambda)}) + (\kappa x_i^*)(c\kappa y_m^* e^{-\sigma(\varepsilon+\lambda)})]\lambda^2 \\
&\quad + [(\gamma + \kappa y_m^*)(2\beta x_m^* + \rho y_m^* - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(\xi(1 - e^{-\sigma\lambda})) \\
&\quad + (\gamma + \kappa y_m^*)(\rho x_m^*)(c\rho y_m^* e^{-\sigma(\varepsilon+\lambda)}) \\
&\quad + (\alpha - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(\rho x_m^*)(c\kappa y_m^* e^{-\sigma(\varepsilon+\lambda)}) \\
&\quad + (\kappa x_i^*)(2\beta x_m^* + \rho y_m^* - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(c\kappa y_m^* e^{-\sigma(\varepsilon+\lambda)}) \\
&\quad + (\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\rho y_m^* e^{-\sigma(\varepsilon+\lambda)})(1 - e^{-\tau\lambda}) \\
&\quad + (\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\varepsilon+\lambda)})(e^{-\gamma\lambda} - 1)]\lambda \\
&\quad + [(\gamma + \kappa y_m^*)(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\rho y_m^* e^{-\sigma(\varepsilon+\lambda)})(1 - e^{-\tau\lambda}) \\
&\quad + (\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(2\beta x_m^* + \rho y_m^* - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)}) \\
&\qquad\qquad (c\kappa y_m^* e^{-\sigma(\varepsilon+\lambda)})(e^{-\tau\lambda} - 1) \\
&\quad - (\alpha - \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\varepsilon+\lambda)})(e^{-\tau\lambda} - 1)] = 0
\end{aligned}$$

Then moving those expressions in the equation that involve exponential functions in λ over to the right hand side of the equal sign we get,

$$\lambda^4 + [(\gamma + \kappa y_m^*) + (2\beta x_m^* + \rho y_m^*) + \xi]\lambda^3$$

$$+ [(\gamma + \kappa y_m^*)(2\beta x_m^* + \rho y_m^*) + (\gamma + \kappa y_m^*)\xi + (2\beta x_m^* + \rho y_m^*)\xi]\lambda^2$$

$$+ [(\gamma + \kappa y_m^*)(2\beta x_m^* + \rho y_m^*)\xi]\lambda$$

$$= [\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)} + \xi e^{-\sigma\lambda}]\lambda^3$$

$$+ [(\gamma + \kappa y_m^*)(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)}) + (\gamma + \kappa y_m^*)\xi e^{-\sigma\lambda}$$

$$+ (\xi\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)}) + (2\beta x_m^* + \rho y_m^*)\xi e^{-\sigma\lambda} - \alpha\xi e^{-\tau(\gamma+\kappa y_m^*+\lambda)} e^{-\sigma\lambda}$$

$$- \rho x_m^*(c\rho y_m^* e^{-\sigma(\epsilon+\lambda)}) - (\kappa x_i^*)(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})]\lambda^2$$

$$+ [(\gamma + \kappa y_m^*)(2\beta x_m^* + \rho y_m^*)\xi e^{-\sigma\lambda} + (\gamma + \kappa y_m^*)\xi(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})$$

$$- (\gamma + \kappa y_m^*)(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)}\xi e^{-\sigma\lambda} - (\gamma + \kappa y_m^*)(c\rho^2 x_m^* y_m^*)e^{-\sigma(\epsilon+\lambda)})$$

$$- (\alpha\rho x_m^* c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)}) + (\rho x_m^* \alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})$$

$$- (\kappa x_i^*)(2\beta x_m^* + \rho y_m^*)(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})$$

$$+ (\kappa x_i^*)(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})$$

$$- (\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\rho y_m^* e^{-\sigma(\epsilon+\lambda)})$$

$$+ (\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\rho y_m^* e^{-\sigma(\xi+\lambda)})e^{-\tau\lambda}$$

$$+ (\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})$$

$$
\begin{aligned}
&-(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})e^{-\tau\lambda}]\lambda \\
&+[-(\gamma+\kappa y_m^*)(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\rho y_m^*)e^{-\sigma(\epsilon+\lambda)} \\
&+(\gamma+\kappa y_m^*)(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\rho y_m^*)e^{-\sigma(\epsilon+\lambda)}e^{-\tau\lambda} \\
&+(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(2\beta x_m^*+\rho y_m^*)(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)}) \\
&-(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(2\beta x_m^*+\rho y_m^*)(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})e^{-\tau\lambda} \\
&-(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)}) \\
&+(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})e^{-\tau\lambda} \\
&-(\alpha^2\kappa x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)}) \\
&+(\alpha^2\kappa x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})e^{-\tau\lambda} \\
&+(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)}) \\
&-(\alpha e^{-\tau(\gamma+\kappa y_m^*+\lambda)})(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})(c\kappa y_m^* e^{-\sigma(\epsilon+\lambda)})e^{-\tau\lambda}]
\end{aligned}
$$

Grouping like terms in $\lambda, e^{-\tau\lambda}, e^{-\sigma\lambda}$ and $e^{-\lambda(\tau+\sigma)}$ we get,

$$
\begin{aligned}
&\lambda^4+[(\gamma+\kappa y_m^*)+(2\beta x_m^*+\rho y_m^*)+\xi]\lambda^3 \\
&\quad+[(\gamma+\kappa y_m^*)(2\beta x_m^*+\rho y_m^*+\xi)+(2\beta x_m^*+\rho y_m^*)\xi]\lambda^2 \\
&\quad+[(\gamma+\kappa y_m^*)(2\beta x_m^*+\rho y_m^*)\xi]\lambda
\end{aligned}
$$

$$= [\alpha e^{-\tau(\gamma+\kappa y_m^*)} e^{-\tau\lambda} + \xi e^{-\sigma\lambda}]\lambda^3$$

$$+ [\{(\gamma + \kappa y_m^* + \xi)(\alpha e^{-\tau(\gamma+\kappa y_m^*)})\} e^{-\tau\lambda}$$

$$+ \{(\gamma + \kappa y_m^*)\xi + (2\beta x_m^* + \rho y_m^*)\xi - \rho x_m^*(c\rho y_m^* e^{-\sigma\varepsilon}) - c\kappa^2 x_i^* y_m^* e^{-\sigma\varepsilon}\} e^{-\sigma\lambda}$$

$$+ \{\alpha\xi e^{-\tau(\gamma+\kappa y_m^*)}\} e^{-(\tau+\sigma)\lambda}]\lambda^2$$

$$+ [\{(\gamma + \kappa y_m^*)\xi(\alpha e^{-\tau(\gamma+\kappa y_m^*)})\} e^{-\tau\lambda}$$

$$+ \{(\gamma + \kappa y_m^*)(\xi(2\beta x_m^* + \rho y_m^*) - (\rho x_m^* c\rho y_m^* e^{-\sigma\varepsilon}))$$

$$- (c\kappa y_m^* e^{-\sigma\varepsilon})(\alpha\rho x_m^* + \kappa x_i^*(2\beta x_m^* + \rho y_m^*) - \kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})$$

$$- (c\rho y_m^* e^{-\sigma\varepsilon})(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})\} e^{-\sigma\lambda}$$

$$- \{(\alpha e^{-\tau(\gamma+\kappa y_m^*)})((\gamma + \kappa y_m^*)\xi - \rho x_m^* c\kappa y_m^* e^{-\sigma\varepsilon} - c\kappa^2 x_i^* y_m^* e^{-\sigma\varepsilon}$$

$$- c\rho\kappa x_m^* y_m^* e^{-\sigma\varepsilon} + c\kappa^2 x_m^* y_m^* e^{-\sigma\varepsilon})\} e^{-(\tau+\sigma)\lambda}]\lambda$$

$$+ \{(\kappa\alpha x_m^* e^{-\tau(\gamma+\kappa y_m^*)})((\gamma + \kappa x_m^*)(c\rho y_m^* e^{-\sigma\varepsilon})$$

$$- (2\beta x_m^* + \rho y_m^* - \alpha)(c\kappa y_m^* e^{-\sigma\varepsilon}))\} e^{-\sigma\lambda}(e^{-\tau\lambda} - 1) \tag{4.19}$$

We see immediately that $\lambda = 0$ is a root of the characteristic equation (4.19). We choose as a Hopf parameter the value c, which is the rate at which prey that are caught by predators are transformed into predator biomass. To satisfy the Hopf hypothesis, we need a value of c, call it c_H, for which the following statements are true:

1) the real part of all eigenvalues, except for that belonging to one conjugate pair which we call λ_{H_1}, and λ_{H_2}, must be negative,
2) The real parts of λ_{H_1} and λ_{H_2} must be zero,

3) The imaginary parts of λ_{H_1} and λ_{H_2} are nonzero,

4) As a function of the Hopf parameter c, the derivatives of the real parts of λ_{H_1} and λ_{H_2} with respect to c must be nonzero when $c = c_H$.

We immediately see that the augmented system (4.10) does not satisfy the conditions in the Hopf hypothesis since $\lambda = 0$ is always an eigenvalue of the system. However, we suspect that no admissible initial function has any component in the eigenspace corresponding to this eigenvalue, and that despite the presence of this zero eigenvalue a Hopf bifurcation does indeed exist in the augmented system. Relation (4.11) would then ensure that we would have a Hopf bifurcation in the original system (4.1) as well, at the same value c_H of the Hopf parameter c. Numerical evidence seems to give support to the truth of this conjecture. We should also remark at this point that the invariant integral condition satisfied by $x_i(t)$ and $y_i(t)$ defines for us an invariante manifold, which may enable us to drop the $\lambda = 0$ eigenvalue and study the Hopf bifurcation in the invariant manifold containing the solutions, giving us another approach to the resolution of the matter of the zero eigenvalue.

4.7. Computer Simulations and Examples

To further investigate the possibility of a Hopf bifurcation in the predator-prey model, we consider the specific system,

$$
\begin{aligned}
\dot{x}_i(t) &= 2.0x_m(t) - 0.3x_i(t) - 0.2y_m(t)x_i(t) \\
&\qquad - 2.0x_m(t-0.2)e^{-0.3\times 0.2}e^{-0.2\int_{t-0.2}^{t} y_m(s)ds} \\
\dot{x}_m(t) &= 2.0x_m(t-0.2)e^{-0.3\times 0.2}e^{-0.2\int_{t-0.2}^{t} y_m(s)ds} - 0.1x_m^2(t) - 0.6y_m(t)x_m(t) \\
\dot{y}_i(t) &= cy_m(t)[0.2x_i(t) + 0.6x_m(t)] - 0.4y_i(t) \\
&\qquad - ce^{-0.4}y_m(t-1.0)[0.2x_i(t-1.0) + 0.6x_m(t-1.0)] \\
\dot{y}_m(t) &= ce^{-0.4}y_m(t-1.0)[0.2x_i(t-1.0) + 0.6x_m(t-1.0)] - 0.3y_m(t)
\end{aligned}
\tag{4.20}
$$

where c, the rate at which the prey biomass that has been captured by the predator is converted into predator biomass, is variable. For initial conditions we assume a constant $\phi_m(t)$ and a constant $\theta_m(t)$, with the values $\phi_i(t)$ and $\theta_i(t)$ being evaluated accordingly.

The figures show the results of numerical computations using subroutine DELAYS with this example. These phase plane diagrams plot the concentration of mature prey on the x-axis versus the concentration of mature predator on the y-axis for eight different values of c. Figure 4.1, with a value of c equal to 0.1, indicates that the interior equilibrium near (2.5, 6.6, 0.67, 1.8) shows all indications of being stable. As the value of c increases to 0.14 in figure 4.2, to 0.16 in figure 4.3 and to 0.18 in figure 4.4, we see that the interior equilibrium appears to be becoming less stable, with the solutions approaching the equilibrium more and more slowly. The equilibrium also moves in the direction of the point (1.4, 3.7, 0.83, 2.25) in the process.

Then as c increases to 0.20 in figure 4.5, to 0.22 in figure 4.6, and to 0.24 in figure 4.7, the interior equilibrium appears to destabilize, going from stable to unstable. The application of several root finders for finding roots of nonlinear systems to this problem gave inconclusive results, but they seemed to indicate that the real part of one conjugate pair of eigenvalues goes from negative to positive as c increases. Of course, it is very difficult to tell that an equilibrium is stable or unstable by looking at phase plane diagrams, since a small amplitude periodic solution is often indistinguishable from a stable equilibrium point when the real part of an eigenvalue is sufficiently small in absolute value. However, we can readily see in figure 4.9 and figure 4.10 that a periodic solution to the four dimensional system may very well exist, as solutions starting sufficiently distant from the interior equilibrium spiral inwards, while solutions starting sufficiently close to the equilibrium spiral outwards from the equilibrium.

4.8. Discussion

To summarize, we have shown that system (4.1) is meaningful as a model for predator-prey population dynamics both biologically and mathematically in that the values that result from solving the system with admissible initial conditions neither become negative, nor do they become unbounded. We also showed that the equilibrium at the origin is always an unstable "saddle" , and that there exists an equilibrium in the prey plane that may be either unstable or stable, depending on whether or not the predator can survive on the prey available.

We also showed that when the boundary point is unstable, at least one interior equilibrium point exists.

Looking at the characteristic equation about an interior equilibrium, we saw that $\lambda = 0$ is always an eigenvalue of the system, so that the Hopf hypothesis is not applicable. However, numerical simulation indicates that using the value c as a variable parameter, the system undergoes what appears to be a Hopf bifurcation notwithstanding the zero eigenvalue. With our example, that value of c_H appears to be somewhere between 0.18 and 0.22.

Thus we conjecture that despite the zero eigenvalue that always exists, system (4.1) undergoes a Hopf bifurcation for properly chosen values of a Hopf parameter, giving us stable periodic solutions of the system for appropriate parameter values.

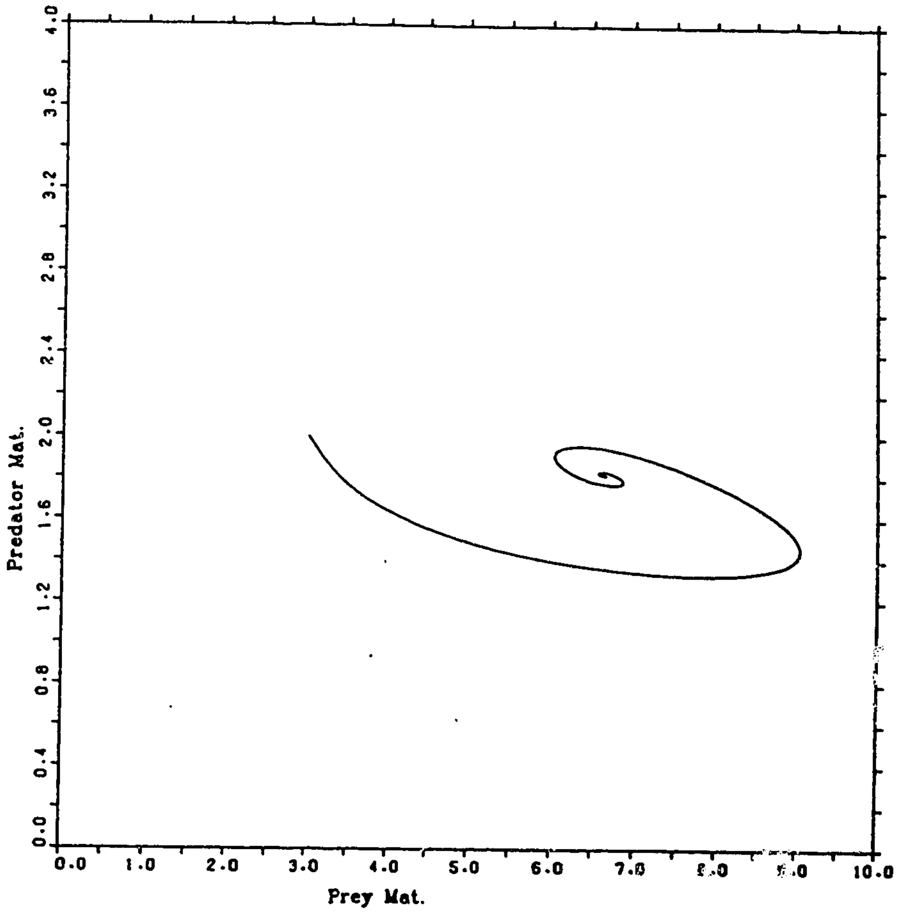
Of course it is difficult to judge whether or not the particular parameters we chose to make up the particular example we investigated have any merit in the field. For example, the values of 0.2 for the predation on immature prey and 0.6 for mature prey may appear to be unrealistic. However, it may be that the prey species strongly protects its young, with the weight of predation falling mostly on its aged members. This would make this particular example meaningful in the real world.

As well, there is no particular reason why the prey to predator conversion factor c is the only choice for the "Hopf" parameter. For instance, it might be informative to choose the predator gestation period σ as a "Hopf" parameter.

We should also note here that the use of a single value c for the conversion of prey into predator biomass constant for both immature and mature prey is unrealistic. Subsequent models that incorporate stage structure should use different values of c for immature and mature prey conversion to predator biomass.

It might also be informative to get away from the Lotka-Volterra dynamics that we assumed in our model. One generalization that readily comes to mind is to make the predator response functions on the immature and mature prey populations something other than the constants κ and ρ that we used. A more meaningful choice for predator response functions might be to have the predation on immatures a function of not only predator concentration, but of mature prey concentration and immature prey concentration, giving us a function $\kappa(x_i, x_m, y_m)$. As well, predation on matures could also be expressed as a function of predator matures, prey immatures, and prey matures, giving us a function $\rho(x_i, x_m, y_m)$. In this manner, factors such as group defense, protection of immature prey by mature prey or risk involved to mature prey trying to protect relatively large numbers of immature prey may be considered. It may be that study of such generalized systems will have to rely more heavily on numerical simulation, but the richer dynamics may well make the effort worthwhile.

Figure 4.1 Predator-Prey Set #5



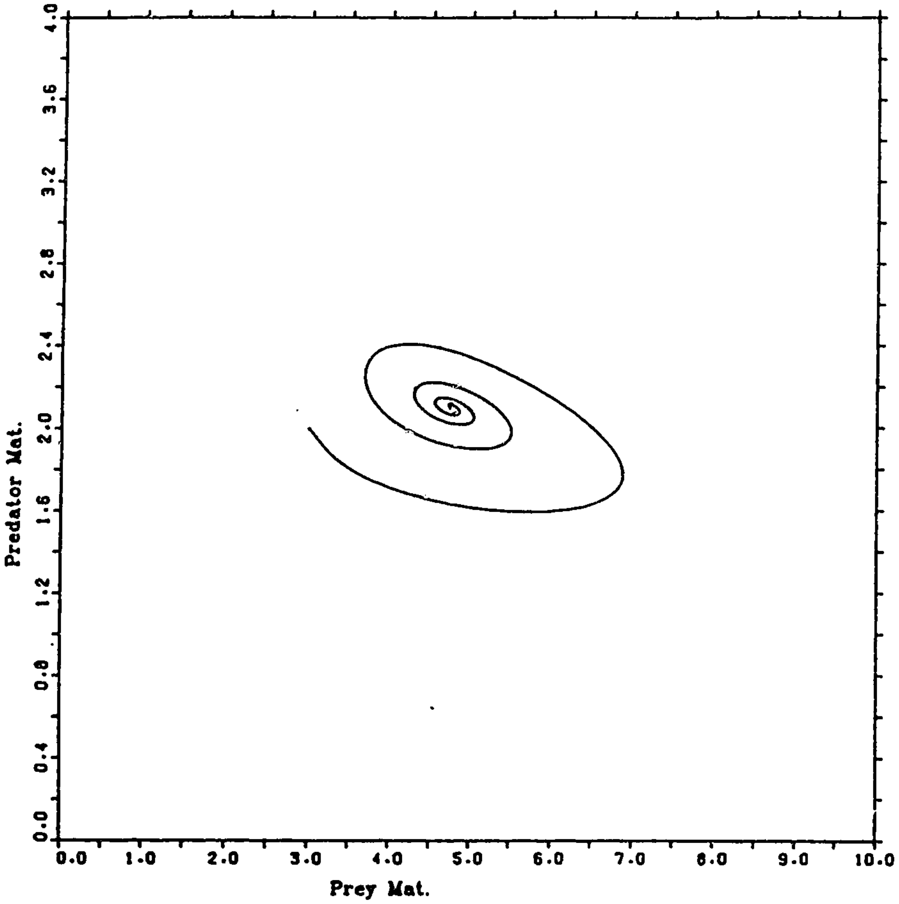
Predator-Prey Data Set #5

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.10000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium: Xi = 7.313
Xm = 18.835

Predator Efficiency 0.85557530

Figure 4.2 Predator-Prey Set #6



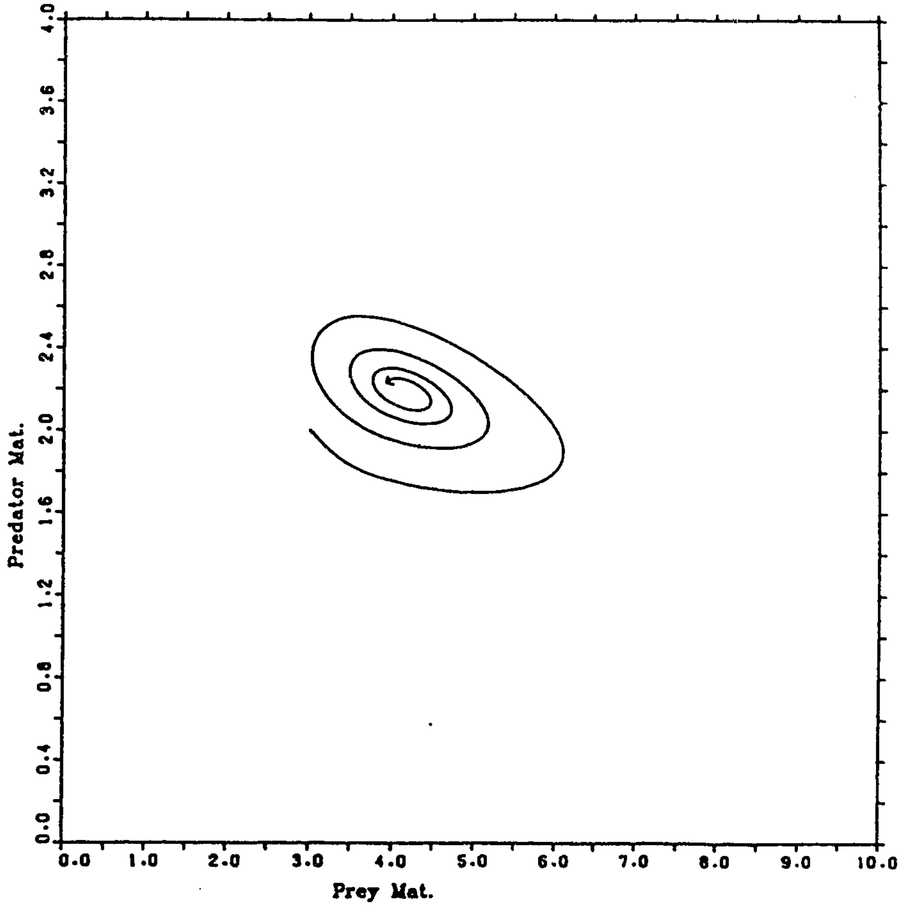
Predator-Prey Data Set #6

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.14000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium Xi = 7.313
Xm = 18.835

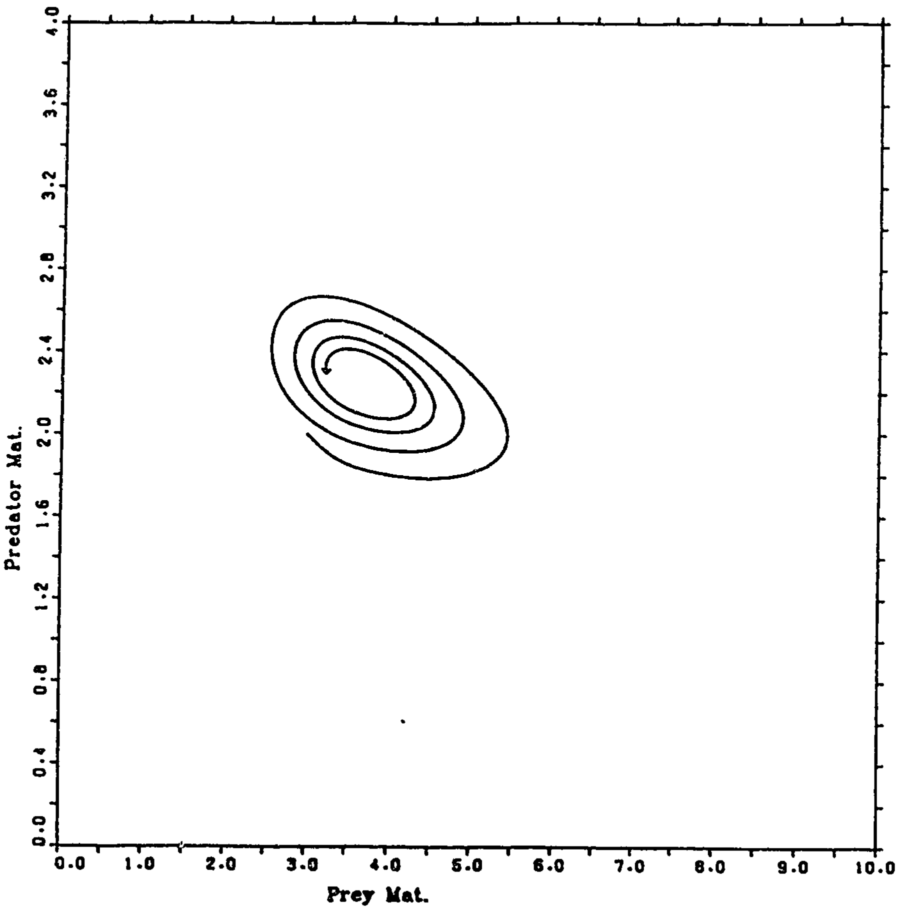
Predator Efficiency 1.19780542

Figure 4.3 Predator-Prey Set #7



```
  Predator-Prey Data Set #7

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.16000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium    Xi = 7.313
                        Xm = 18.835

Predator Efficiency        1.36892048
```

Figure 4.4 Predator-Prey Set #8



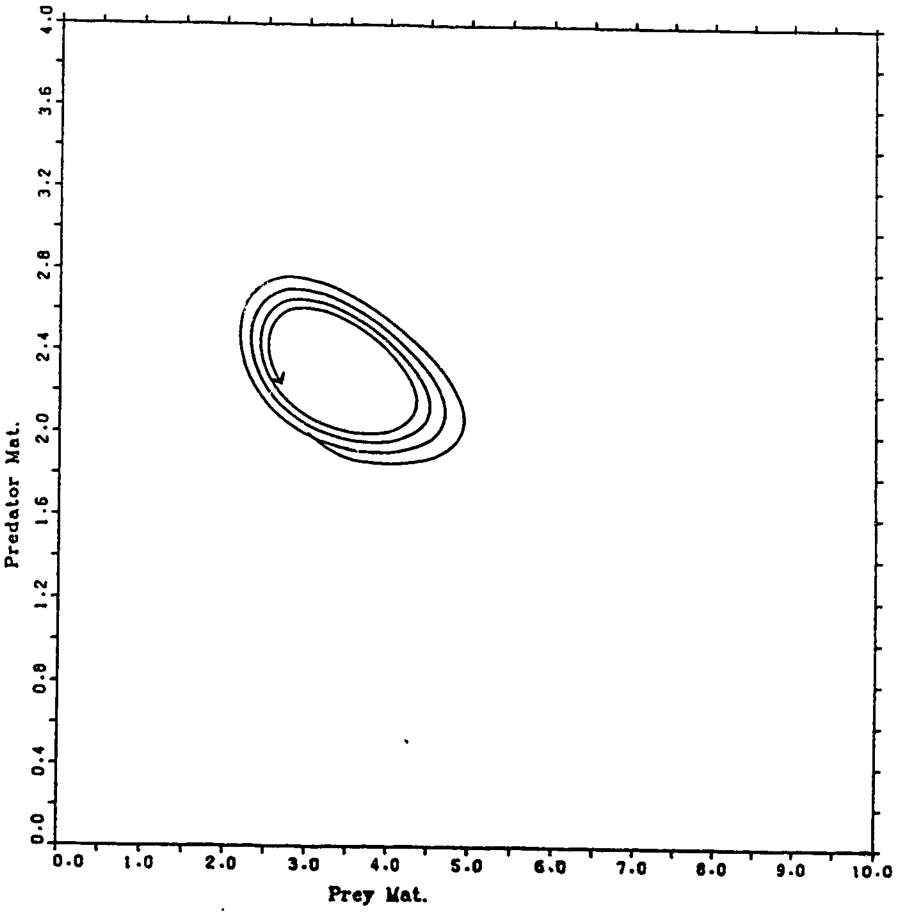
Predator-Prey Data Set #8

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.18000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium Xi = 7.313
Xm = 18.835

Predator Efficiency 1.54003554

Figure 4.5 Predator-Prey Set #9



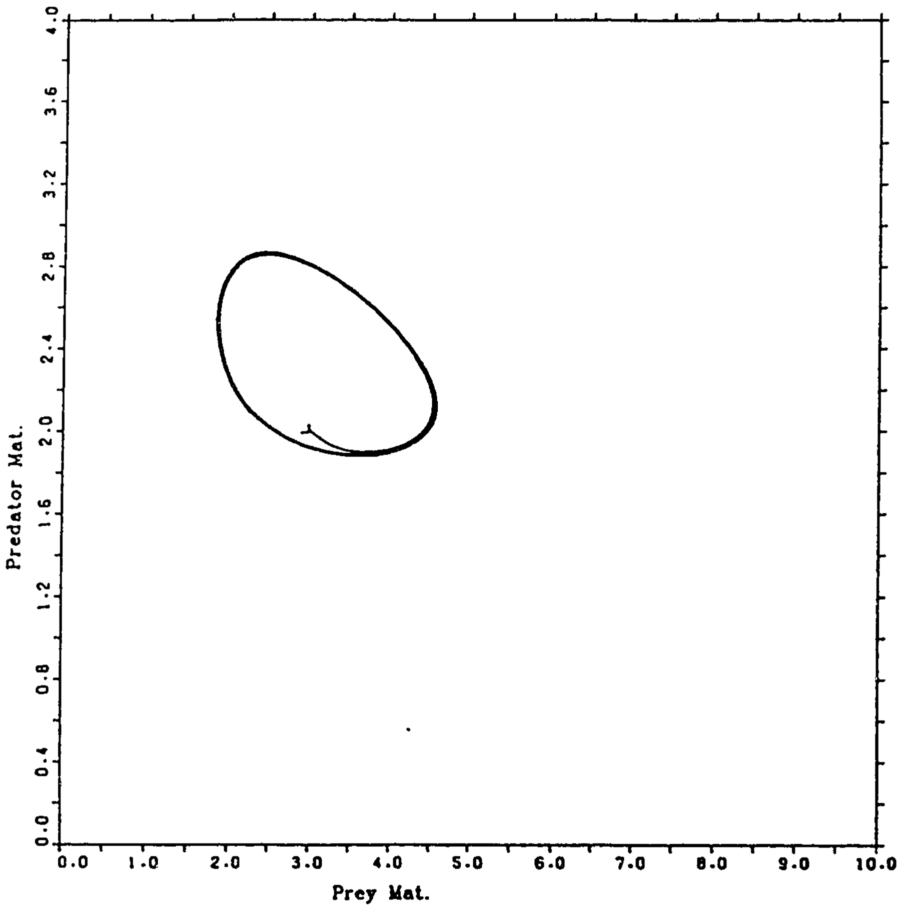
Predator-Prey Data Set #9

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.20000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium Xi = 7.313
Xm = 18.835

Predator Efficiency 1.71115060

Figure 4.6 Predator-Prey Set #10



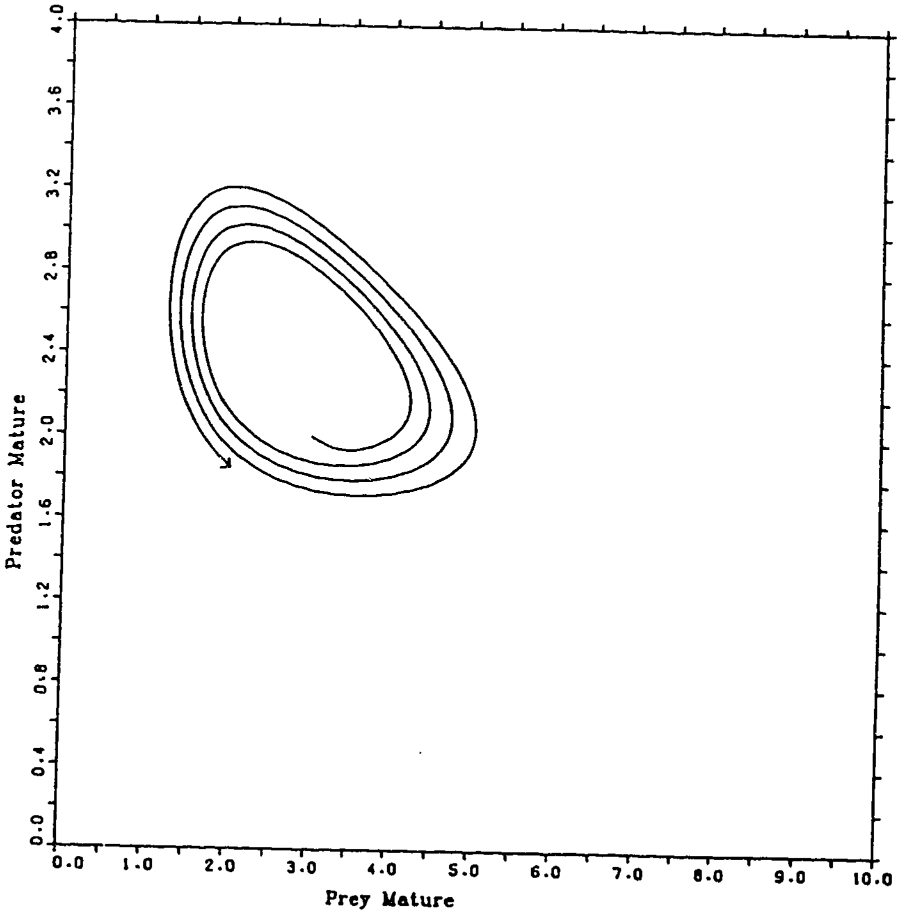
Predator-Prey Data Set #10

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.22000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium Xi = 7.313
Xm = 18.835

Predator Efficiency 1.88226566

Figure 4.7 Predator-Prey Set #11



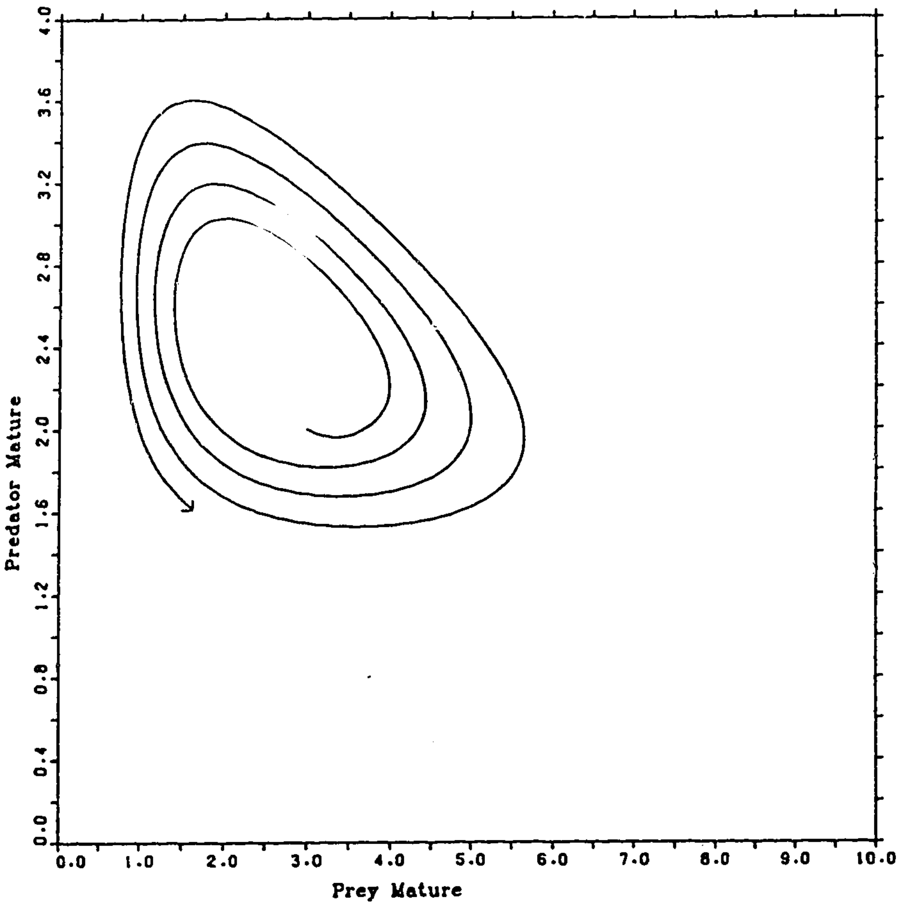
Predator-Prey Data Set #11

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.24000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium Xi = 7.313
Xm = 18.835

Predator Efficiency 2.05338072

Figure 4.8 Predator-Prey Set #12



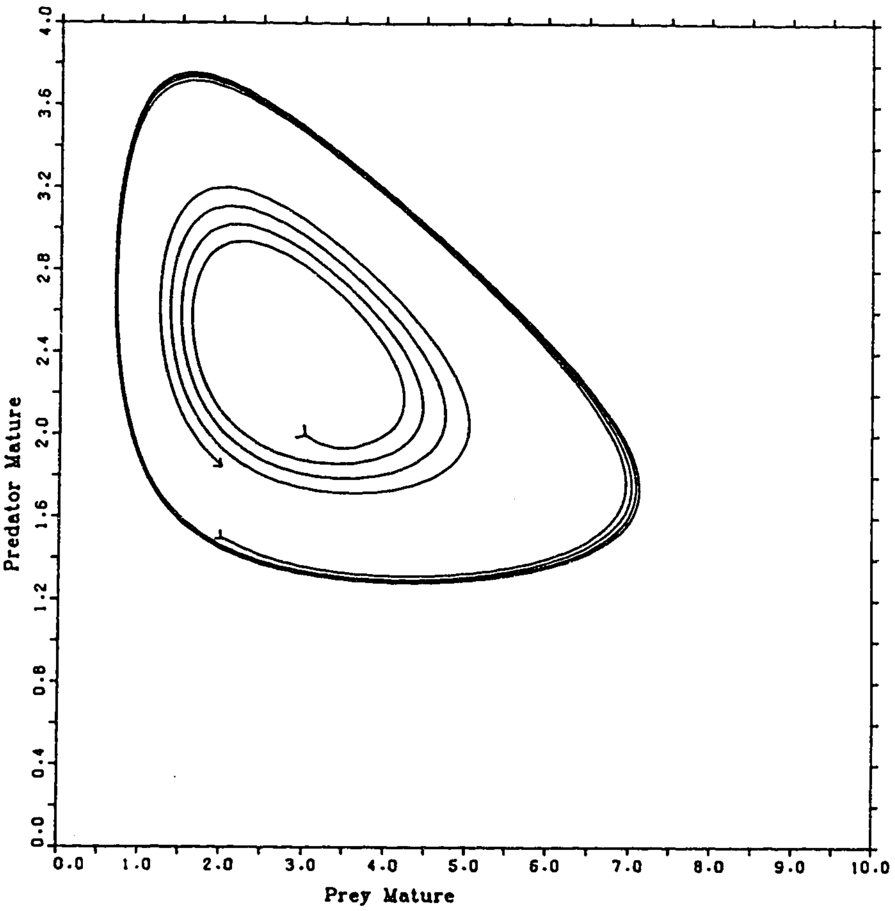
Predator-Prey Data Set #12

Prey Intrinsic Growth Rate: 2.00000
Prey Mature Death Rate: 0.10000
Prey Immature Death Rate: 0.30000
Immature Prey Predation Constant: 0.20000
Mature Prey Predation Constant: 0.60000
Prey Maturation Period: 0.20000
Predator => Prey Conversion Factor: 0.26000000
Predator Immature Death Rate 0.40000
Predator Mature Death Rate: 0.30000
Predator Maturation Period: 1.00000

Boundary Equilibrium Xi = 7.313
Xm = 18.835

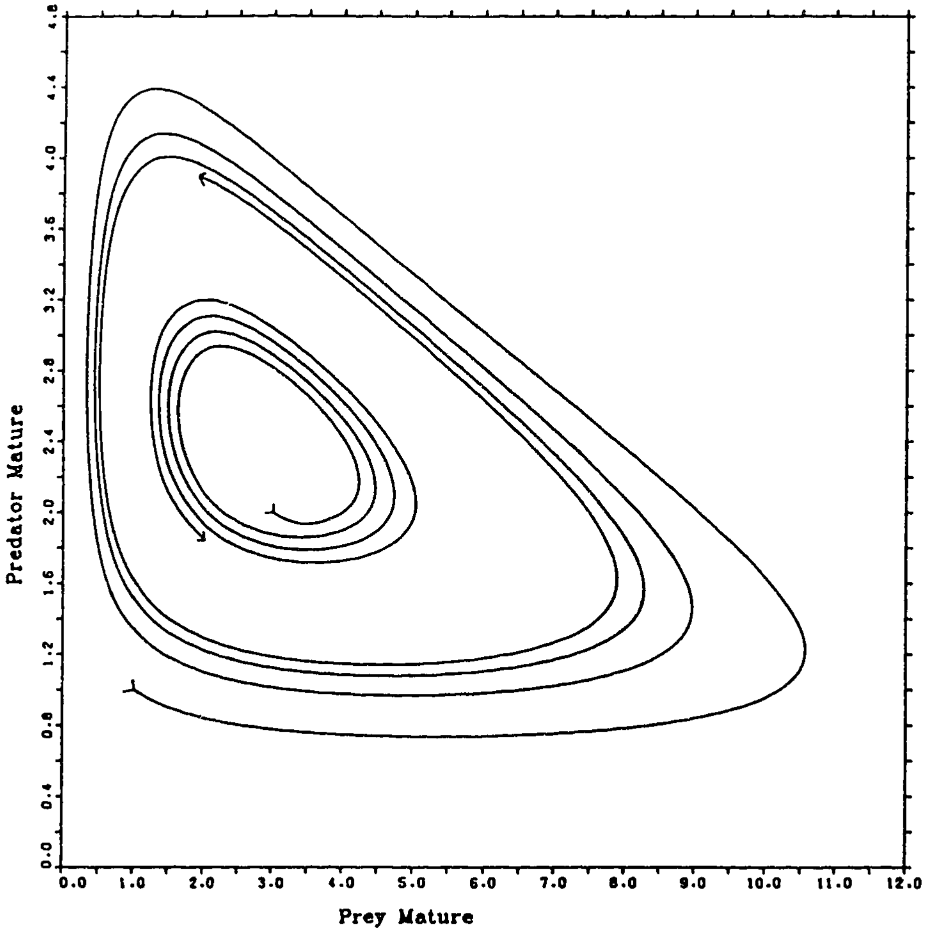
Predator Efficiency 2.22449578

Figure 4.9 Predator-Prey Set #10



Predator-Prey Set #10

Figure 4.10 Predator-Prey Set #11



Predator-Prey Set #11

CHAPTER FIVE

SINGLE SPECIES GROWTH WITH STATE DEPENDENT TIME DELAY

5.1. Introduction

In chapter two, a stage-structured model of population growth consisting of immature and mature individuals was developed and analyzed, where the stage-structure was modeled by the introduction of a constant time delay. As we mentioned in the introduction to chapter two, many other models of population growth with time delays have been covered in the literature. Included in these investigations are studies by Aiello (1990), Fisher and Goh (1984), Freedman and Gopalsamy (1986), Gurney, Blythe, and Nisbet (1980), Gurney and Nisbet (1985), Koselsov (1983), May, Hassell, Conway, and Southwood (1974), Rosen (1987), and Wangersky and Cunningham (1956). In addition age and stage structured models using both discrete and distributed time delays, as well as stochastic time delays, have been considered. Some of the work using models of these types include Barclay and Van denDriessche (1980), Gurney, Nisbet, and Lawton (1983), Landahl and Hanson (1975), Tognetti (1975), and Wood, Blythe, Gurney, and Nisbet (1989).

In Gambell (1985), it was observed that for Antarctic whale and seal populations, the length of time to maturity is a function of the amount of food (mostly krill) available. Previous to the Second World War, it was observed that individual seals took five years to mature, small whales took seven to ten years and large whale species took twelve to fifteen years to mature. Subsequent to the introduction of factory ships after the war and with it a depletion of the large whale populations, there was an increase in the krill available for the seals and the remaining whales. It was then noted that seals took three to four years to mature and small whales now only took five years. Maturation time for large whales also significantly decreased.

Since the amount of food available per biomass for a fixed food supply in a closed environment is a function of the total consumer biomass, we modify the model considered in chapter two to include a monotonically increasing, density dependent time delay. It is the purpose of this chapter to analyze as best we can the proposed model.

In the next section, we develop our model. In Section 3, we obtain positivity and boundedness results. An equilibrium analysis will follow in Section 4. In particular, we show that multiple positive equilibria can exist (where the constant time delay case only allows at most one), and we obtain criteria for the uniqueness of an equilibrium and for its asymptotic stability. In Section 5, we examine the gobal behavior of solutions. A brief discussion follows in Section 6.

5.2. Derivation of the Model

In chapter two, we utilized the system

$$\begin{aligned} \dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau) \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t) \end{aligned} \tag{5.1}$$

where $x_i(t)$ and $x_m(t)$ represented the immature and mature population densities respectively in modeling stage-structured population growth. There, τ

represented a constant time to maturity, and α, β, γ were positive constants. Integrating the equation for the immature population in system (5.1) under the assumption that $x_i(0) = \int_{-\tau}^{0} \alpha x_m(s) e^{\gamma s} ds$, we get that the number of immature individuals who are born during the time interval $t - \tau$ to t and who survive until time t is given by the expression,

$$\int_{t-\tau}^{t} \alpha x_m(s) e^{\gamma(s-t)} ds \text{ for all } t \geq 0.$$

Given the invariant intergral condition and the initial conditions of this system the expression also represents the total population of immatures at time t. Biologically this represents the fact that $x_i(t)$ is the accumulated survivors of those members of the immature population born between times $t - \tau$ and t.

Here we modify system (5.1) to account for the observed dependence of τ on the population density. We then let $\tau(x_i + x_m)$ be an increasing function of $x_i + x_m$ whose range lies in the interval $[\tau_m, \tau_M]$. Hence we consider the system, where $z(t) = x_i(t) + x_m(t)$,

$$\dot{x}_i(t) = \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma \tau(z(t))} x_m(t - \tau(z(t))) \tag{5.2a}$$

$$\dot{x}_m(t) = \alpha e^{-\gamma \tau(z(t))} x_m(t - \tau(z(t))) - \beta x_m^2(t) \tag{5.2b}$$

where $x_m(t) = \varphi_m(t) > 0, -\tau_M \leq t \leq 0$, and $\varphi_i(t)$ is defined below. Here, $\cdot = \frac{d}{dt}, \alpha > 0, \beta > 0, \gamma > 0$, and $0 < \tau_m \leq \tau(z) \leq \tau_M < \infty$. Since $\tau(z)$ is observed to be an increasing function of population density with a lower limit, we further assume that $\frac{d}{dt}\tau(z)$ exists, so that

$$\frac{d}{dt}\tau(z) \geq 0, \quad \text{and that } 0 < \tau_m \leq \tau(z) \leq \tau_M.$$

$\varphi_m(t)$ represents the number of matures in the population at time t, $-\tau_M \leq t \leq 0$.

Now, in order for the model to make sense, we must impose conditions on $\tau(z(t))$ so that $t - \tau(z(t))$ is a monotone increasing function of t. Thus we need $\frac{d}{dt}\tau(z) = \tau'(z)\dot{z}(t) < 1$. This is equivalent to,

$$\tau'(z)(\dot{x}_i(t) + \dot{x}_m(t)) < 1,$$

or

$$\tau'(z)(\alpha x_m(t) - \gamma x_i(t) - \beta x_m^2(t)) < 1.$$

We know that $\tau'(z) \geq 0$ is true. Then, if $\tau'(z) = 0$, we have a constant delay, so that $t - \tau(z(t))$ is monotone increasing. So assuming $\tau'(z) > 0$,

$$\tau'(z)(\alpha x_m(t) - \gamma x_i(t) - \beta x_m^2(t)) \leq \tau'(z)(\alpha x_m(t) - \beta x_m^2(t)),$$

provided of course that $x_i(t) \geq 0$. Thus if $\tau'(z)(\alpha x_m(t) - \beta x_m^2(t)) < 1$, $t - \tau(z(t))$ is monotone increasing. But $(\alpha x_m(t) - \beta x_m^2(t))$ attains its maximum value of $\alpha^2/4\beta$ when $x_m = \alpha/2\beta$. Thus if

$$\tau'(z) < 4\beta/\alpha^2,$$

$t - \tau(z(t))$ will be monotone increasing.

Now, let τ_s be defined so that

$$\tau_s = \tau(\varphi_m(0) + \int_{-\tau_s}^{0} \alpha\varphi_m(s)e^{\gamma s}ds). \tag{5.3}$$

Such a τ_s exists, since if we regard equation (5.3) as an expression in which τ_s is a variable, as the left hand side increases from zero towards infinity, the right hand side will increase, but staying between the values τ_m and τ_M. The value τ_s so defined may not be unique, so we set

$$\tau_s = \inf_{\tau_t}\{\tau_t : \ \tau_t = \tau(\varphi_m(0) + \int_{-\tau_t}^{0} \alpha\varphi_m(s)e^{\gamma s}ds)\}.$$

We then define $\varphi_i(0) = \int_{-\tau_s}^{0} \alpha\varphi_m(s)e^{\gamma s}ds$, which by a change of variable $r = s + \tau_1$ and then resubstituting s for r becomes,

$$\varphi_i(0) = \int_0^{\tau_s} \alpha\varphi_m(s - \tau_s)e^{\gamma(s-\tau_s)}ds.$$

In this manner, $\varphi_i(0)$ represents the accumulated survivors of those members of the immature population born between time $-\tau_s$ and 0.

For values of t, $-\tau_s \leq t \leq 0$ we understand that $x_m(t) = \varphi_m(t)$, and that $x_i(0) = \varphi_i(0)$.

Note also that $\tau(z(0)) = \tau_s$.

5.3. Positivity and Boundedness

In order that our model (5.2) makes sense, we must show that solutions to the system do not become negative, and that those solutions remain bounded. Boundedness may be interpreted as a natural restriction on the size of populations as a consequence of limited space and other resouces.

THEOREM 5.1. *Let* $\varphi_m(t) > 0$ *for* $-\tau_M \leq t \leq 0$. *Then* $x_m(t) > 0$ *for* $t > 0$.

PROOF: Suppose $x_m(t) = 0$ for some value of t, Since $x_m(0) > 0$, by continuity of solutions, such a value of t must be strictly greater than zero. Let $t^* = \inf\{t :$

$t > 0, x_m(t) = 0\}$. Then from equation (5.2) $\dot{x}_m(t^*) = \alpha e^{-\gamma\tau(z(t^*))}(x_m(t^* - \tau(z(t^*)))$. Since $\tau(z) > 0$, $t^* - \tau(z(t^*)) < t^*$, implying that $x_m(t^* - \tau(z(t^*))) > 0$ by definition of t^*. This in turn implies that $\dot{x}_m(t^*) > 0$, giving us a contradiction. Therefore no such t^* exists, and the theorem is proved.

THEOREM 5.2. *Let $\varphi_m(t) > 0$ for $-\tau_M \le t \le 0$. Then there exists a $\delta_m = \delta_m(\varphi_m) > 0$ such that $x_m(t) > \delta_m$ for all $t \ge 0$.*

PROOF: Let $\delta_m(\varphi_m) = \frac{1}{2}\min\{\inf_{-\tau_M \le t \le 0} \varphi_m(t), \alpha\beta^{-1}e^{-\gamma\tau_M}\}$. Then assume there exists a t^* such that $t^* = \inf\{t : t \ge 0, x_m(t) = \delta_m\}$. Since $x_m(0) = \varphi_m(0)$, and $\varphi_m(0) \ge 2\delta_m$, by continuity $t^* > 0$. Then,

$$\begin{aligned} \dot{x}_m(t^*) =& \alpha e^{-\gamma\tau(z(t^*))} x_m(t^* - \tau(z(t^*))) - \beta x_m^2(t^*) > \\ & \alpha e^{-\gamma\tau_M}\delta_m - \beta\delta_m^2 \ge \\ & \alpha e^{-\gamma\tau_M}\delta_m - \frac{1}{2}\alpha e^{-\gamma\tau_M}\delta_m = \frac{1}{2}\alpha e^{-\gamma\tau_M}\delta_m > 0. \end{aligned}$$

Since $\dot{x}(t^*) > 0$ is impossible by definition of t^*, we have a contradiction. Therefore no such t^* exists and $x_m(t) > \delta_m(\varphi_m)$ for all $t > 0$. This proves the theorem.

THEOREM 5.3. *Let $\varphi_m(t) > 0$ for $-\tau_M \le t \le 0$. Then there exists $\Delta_m = \Delta_m(\varphi_m) > 0$ such that $x_m(t) \le \Delta_m$ for $t \ge 0$.*

PROOF: Assume the contrary. Our proof is split into two cases.

(a) First suppose that $\dot{x}_m(t) \geq 0$ for all $t > T$ for some $T \geq 0$. Then for $t > T + \tau_M$,

$$0 \leq \dot{x}_m(t) = \alpha e^{-\gamma\tau(z(t))} x_m(t - \tau(z(t))) - \beta x_m^2(t)$$
$$\leq \alpha e^{-\gamma\tau(z(t))} x_m(t) - \beta x_m^2(t)$$

since $x_m(t - \tau(z(t))) \leq x_m(t)$. This in turn implies that

$$x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau(z(t))} \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$$

for $t > T$, since $x_m(t) > 0$, giving us our desired result.

(b) Now assume that there exists a sequence $\{t_n\}_{n=1}^{\infty}$ such that $\dot{x}_m(t_n) = 0$, ans such that $x_m(t_n)$ is a local maximum where $x_m(t) \leq x_m(t_n)$, $0 < t < t_n$, for all n. Then at $t = t_n$,

$$0 = \dot{x}_m(t_n) = \alpha e^{-\gamma\tau(z(t_n))} x_m(t_n - \tau(z(t_n))) - \beta x_m^2(t_n)$$
$$\leq \alpha e^{-\gamma\tau(z(t_n))} x_m(t_n) - \beta x_m^2(t_n)$$

which again implies that $x_m(t_n) \leq \alpha\beta^{-1}e^{-\gamma\tau(z(t_n))} \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$,.

Thus $\Delta_m(\varphi_m) = \max\{\sup_{-\tau_M \leq t \leq 0} \varphi_m(t), \alpha\beta^{-1}e^{-\gamma\tau_m}\}$ This proves the theorem.

Now, Theorems 5.2 and 5.3 show that, given an admissible set of initial conditions, solutions $x_m(t)$ to system (5.2) will remain positive and will be bounded. We can also prove that solutions $x_i(t)$ will be bounded above by a bound that depends on initial conditions.

THEOREM 5.4. *Let $\varphi_m(t) > 0$ for $-\tau_m \le t \le 0$. Then there exists a $\Delta_i(\varphi_m) = \alpha x_i(0) + \alpha\gamma^{-1}\Delta_m$ such that $x_i(t) < \Delta_i$ for all t.*

PROOF: First we observe that since $x_i(0) = \int_{-\tau_s}^{0} \alpha\varphi_m(s)e^{\gamma s}ds$ as discussed in the previous section, Δ_i is indeed a functional depending only on $\varphi_m(t)$. Then from system (5.2),

$$\dot{x}_i(t) = \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau(z(t))}x_m(t - \tau(z(t))).$$

Integrating this expression we get for $t > 0$,

$$\begin{aligned} x_i(t) = \alpha e^{-\gamma t}x_i(0) + \alpha e^{-\gamma t}\int_0^t e^{\gamma s}x_m(s)ds \\ - \alpha e^{-\gamma t}\int_0^t e^{\gamma s}e^{-\gamma\tau(z(s))}x_m(s - \tau(z(s)))ds. \end{aligned}$$

Hence

$$\begin{aligned} x_i(t) &< \alpha e^{-\gamma t}x_i(0) + \alpha e^{-\gamma t}\int_0^t e^{\gamma s}x_m(s)ds \\ &\le \alpha e^{-\gamma t}x_i(0) + \alpha e^{-\gamma t}\int_0^t \Delta_m e^{\gamma s}ds \\ &= \alpha e^{-\gamma t}x_i(0) + \alpha e^{-\gamma t}\gamma^{-1}\Delta_m(e^{\gamma t} - 1) \\ &= \alpha e^{-\gamma t}x_i(0) + \alpha\gamma^{-1}\Delta_m(1 - e^{-\gamma t}) \\ &< \alpha x_i(0) + \alpha\gamma^{-1}\Delta_m \end{aligned}$$

proving the theorem.

Finally, we would like to prove that $x_i(t) > 0$ for all values of t. However, this does not seem to be possible without placing additional restrictions on either the initial conditions or on the delay function $\tau(z)$. For example, if we assume that $\tau'(z) \equiv 0$, then we have seen in chapter two that $x_i(t)$ remains positive for all t, but then we have no state dependence of the time delay.

However, we can impose less stringent conditions on $\tau'(z)$ that for a given set of initial conditions will give us the positivity of $x_i(t)$ that we need while still maintaining some of the character of the state dependent time delay.

THEOREM 5.5. *Suppose $\tau'(z) > 0$ is small enough so that the inequality $\delta_m \int_{t-\tau_m}^{t} e^{\gamma s} ds > \Delta_m \int_{\tau_s}^{t-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$ holds for all values of t. Then $x_i(t) > 0$ for all $t \geq 0$.*

PROOF: Suppose $x_i(t) = 0$ for some value of t. Then let $t^* = \inf\{t > 0 : x_i(t) = 0\}$. Since $x_i(0) > 0$, $t^* > 0$ by continuity. Then integrating equation (5.2a) we get,

$$\begin{aligned} 0 = x_i(t^*) = e^{-\gamma t^*} x_i(0) + \alpha e^{-\gamma t^*} &\int_0^{t^*} e^{\gamma s} x_m(s) ds \\ - \alpha e^{-\gamma t^*} &\int_0^{t^*} e^{\gamma s} e^{-\tau(z(s))} x_m(s - \tau(z(s))) ds. \end{aligned}$$

Since $x_i(t^*) = 0$ and since $x_i(0) = \int_{-\tau_s}^{0} \alpha e^{\gamma s} x_m(s) ds$ this is equivalent to

$$\begin{aligned} \alpha e^{-\gamma t^*} \int_{-\tau_s}^{0} e^{\gamma s} x_m(s) ds + \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma s} x_m(s) ds \\ = \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma(s - \tau(z(s)))} x_m(s - \tau(z(t))) ds \end{aligned}$$

or,

$$\int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s) ds = \int_0^{t^*} e^{\gamma(s - \tau(z(s)))} x_m(s - \tau(z(s))) ds. \tag{5.5}$$

Substituting $r = s - \tau(z(s))$ into the right hand side of equation (5.5) and then resubstituting r for s we get,

$$\int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s)ds = \int_{-\tau_s}^{t^*-\tau(z(t^*))} \frac{e^{\gamma s} x_m(s)}{1-\tau'(z)\dot{z}(s)} ds.$$

Now, since $x_i(t) > 0$ for $t < t^*$ we have $t - \tau(z(t))$ an increasing function of t for $t \leq t^*$, so that $1 - \tau'(z)\dot{z}(t) > 0$ holds for $-\tau_s \leq t \leq t^* - \tau(z(t^*))$. Since $x_m(t) > 0$ as well, we get the inequality

$$\int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s)ds \leq \int_{-\tau_s}^{t^*-\tau_m} \frac{e^{\gamma s} x_m(s)}{1-\tau'(z)\dot{z}(s)} ds.$$

This gives us,

$$\begin{aligned} \int_{t^*-\tau_m}^{t^*} e^{\gamma s} x_m(s)ds &\leq \int_{-\tau_s}^{t^*-\tau_m} \left(\frac{1}{1-\tau'(z)\dot{z}(s)} - 1\right) e^{\gamma s} x_m(s)ds \\ &= \int_{-\tau_s}^{t^*-\tau_m} \frac{\tau'\dot{z}(s)}{1-\tau'(t)\dot{z}(s)} e^{\gamma s} x_m(s)ds \end{aligned} \tag{5.6}$$

Now the left hand side of inequality (5.6) satisfies

$$\int_{t^*-\tau_m}^{t^*} e^{\gamma s} x_m(s)ds \geq \delta_m \int_{t^*-\tau_m}^{t^*} e^{\gamma s} ds. \tag{5.7}$$

The right hand side satisfies,

$$\int_{-\tau_s}^{t^*-\tau_m} \frac{\tau'(z)\dot{z}(s)}{1-\tau'(z)\dot{z}(s)} e^{\gamma s} x_m(s)ds \leq \int_{-\tau_s}^{t^*-\tau_m} \Delta_m \frac{\tau'(z)z}{1-\tau'(z)z}$$

But $\tau'(z) > 0$, and $t'(z)\dot{z}(t) > 1$, so since $\frac{x}{1-x}$ is an increasing function for $1 < x < +\infty$, $\frac{\tau'(z)\dot{z}(t)}{1-\tau'(z)\dot{z}(t)}$ is maximized when $\dot{z}(t)$ is at its maximum value, which as we saw in the previous section is $\dot{z}(t) = \alpha^2/4\beta$. So we have that,

$$\int_{-\tau_s}^{t^*-\tau_m} \Delta_m \frac{\tau'(z)\dot{z}(s)}{1-\tau'(z)\dot{z}(s)} e^{\gamma s} ds \leq \Delta_m \int_{-\tau_s}^{t^*-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$$

is true. Thus we have the following inequality,

$$\int_{-\tau_s}^{t^*-\tau_m} \frac{\tau'(z)\dot{z}(s)}{1-\tau'(t)\dot{z}(s)} e^{\gamma s} x_m(s)\,ds \le \Delta_m \int_{-\tau_s}^{t^*-\tau_m} \frac{\alpha^2\tau'(z)}{4\beta-\alpha^2\tau'(z)} e^{\gamma s}\,ds \tag{5.8}$$

Finally putting inequality (5.6), inequality (5.7) and inequality (5.8) together we get that at t^*

$$\delta_m \int_{t^*-\tau_m}^{t^*} e^{\gamma s}\,ds \le \Delta_m \int_{-\tau_s}^{t^*-\tau_m} \frac{\alpha^2\tau'(z)}{4\beta_\alpha^2\tau'(z)} e^{\gamma s}\,ds$$

must be true. This contradicts the hypothesis of our theorem, so no such t^* can exist and $x_i(t) > 0$ for all $t > 0$. This proves the theorem.

Whether or not theorem 5.5 imposes conditions on $\tau'(z)$ that are too stringent must remain the subject of further research. For the rest of this chapter, however, we must assume that $x_i(t)$ is positive for all t. In any case, since our conditions for $x_i(t)$ remaining positive depend in part on $\delta_m(\varphi_m)$ and on $\Delta_m(\varphi_m)$, a given set of initial conditions for system (5.2) may or may not be admissible depending on the system parameters. Thus we achieve sufficient conditions for the positivity of $x_i(t)$ by placing restrictions on both $\tau'(z)$ and on the initial conditions.

However, noting that Theorem 5.5 gives only sufficient conditions for an initial function to give a meaningful solution, we can also state the following

THEOREM 5.6. *Suppose* $e^{-\gamma\tau_m} \le \frac{\delta_m}{\Delta_m}$. *Then* $x_i(t) > 0$ *for all* $t \ge 0$.

PROOF: From the proof of Theorem 5.5, we know that if $t^* = \inf\{t > 0 : x_i(t) > 0\} < \infty$, then equation (5.5)

$$\int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s)ds = \int_0^{t^*} e^{\gamma(s-\tau(z(s)))} x_m(s-\tau(z(s)))ds$$

is true. The left hand side of equation (5.5) satisfies,

$$\delta_m \gamma^{-1}(e^{\gamma t^*} - e^{-\gamma\tau_s}) \le \int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s)ds \tag{5.9}$$

by substituting the lower bound δ_m for the function $x_m(s)$ and integrating. In a similar manner, the right hand side of equation (5.5) satisfies,

$$\int_0^{t^*} e^{\gamma(s-\tau(z(s)))} x_m(s-\tau(z(s)))ds \le \Delta_m \gamma^{-1} e^{-\gamma\tau_m}(e^{\gamma t^*} - 1). \tag{5.10}$$

Now, let

$$f_1(t) = \delta_m \gamma^{-1}(e^{\gamma t} - e^{-\gamma\tau_s}),$$

and

$$f_2(t) = \Delta_m \gamma^{-1} e^{-\gamma\tau_m}(e^{\gamma t} - 1).$$

As well, $f_1'(t) = \delta_m e^{\gamma t}$ and $f_2'(t) = \Delta_m e^{-\gamma\tau_m} e^{\gamma t}$. Then, if $e^{-\gamma\tau_m} \le \frac{\delta_m}{\Delta_m}$ were true, then $f_2'(t) \le f_1'(t)$ would be true for all t. Since $f_2(0) < f_1(0)$ is true, then $f_2(t) < f_1(t)$ would have to be true for all t if $e^{-\gamma\tau_m} < \delta_m/\Delta_m$ were to hold. But equation (5.5) together with equation (5.9) and equation (5.10) imply that $f_1(t^*) \le f_2(t^*)$. Therefore if $e^{-\gamma\tau_m} < \delta_m/\Delta_m$ then no such t^* could exist, and $x_i(t) = 0$ would be impossible for any t. This proves the theorem.

Theorem 5.5 seems to imply that as $\tau'(z)$ gets larger, the more restricted becomes the set of admissible initial functions, and that if $\tau'(z)$ approaches the value $4\beta/\alpha^2$ for some value of $z(t)$ that the set of admissible functions approaches the null set. Theorem 5.6, however, seems to imply that there will always be some initial function that gives a solution to the system where $x_i(t)$ remains positive, independent of any behaviour of $\tau(z)$.

We are not able, however, to bound $x_i(t)$ below by any value strictly greater than zero. Just what conditions we must impose on the system and its initial conditions to get such a strictly positive lower bound for $x_i(t)$ remains a subject for further study. However, in section five we will see that the limit a t approaches infinity of $x_i(t)$ is strictly positive given some simple assumptions on $\tau(z)$.

5.4. Equilibria: Existence and Local Stability.

There are only two types of equilibria, namely the origin (denoted $E_0(0,0)$) and one or more interior equilibria (denoted $\hat{E}(\hat{x}_i, \hat{x}_m)$).

Clearly there are no axial equilibria other than E_0. This is obvious biologically as well since the mature population cannot survive without the immatures, and vice versa.

To show that $\hat{E}$ always exists is equivalent to showing that the algebraic system

$$\alpha x_m - \gamma x_i - \alpha e^{-\gamma\tau(z)} x_m = 0 \qquad (5.11)$$

$$\alpha e^{-\gamma\tau(z)} - \beta x_m = 0 \qquad (5.12)$$

always has at least one positive solution. Let Γ_1 be the solution curve for $x_i \geq 0$, $x_m \geq 0$ of equation (5.11) and let Γ_2 be the solution curve for equation (5.12).

Let us first consider the solution curve Γ_2. This curve is strictly decreasing, passing through $(0, a)$ in the $x_i - x_m$ plane, where a is the unique positive root of $\beta a = \alpha e^{-\gamma\tau(a)}$. To show that Γ_2 is strictly decreasing, we compute $\frac{dx_m}{dx_i}$ along Γ_2. From equation (5.12) we have that $x_m = \alpha\beta^{-1}e^{-\gamma\tau(z)}$, so that differentiating equation (5.12) we get,

$$\frac{dx_m}{dx_i} = -\alpha\beta^{-1}\gamma e^{-\gamma\tau(z)}\tau'(z)(1 + \frac{dx_m}{dx_i}),$$

or,

$$\frac{dx_m}{dx_i}(1 + \alpha\beta^{-1}\gamma e^{-\gamma\tau(z)}\tau'(z)) = -\alpha\beta^{-1}\gamma e^{-\gamma\tau(z)}\tau'(z).$$

Hence,

$$\frac{dx_m}{dx_i} = -\frac{\alpha\gamma e^{-\gamma\tau(z)}\tau'(z)}{\beta + \alpha\gamma e^{-\gamma\tau(z)}\tau'(z)},$$

which is always less than zero since $\tau'(z) > 0$ is assumed. Further, $\lim_{x_i \to \infty} x_m(x_i) = b$ along Γ_2, where $b = \beta^{-1}\alpha e^{-\gamma\tau_M}$.

Γ_1 has the following properties. $(0,0) \in \Gamma_1$. Further, on Γ_1, $\lim_{x_i \to \infty} x_m(x_i) = \infty$. Hence Γ_1 and Γ_2 must intersect at positive values, establishing the existence of $\hat{E}$.

It is not necessarily the case that $\hat{E}$ is unique, since Γ_1 and Γ_2 may intersect at more than one point.

It is therefore desirable to obtain criteria for there to exist a unique equilibrium. Both Γ_1 and Γ_2 define x_m as a function of x_i, $x_m = g_1(x_i)$ and $x_m = g_2(x_i)$, respectively. Then $\hat{E}$ will be unique provided $g_1'(\hat{x}_i) > g_2'(\hat{x}_i)$ for every such $\hat{E}$, since if there were more than one $\hat{E}$, the reverse inequality must hold for alternate equilibria.

Now from equation (5.11) we have that $\alpha x_m - \gamma x_i - \alpha e^{-\gamma\tau(z)} x_m = 0$ along Γ_1. Hence along this curve,

$$x_m(\alpha - \alpha e^{-\gamma\tau(z)}) = \gamma x_i.$$

Taking derivatives with respect to x_i gives us,

$$\frac{dx_m}{dx_i}(\alpha - \alpha e^{-\gamma\tau(z)}) + x_m \alpha\gamma e^{-\gamma\tau(z)}\tau'(z)(1 + \frac{dx_m}{dx_i}) = \gamma$$

so that,

$$\frac{dx_m}{dx_i}[(\alpha - \alpha e^{-\gamma\tau(z)}) + \alpha\gamma x_m e^{-\gamma\tau(z)}\tau'(z)] = \gamma(1 - \alpha x_m e^{-\gamma\tau(z)}\tau'(z))$$

which gives us,

$$g_1'(x_i) = \frac{\gamma(1 - \alpha x_m e^{-\gamma\tau(z)}\tau'(z))}{\alpha(1 - e^{-\gamma\tau(z)} + \gamma x_m e^{-\gamma\tau(z)}\tau'(z))}, \tag{5.13}$$

From equation (5.12), we saw that

$$g_2'(x_i) = -\frac{\alpha\gamma e^{-\tau(z)}\tau'(z)}{\beta + \alpha\gamma e^{-\gamma\tau(z)}\tau'(z)}, \tag{5.14}$$

where in equation (5.13) and equation (5.14), x_m is the appropriate function of x_i.

Now from equation (5.12) and equation (5.11) we get the relations,

$$\begin{aligned} e^{-\gamma\tau(\hat{z})} &= \alpha^{-1}\beta\hat{x}_m, \\ \hat{x}_i &= \gamma^{-1}(\alpha - \beta\hat{x}_m)\hat{x}_m, \end{aligned} \tag{5.15}$$

and also

$$\begin{aligned} g_1'(\hat{x}_i) &= \frac{\gamma[1 - \beta\hat{x}_m^2\tau'(\hat{z})]}{\alpha - \beta\hat{x}_m + \beta\gamma\hat{x}_m^2\tau'(\hat{z})}, \\ g_2'(\hat{x}_i) &= -\frac{\gamma\hat{x}_m\tau'(\hat{z})}{1 + \gamma\hat{x}_m\tau'(\hat{z})}. \end{aligned} \tag{5.16}$$

Hence $g_1'(\hat{x}_i) > g_2'(\hat{x}_i)$ provided

$$\frac{\gamma[1 - \beta\hat{x}_m^2\tau'(\hat{z})]}{\alpha - \beta\hat{x}_m + \beta\gamma\hat{x}_m^2\tau'(\hat{z})} > -\frac{\gamma\hat{x}_m\tau'(\hat{z})}{1 + \gamma\hat{x}_m\tau'(\hat{z})}. \tag{5.17}$$

Now from equation (5.12), clearly $\hat{x}_m < \alpha\beta^{-1}$. Hence $\alpha - \beta\hat{x}_m + \beta\gamma\hat{x}_m^2\tau'(\hat{z}) > \beta\gamma\hat{x}_m^2\tau'(\hat{z}) \geq 0$. Hence inequality (5.17) is equivalent to

$$(1 + \gamma\hat{x}_m\tau'(\hat{z}))(1 - \beta\hat{x}_m^2\tau'(\hat{z})) > \hat{x}_m\tau'(\hat{z})(-\alpha + \beta\hat{x}_m - \beta\gamma\hat{x}_m^2\tau'(\hat{z})).$$

But the left hand side of this equality becomes,

$$1 + \gamma\hat{x}_m\tau'(\hat{z}) - \beta\hat{x}_m^2\tau'(\hat{z}) - \beta\gamma\hat{x}_m^3\tau'(\hat{z})^2,$$

or

$$1 + \hat{x}_m \tau'(\hat{z})(\gamma - \beta \hat{x}_m) - \beta\gamma \hat{x}_m^3 \tau'(\hat{z})^2.$$

Thus the inequality becomes,

$$1 + \hat{x}_m(\gamma - \beta\hat{x}_m)\tau'(\hat{z}) - \beta\gamma\hat{x}_m^3\tau'(\hat{z})^2 > \hat{x}_m\tau'(\hat{z})\big(- \alpha + \beta\hat{x}_m - \beta\gamma\hat{x}_m^2\tau'(\hat{z})\big),$$

which by combining terms gives us that $g_1'(\hat{x}_i) > g_2'(\hat{x}_i)$ provided,

$$1 + \hat{x}_m\tau'(\hat{z})(\alpha + \gamma - 2\beta\hat{x}_m) > 0. \tag{5.18}$$

We are now ready to state and prove a theorem giving criteria for uniqueness of $\hat{E}$.

THEOREM 5.7. *If any one of* *(i)* $\gamma > \alpha$; *(ii)* $\hat{x}_m < \frac{\alpha+\gamma}{2\beta}$ *for all* $\hat{x}_m$; *(iii)* $\tau'(z) < \frac{1}{\hat{x}_m(2\beta\hat{x}_m - \alpha - \gamma)}$ *holds, then* $\hat{E}$ *is unique.*

PROOF: If (ii) holds, then inequality (5.18) is valid. Since $\hat{x}_m < \alpha\beta^{-1}$, if (i) holds then (ii) holds. Finally, it is clear that if (iii) holds, then inequality (5.18) is valid. This proves the theorem.

We carry out as much as we can a stability analysis of the equilibria noting that the linearized stability theory for state dependent delays is not yet completely developed. The following analysis, then, is only formal in nature. Let $E^*(x_i^*, x_m^*)$ be an arbitrary equilibrium. Then the variational system of system (5.2) about E^* is given by

$$\begin{aligned} \frac{d}{dt}\begin{pmatrix} x_i(t) \\ x_m(t) \end{pmatrix} &= \begin{pmatrix} -\gamma + \xi^* & \alpha + \xi^* \\ -\xi^* & -2\beta x_m^* - \xi^* \end{pmatrix} \begin{pmatrix} x_i(t) \\ x_m(t) \end{pmatrix} \\ &\quad + \begin{pmatrix} 0 & -\alpha e^{-\gamma\tau(z^*)} \\ 0 & \alpha e^{-\gamma\tau(z^*)} \end{pmatrix} \begin{pmatrix} x_i(t - \tau(z^*)) \\ x_m(t - \tau(z^*)) \end{pmatrix}, \end{aligned} \tag{5.19}$$

where

$$\xi^* = \alpha\gamma e^{-\gamma\tau(z^*)}\tau'(z^*)x_m^*. \tag{5.20}$$

This leads to a characteristic equation given by

$$\det \begin{vmatrix} \lambda+\gamma-\xi^* & \alpha e^{-\tau(z^*)(\lambda+\gamma)}-\alpha-\xi^* \\ \xi^* & \lambda+2\beta x_m^*+\xi^*-\alpha e^{-\tau(z^*)(\lambda+\gamma)} \end{vmatrix} = 0. \tag{5.21}$$

For the equilibrium $E_0(0,0)$, clearly $\xi^* = 0$ and equation (5.21) reduces to

$$(\lambda+\gamma)(\lambda-\alpha e^{-\tau_m(\lambda+\gamma)}) = 0.$$

$\lambda = -\gamma$ is one of the eigenvalues. All other eigenvalues are given by solutions of

$$\lambda = \alpha e^{-\tau_m(\lambda+\gamma)},$$

which always has a real, positive solution. Hence E_0 is a saddle point.

For any interior equilibrium, $\hat{E}(\hat{x}_i, \hat{x}_m)$, we set

$$\hat{\xi} = \alpha\gamma e^{-\gamma\tau(\hat{z})}\tau'(\hat{z})\hat{x}_m = \beta\gamma\hat{x}_m^2\tau'(\hat{z}).$$

Expanding the characteristic equation (5.21) gives us,

$$\begin{aligned} &\lambda^2 + [\gamma+2\beta\hat{x}_m-\alpha e^{-\tau(\hat{z})(\gamma+\lambda)}]\lambda \\ &\quad + \gamma(\hat{\xi}+2\beta\hat{x}_m-\alpha e^{-\tau(\hat{z})(\gamma+\lambda)} - \hat{\xi}(\hat{\xi}+2\beta\hat{x}_m-\alpha e^{-\tau(\hat{z})(\gamma+\lambda)} \\ &\qquad = \hat{\xi}(-\alpha-\hat{\xi}+\alpha e^{-\tau(\hat{z})(\gamma+\lambda)}) \end{aligned}$$

which is equivalent to,

$$\begin{aligned} \lambda^2 + [\gamma+2\beta\hat{x}_m-\alpha e^{-\tau(\hat{z})(\lambda+\gamma)}]\lambda + \gamma(\hat{\xi}+2\beta\hat{x}_m-\alpha e^{-\tau(\hat{z})(\lambda+\gamma)}) \\ -\hat{\xi}(2\beta\hat{x}_m) = -\alpha\hat{\xi} \end{aligned}$$

so that

$$\lambda^2 + [\gamma + 2\beta\hat{x}_m]\lambda + \gamma(\hat{\xi} + 2\beta\hat{x}_m) - \hat{\xi}2\beta\hat{x}_m + \alpha\hat{\xi}$$
$$= \alpha e^{-\tau(\hat{z})(\lambda+\gamma)})(\lambda + \gamma)$$

Then, since $\hat{\xi} = \alpha\gamma e^{-\gamma\tau(\hat{z})}\tau'(\hat{z})\hat{x}_m = \beta\gamma\hat{x}_m^2\tau'(\hat{z})$ we have

$$\lambda^2 + [\gamma + 2\beta\hat{x}_m]\lambda + \beta\gamma\hat{x}_m[\gamma\hat{x}_m\tau'(\hat{z}) + 2 - 2\beta\hat{x}_m^2\tau'(\hat{z}) + \alpha\hat{x}_m\tau'(\hat{z})]$$
$$= \beta\hat{x}_m e^{-\gamma\tau(\hat{z})}(\lambda + \gamma)$$

which gives us

$$\begin{aligned} &\lambda^2 + [2\beta\hat{x}_m + \gamma]\lambda + \beta\gamma\hat{x}_m[2 + \hat{x}_m(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z})] \\ &= \beta\hat{x}_m e^{-\gamma\tau(\hat{z})\lambda}(\lambda + \gamma) \end{aligned} \tag{5.22}$$

as the characteristic equation.

In chapter two, where $\tau'(z) \equiv 0$, it was shown that $\hat{E}$ is globally asymptotically stable. Our first stability result for a density varying time delay is that if $\tau'(\hat{z}) = 0$, local asymptotic stability holds.

THEOREM 5.8. *Let $\tau'(\hat{z}) = 0$. Then $\hat{E}$ is asymptotically stable.*

PROOF: If $\tau'(\hat{z}) = 0$, the characteristic equation (5.22) can be written as,

$$\lambda^2 + 2\beta\hat{x}_m(\lambda + \gamma) + \gamma\lambda = \beta\hat{x}_m\hat{x}e^{-\gamma\tau(\hat{z})\lambda}(\lambda + \gamma)$$

or,

$$(\lambda + \gamma)(\lambda + 2\beta\hat{x}_m - \beta\hat{x}_m e^{-\gamma\tau(\hat{z})\lambda}) = 0. \tag{5.23}$$

Again $\lambda = -\gamma$ is one eigenvalue, and the others are given by the equation

$$\lambda + 2\beta\hat{x}_m = \beta\hat{x}_m e^{-\gamma\tau(\hat{z})\lambda}. \tag{5.24}$$

From equation (5.24) we compute the real parts of λ and get

$$\begin{aligned}\Re\mathrm{e}\,\lambda + 2\beta\hat{x}_m &= \beta\hat{x}_m e^{-\gamma\tau(\hat{z})\Re\mathrm{e}\,\lambda}\cos\left(\tau(\hat{z})\Im\mathrm{m}\,\lambda\right)\\ &\leq \beta\hat{x}_m.\end{aligned}$$

Hence $\Re\mathrm{e}\,\lambda \leq -\beta\hat{x}_m < 0$, proving the theorem.

We now consider the case where $\tau'(\hat{z}) > 0$. We let $\lambda = \mu + i\nu$ and separate the characteristic equation (5.22) into real and imaginary parts giving

$$\begin{aligned}\mu^2 - \nu^2 + (2\beta\hat{x}_m + \gamma)\mu + \eta &= \beta\hat{x}_m e^{-\hat{\tau}\mu}[(\gamma+\mu)\cos\hat{\tau}\nu + \nu\sin\hat{\tau}\nu]\\ 2\mu\nu + (2\beta\hat{x}_m + \gamma)\nu &= \beta\hat{x}_m e^{-\hat{\tau}\mu}[\nu\cos\hat{\tau}\nu - (\gamma+\mu)\sin\hat{\tau}\nu],\end{aligned} \tag{5.25}$$

where

$$\hat{\tau} = \gamma\tau(\hat{z}), \quad \eta = \beta\gamma\hat{x}_m[2 + \hat{x}_m(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z})].$$

We will think of η as a parameter which varies with $\tau'(\hat{z})$. When $\tau'(\hat{z}) = 0$, then $\eta = 2\beta\gamma\hat{x}_m$, and for this value of η, $\hat{E}$ is asymptotically stable.

Suppose, now that there is a first value of $\tau'(\hat{z}) > 0$ such that for this value $\eta = \bar{\eta}$ gives us that $\mu = 0$, so that $\hat{E}$ loses its stability. Then equation (5.25) becomes

$$\begin{aligned}\nu^2 - \bar{\eta} &= -\beta\hat{x}_m[\gamma\cos\hat{\tau}\nu + \nu\sin\hat{\tau}\nu]\\ (2\beta\hat{x}_m + \gamma)\nu &= \beta\hat{x}_m[\nu\cos\hat{\tau}\nu - \gamma\sin\hat{\tau}\nu].\end{aligned} \tag{5.26}$$

Squaring and adding equation (5.26) gives the equation

$$\nu^4 + [(2\beta\hat{x}_m + \gamma)^2 - 2\bar{\eta}]\nu^2 + \bar{\eta}^2 = \beta^2\hat{x}_m^2(\nu^2 + \gamma^2)$$

or

$$\nu^4 + [3\beta^2\hat{x}_m^2 + 4\beta\gamma\hat{x}_m + \gamma^2 - 2\bar{\eta}]\nu^2 + [\bar{\eta}^2 - \beta^2\gamma^2\hat{x}_m^2] = 0. \qquad (5.27)$$

In order for such $\bar{\eta}$ to exist, equation (5.27) must have real roots. Hence we can now prove the following theorem.

THEOREM 5.9. *If either* (i) $\hat{x}_m \leq \frac{\alpha+\gamma}{2\beta}$ or (ii) $\hat{x}_m > \frac{\alpha+\gamma}{2\beta}$ and $\tau'(\hat{z}) \leq \frac{3}{4\hat{x}_m(2\beta\hat{x}_m-\alpha-\gamma)}$ *holds, then* $\hat{E}$ *is asymptotically stable.*

PROOF: After substituting for $\bar{\eta}$ equation (5.27) becomes

$$\nu^4 + [3\beta^2\hat{x}_m^2 + 4\beta\gamma\hat{x}_m + \gamma^2 - 2\beta\gamma\hat{x}_m(2 + \hat{x}_m(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z}))]\nu^2$$
$$+ \beta^2\gamma^2x_m^2(4 + 4\hat{x}_m(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z}) + [\hat{x}_m(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z})]^2)$$
$$- \beta^2\gamma^2x_m^2 = 0.$$

Then, combining like terms, and rearranging,

$$\nu^4 - 2\beta\gamma\hat{x}_m^2(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z}) + \beta^2\gamma^2\hat{x}_m^4[(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z})]^2$$
$$+ [3\beta^2\hat{x}_m^2 + \gamma^2]\nu^2 + 3\beta^2\gamma^2x_m^2 + 4\beta^2\gamma^2x_m^3(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z}) = 0.$$

so that we get the relation,

$$f(\nu^2) = [\nu^2 - \beta\gamma\hat{x}_m^2\tau'(\hat{z})(\alpha+\gamma-2\beta\hat{x}_m)]^2 + [3\beta^2\hat{x}_m^2 + \gamma^2]\nu^2$$
$$+ 3\beta^2\gamma^2\hat{x}_m^2 + 4\beta^2\gamma^2\hat{x}_m^3(\alpha+\gamma-2\beta\hat{x}_m)\tau'(\hat{z}) = 0.$$

Observe that the first three expressions in $f(\nu^2)$ are always positive. So, if $x_m \leq \frac{\alpha+\gamma}{2\beta}$ the last expression is also positive since $\hat{x}_m > 0$, $\tau'(\hat{z}) > 0$ by assumption, and $(\alpha + \gamma - 2\beta\hat{x}_m) > 0$ will be true. Hence $f(\nu^2) > 0$, and no such $\hat{\eta}$ can exist.

Now, if $\hat{x}_m > \frac{\alpha+\gamma}{2\beta}$, then $(\alpha+\gamma-2\beta\hat{x}_m) < 0$. Then if $\tau'(z) < \frac{3}{4}(\hat{x}_m(2\beta\hat{x}_m - \alpha - \gamma))$ we have,

$$3\beta^2\gamma^2\hat{x}_m^2 + 4\beta^2\gamma^2\hat{x}_m^3(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z}) \geq 3\beta^2\gamma^2\hat{x}_m^2 - 4\beta^2\gamma^2\hat{x}_m^3 \cdot \frac{3}{4\hat{x}_m} = 0.$$

Since the first two terms of $f(\nu^2)$ are positive, then $f(\nu^2) > 0$ must hold. So if either (i) or (ii) holds, then $f(\nu^2) > 0$ for all $\nu^2 \geq 0$ and equation (5.27) has no real solution. Then for that value of $\tau'(\hat{z})$, $\mu = 0$ is impossible. Hence, since $\mu < 0$ when $\tau'(\hat{z}) = 0$, by continuity, $\mu < 0$ for that value of $\tau'(\hat{z})$ proving the theorem.

We note that in the case that $\hat{E}$ is not unique, unstable (saddle point) equilibria must exist.

5.5 Global Behavior of Solutions

In this section we are interested in obtaining some global properties of the solutions of our model. In particular, we wish to ascertain that their behavior is reasonable provided the initial inputs are reasonable.

The first results show that if the mature population remains below or above a certain value for length of time τ_M, it will do so from then on.

THEOREM 5.10. *Let $x_i(t)$, $x_m(t)$ be a solution of system (5.2).*

(i) If there exists $t_1 \geq -\tau_m$ such that $x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for $t_1 \leq t \leq t_1+\tau_M$, then $x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for all $t \geq t_1$.

(ii) If there exists $t_2 \geq -\tau_m$ *such that* $x_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_M}$ *for* $t_2 \leq t \leq t_2+\tau_M$, *then* $x_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_M}$ *for all* $t \geq t_2$.

PROOF: We prove the result for case (i). The proof of case (ii) follows analogously. Suppose there exists $t^* > t_1 + \tau_M$ such that $x_m(t^*) = \alpha\beta^{-1}e^{-\gamma\tau_m}$ and $x_m(t) < \alpha\beta^{-1}e^{-\gamma\tau_m}$ for $t_1 \leq t < t^*$. Then $\dot{x}_m(t^*) \geq 0$. However, from system (5.2),

$$\begin{aligned}
\dot{x}_m(t^*) &= \alpha e^{-\gamma\tau(z)} x_m\big(t^* - \tau(z)\big) - \beta x_m^2(t^*) \\
&= \alpha e^{-\gamma\tau(z)} x_m\big(t^* - \tau(z)\big) - \alpha^2\beta^{-1}e^{-2\gamma\tau_m} \\
&\leq \alpha e^{-\gamma\tau_m}\big[x_m\big(t^* - \tau(z)\big) - \alpha\beta^{-1}e^{-\gamma\tau_m}\big] < 0,
\end{aligned}$$

a contradiction.

From this theorem, the following corollary follows immediately.

COROLLARY 5.11. *(i) If* $\varphi_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$, $-\tau_M \leq t \leq 0$, *then* $x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$ *for all* $t \geq 0$. *(ii) If* $\varphi_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_M}$, $-\tau_M \leq t \leq 0$, *then* $x_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_M}$ *for all* $t \geq 0$.

In the case where we know that $x_m(t)$ is monotone, then we can show that the limit as $t \to \infty$ of $x_m(t)$ lies in a certain bounded interval.

THEOREM 5.12. *Suppose* $x_m(t)$ *is eventually monotonic. Then* $\alpha\beta^{-1}e^{-\gamma\tau_M} \leq \lim_{t\to\infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$.

PROOF: Since $x_m(t)$ is eventually monotonic and $x_m(t)$ is bounded, there exists $0 < \bar{x}_m < \infty$ such that $\lim_{t\to\infty} x_m(t) = \bar{x}_m$, $\lim_{t\to\infty} \dot{x}_m(t) = 0$. Hence from system (5.2), taking the limit superior as $t \to \infty$, we have that,

$$0 = \bar{x}_m\big(\alpha e^{-\gamma\tau(\overline{\lim}_{t\to\infty} x_i(t)+\bar{x}_m)} - \beta\bar{x}_m\big).$$

Thus $\bar{x}_m = \alpha\beta^{-1}e^{-\gamma\tau(\overline{\lim}_{t\to\infty}\ x_i(t)+\bar{x}_m)}$, so that $\alpha\beta^{-1}e^{-\gamma\tau_M} \leq \bar{x}_m \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$, proving the theorem.

We are now in a position to state bounds on the eventual behaviour of $x_m(t)$, independent of admissible initial conditions.

THEOREM 5.13. *Let* $(x_i(t), x_m(t))$ *be a solution of system (5.2). Then*

$$\alpha\beta^{-1}e^{-\gamma\tau_M} \leq \liminf_{t\to\infty} x_m(t) \leq \limsup_{t\to\infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}. \tag{5.28}$$

PROOF: If $x_m(t)$ is eventually monotonic, the result follows from Theorem 5.12. Hence we assume that $x_m(t)$ is oscillatory. We prove that $\limsup_{t\to\infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$. The other inequality follows analogously.

Define the sequence $\{t_k\}$ as those times for which $x_m(t)$ achieve a maximum, i.e. $\dot{x}_m(t_k) = 0$, $\ddot{x}_m(t_k) < 0$. Define

$$\tilde{x}_m = \limsup_{k\to\infty}\{x_m(t_k)\}. \tag{5.29}$$

Then $0 < \tilde{x}_m < \infty$ and $\limsup_{t\to\infty} x_m(t) = \tilde{x}_m$.

If $\tilde{x}_m \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$, we are done. Hence assume that

$$\tilde{x}_m > \alpha\beta^{-1}e^{-\gamma\tau_m}. \tag{5.30}$$

Then from system (5.2), $0 = \dot{x}_m(t_k) = \alpha e^{-\gamma\tau(z_k)} x_m(t_k - \tau(z_k)) - \beta x_m(t_k)^2$, where $z_k = x_i(t_k) + x_m(t_k)$.

We now choose a subsequence of $\{t_k\}$ relabelled as $\{t_k\}$ so that $\lim\limits_{k\to\infty} x_m(t_k) = \tilde{x}_m$ and $t_{k+1} \geq t_k + \tau_M$. We then choose a further subsequence of $\{t_k\}$, again relabelled $\{t_k\}$ so that $\lim\limits_{k\to\infty} z_k = \tilde{z}$, where $\tilde{z} = \limsup\limits_{k\to\infty} z_k$.

Now let $x_m^{\#} = \limsup\limits_{k\to\infty} x_m(t_k - \tau(z_k))$ for this subsequence $\{t_k\}$. We choose a final subsequence of $\{t_k\}$, once again relabelled $\{t_k\}$, so that

$\lim\limits_{k\to\infty} x_m(t_k - \tau(z_k)) = x_m^{\#}$.

Now from the definition of τ_m and inequality (5.30), we get, taking the limit as $k \to \infty$,

$$0 = \alpha e^{-\gamma\tau(\tilde{z})} x_m^{\#} - \beta \tilde{x}_m^2 < \alpha e^{-\gamma\tau_m}(x_m^{\#} - \tilde{x}_m).$$

If $x_m^{\#} \leq \tilde{x}_m$, we have a contradiction.

Hence we assume that $x_m^{\#} > \tilde{x}_m$. Then we have that for each k, we can choose a value t_i such that $\dot{x}_m(t_i) = 0$, $\ddot{x}_m(t_i) < 0$, and $\limsup\limits_{i\to\infty} x_m(t_i) \geq x_m^{\#} > \tilde{x}_m$. But this contradicts the definition of $\tilde{x}_m$ in expression (5.29), so $x_m^{\#} > \tilde{x}_m$ cannot be true. This eliminates the last possibility and proves the theorem.

We are now in a position to use the above estimates in obtaining estimates on the x_i. We first note that we can find $T(\varepsilon) > 0$ so large that

$$\alpha\beta^{-1}e^{-\gamma\tau_M} - \varepsilon < x_m(t) < \alpha\beta^{-1}e^{-\gamma\tau_m} + \varepsilon \qquad (5.31)$$

for given $\varepsilon > 0$ whenever $t \geq T$. Then the first equation of (2.2) can be written in the integral equation form

$$x_i(t) = e^{-\gamma(t-T)}[x_i(T)+\alpha \int_T^t e^{\gamma(s-T)}\big(x_m(s)-e^{-\gamma\tau(z(s))}x_m\big(s-\tau(z(s))\big)\big)ds. \quad (5.32)$$

Although inequality (5.32) is valid for all t, we will utilize it only for those $t \geq T + \tau_M$.

THEOREM 5.14. *Let* $(x_i(t), x_m(t))$ *be a solution of system (5.2). Then* $\limsup_{t\to\infty} x_i(t) \leq \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M})$.

PROOF: Utilizing inequalities (5.31) and (5.32), we get for $t \geq T + \tau_M$,

$$x_i(t) \leq e^{-\gamma(t-T)}[x_i(T)+\alpha \int_T^t e^{\gamma(s-T)}\big(\alpha\beta^{-1}e^{-\gamma\tau_m}+\varepsilon-e^{-\gamma\tau_M}(\alpha\beta^{-1}e^{-\gamma\tau_M}-\varepsilon)\big)ds], \quad (5.33)$$

where $\varepsilon > 0$ is arbitrary. Hence from equation (5.33) we get that

$$\begin{aligned}\limsup_{t\to\infty} x_i(t) \leq{}& \limsup_{t\to\infty} e^{-\gamma(t-T)}x_i(T)\\ &+ \limsup_{t\to\infty} \alpha e^{-\gamma(t-T)}[\alpha\beta^{-1}e^{-\gamma\tau_m} - \alpha\beta^{-1}e^{-2\gamma\tau_M})\\ &+ \varepsilon(1+e^{-\gamma\tau_M})]\int_T^t e^{\gamma(s-T)}ds\\ ={}& [\alpha^2\beta^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M})\\ &+ \alpha\varepsilon(1+e^{-\gamma\tau_M})] \limsup_{t\to\infty} e^{-\gamma(t-T)}\int_T^t e^{\gamma(s-T)}ds\\ ={}& \gamma^{-1}[\alpha^2\beta^{-1}(e^{-\gamma\tau_m}) - e^{-2\gamma\tau_M}) + \alpha\varepsilon(1-e^{-\gamma\tau_M})](1-\lim_{t\to\infty} e^{-\gamma(t-T)})\\ ={}& \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M}) + \alpha\gamma^{-1}\varepsilon(1-e^{-\gamma\tau_M}).\end{aligned}$$

Since ε is arbitrary, the theorem is proved.

Similarly we can obtain a lower bound on $x_i(t)$.

THEOREM 5.15. *Let $\tau_M < 2\tau_m$. Let $\big(x_i(t), x_m(t)\big)$ be a solution of system (5.2). Then* $\liminf_{t\to\infty} x_i(t) \geq \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_M} - e^{-2\gamma\tau_m})$.

PROOF: The proof for this theorem is symmetrical to the proof of theorem 5.14.

In this theorem for the lower bound, we require that $\tau_M < 2\tau_m$ in order for the lower bound to be positive. Otherwise we do not have any new information. That is, if it is the case that $\tau_M - \tau_m > \tau_m$, (too large a spread) we are unable to obtain an explicit limiting lower bound on $x_i(t)$.

5.6. Discussion

The main purpose of this chapter was to analyze a model of stage-structured population growth where the age to maturity is state dependent. It was found that there always exists a positive equilibrium, but unlike the constant delay case, this equilibrium may not be unique. Criteria for uniqueness were obtained.

In Section 5, we obtained explicit bounds for the eventual behavior of $x_i(t)$ and $x_m(t)$. These bounds were in terms of τ_m and τ_M. In the case that $\tau_M = \tau_m$, i.e. in the case where our system reduces to the constant delay case, then $\lim_{t\to\infty}\big(x_i(t), x_m(t)\big)$ exists and tends to $(\hat{x}_i, \hat{x}_m)$ (which is unique), thus incorporating the results of chapter two. We should note that theorem 5.15 allows for the possibility of the number of immatures, $x_i(t)$, becoming arbitrarily small if $\tau_M < 2\tau_m$. Neither our requirement that $\tau'(z) < 4\beta/\alpha^2$ to avoid retrogression of matures into immatures, nor our requirement for theorem

5.5 that $\delta_m \int_{t-\tau_m}^{t} e^{\gamma s} ds > \Delta_m \int_{-\tau_s}^{t-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$ for all t precludes τ_M from being less than $2\tau_m$, since for any difference $\tau_M - \tau_m$, $\tau'(z)$ can still be made as small as we need to satisfy our requirements for a valid model. In any case, theorem 5.6 assures us that we can find admissible initial functions for a wide variety of cases.

We should also note that the requirement that $\tau'(z) < 4\beta/\alpha^2$ to avoid retrogression and the requirement that $\delta_m \int_{t-\tau_m}^{t} e^{-\gamma s} ds > \Delta_m \int_{-\tau_s}^{t-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$ in theorem 5.5 that gives sufficient conditions for the positivity of $x_i(t)$ are linked; as $\tau'(z)$ approaches the value $4\beta/\alpha^2$ where retrogression of mature and immatures occurs, the set of admissible initial functions allowed by that theorem approaches the null set.

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APPENDIX ONE

Documentation for subroutine DELAYS

```
SUBROUTINE DELAYS (FEVL, G, FINEVL, N, NTD, IWD1, IWD2,
      TINIT, TSTOP, X, H, IDIG, IND, WK1, WK2, WK3, WK4, WK5)
```

SUBROUTINE NAME: DELAYS

SUBROUTINE LIBRARY: MATH:DELAYS.LIB

SUBROUTINE TITLE: Solving Systems of First Order Retarded FDE's with Continuous Initial Conditions and Delays Bounded Away from Zero and Infinity

PRECISION: DOUBLE

ORIGIN/AUTHOR: Walter G. Aiello, Department of Mathematics, UQV

DATE: October, 1989

SOURCE LANGUAGE: FORTRAN

PURPOSE: Subroutine DELAYS uses an Adams-Moulton fourth order predictor-corrector method with varying stepsize to solve the first order system of retarded FDE's of the form,

$$X' = F(T, X(T), X(G_1(T,X)), \ldots, X(G_{ntd}(T,X))$$

Where X is an N-vector, G_i is a function from N+1 dimensional space to the time domain, and F is the defining function which gives X'_i as a function of T, X(T), and the $X(G_i)$'s, for i = 1,...,NTD. Notice that the time delay functions G_i can depend on both the independent and dependent variables, T and X(N). Here N is the number of equations in the system, and NTD is the number of time delays.

The stepsize H is checked at each step to ensure it is small enough for convergence. If not, the stepsize is cut in half. The stepsize may also be doubled in some cases to improve speed without sacrificing accuracy.

USAGE: In program, `CALL DELAYS(FEVL, G, FINEVL, N, NTD, IWD1, IWD2, TINIT, TSTOP, X, H, IDIG, IND, WK1, WK2, WK3, WK4, WK5)`

Compile, then `$RUN -OBJ+MATH:DELAYS.LIB`, where -OBJ is the compiled object program.

PARAMETER LIST: (DOUBLE PRECISION ARGUMENTS)

FEVL User supplied SUBROUTINE that evaluates the derivative of each of the N components of X as a function of T, X(T), and $X(G_i(T,X(T)))$, where i = 1,...,NTD. It must be of the following form:

```
SUBROUTINE FEVL(T, X, XDEL, F)
DOUBLE PRECISION T, X(*N*), XDEL(*NTD*,*N*), F(*N*)
  ...
```

where *NTD* is the actual number of time delays, and *N* is the actual number of equations in the system. X is the dependent variable described below, XDEL returns the values of each of the N components of X at each of the NTD time delays, and F returns the derivatives of X back to the calling program. F must be defined by the user, being a function of T, X, and XDEL. The time delays are given by XDEL, where XDEL(i,j) refers to the i'th time delay of the j'th component of the X vector. FEVL must be declared EXTERNAL by the user in the calling program.

G User supplied FUNCTION program that evaluates the I time delays from time T for a given value of X. G must be bounded away from zero, must have a finite upper bound, and it must be in the following form:

```
DOUBLE PRECISION FUNCTION G(T, X, I)
DOUBLE PRECISION X(*N*), T
  ...
```

where *N* is the number of equations in the system, and where I is supplied to the function routine by the calling program to indicate which time delay is to be evaluated. The user must have G as being a function of T, X, and I in the following manner:

IF (I .EQ. 1)   G = $g_1(T, X)$
IF (I .EQ. 2)   G = $g_2(T, X)$
...
IF (I .EQ. NTD)   G = $g_{ntd}(T, X)$

G must be declared EXTERNAL by the user in the calling program.

FINEVAL User supplied SUBROUTINE that evaluates each of the N components of the initial function at time T. FINEVAL must define an initial function FINIT that is continuous on its closed domain of definition, and it must be in the following form:

```
          SUBROUTINE FINEVL(T, FINIT)
          DOUBLE PRECISION T, FINIT(*N*)
            ...
```

where *N* is the actual number of equations in the system. FINIT returns the N components of the initial function evaluated at time T to the calling program, and must be defined in the subroutine by the user. FINEVL must be declared EXTERNAL by the user in the calling program.

N	Number of equations in the system of FDE's
NTD	Number of time delays in the system of FDE's
IWD1	Workspace dimension. Set equal to 6*(NTD+1)
IWD2	Workspace dimension. Set equal to 3*N + 1
TINIT	On INPUT: Starting point of independent variable. On OUTPUT: Stopping point of independent variable.
TSTOP	Stopping point of independent variable; value at which solution is desired.
X(N)	N-vector of values of components of dependent variable. On input initial values are given by the initial function FINEVL. On output X contains the computed values of the dependent variable X at time TSTOP
H	Initial stepsize, may be changed by program
IDIG	Desired number of digits accuracy
IND	Indicator. To be set to 1 for first call. Program will set IND to 0 for subsequent calls in order to indicate that computed values of X are stored in history arrays.
WK1	Work area dimensioned to (10000, N)
WK2	Work area dimensioned to (10000, N)
WK3	Work area dimensioned to (N, IWD1) where IWD1 = 6*(NTD+1)
WK4	Work area dimensioned to (NTD,IWD2) where IWD2 = 3*N + 1
WK5	Work area dimensioned to (16*N)

REMARKS: 1. Typically, H will be set to a value somewhere between 10^{-5} and 10^{-2}, but in any case H must be smaller than the minimium value the time delay can achieve. The program will increase H to a maximum value of (TSTOP-TINIT)/10. So if H is initially set to too small a value, the storage tables containing past information are likely to overflow. If such an overflow occurs, one should either increase the stepsize H, and/or decrease the number of digits accuracy IDIG.

2. The desired number of digits accuracy IDIG is only a relative figure. One may get more, or less, accuracy than is reflected by IDIG. In general, increasing IDIG will increase accuracy, and decreasing IDIG will decrease accuracy. For some systems too small a value of IDIG will cause problems. Generally, a value of IDIG less than 8 is indicated.

EXAMPLE:

```
      REAL*8 X(2), T, TSTOP, TINCR, H
      REAL*8 WK1(10000,2), WK2(10000,2), WK3(2,24), WK4(3,7), WK5(32)
      INTEGER N, NTD, IWD1, IWD2, IDIG, IND
      EXTERNAL FEVL, G, FINEVL
      N = 2
      NTD = 3
      IWD1 = 6*(NTD+1)
      IWD2 = 3*N + 1
      T = 0.D0
      TSTOP = .1D0
      TINCR = .1D0
      H = .0001D0
      IDIG = 7
      IND = 1
      DO 3000 K=1,5
        CALL  DELAYS(FEVL,  G,  FINEVL,  N, NTD, IWD1, IWD2, T,TSTOP,
     >                     X, H, IDIG, IND, WK1, WK2, WK3, WK4, WK5)
C Write out results here.
        TSTOP = TSTOP + TINCR
 3000 CONTINUE
      STOP
      END
```

```
      SUBROUTINE FEVL(T, X, XDEL, F)
      REAL*8 X(2), XDEL(3,2), F(2), T
C Define the system of FDE's here, eg:
C
C   F(1) = XDEL(3,2) - X(1)
C   F(2) = -XDEL(1,1)*XDEL(2,1) - X(2)
C
C being an example of two equations in three time delays.
C Notice that the first dimension in the array XDEL gives which
C time delay is indicated, and the second dimension gives the
C component of X that is indicated.
C Thus this example would be for the system:
C
C   X'1 = X2(G3) - X1
C   X'2 = -X1(G1)*X1(G2) - X2
C
C where G1, G2, and G3 are functions of X and T.
      RETURN
      END


      DOUBLE PRECISION FUNCTION G(T,X,I)
      REAL*8 X(2), T
C Define the time delay function here. A typical case is for a
C constant time delay: G = T - TAU. If more than one time delay is
C involved, one will need a function of the type:
C
C                             IF (I .EQ. 1) G = T - TAU1
C                             IF (I .EQ. 2) G = T - TAU2
C                             IF (I .EQ. 3) G = T - TAU3
C
C being an example that includes three time delays and no dependence
C on the dependent variable X.
      RETURN
      END


      SUBROUTINE FINEVL(T, FINIT)
      REAL*8 FINIT(2), T
C Define initial function here, eg:
C    FINIT(1) = 1.D0
C    FINIT(2) = DSIN(T)
C being an example for a two-dimensional system.
      RETURN
      END
```

APPENDIX TWO

Fortran source code for subroutine DELAYS

```
      SUBROUTINE DELAYS(FEVL, G, FINEVL, N, NTD, IWD1, IWD2, TINIT,
     >               TSTOP, X, H, IDIG, IND, WK1, WK2, WK3, WK4, WK5)
      INTEGER N, IDIG, IND, NTD
      INTEGER IC1, IC2, ID3, ID4, ID5, ID6, ID7, ID8, ID9, ID10
      INTEGER ID11, ID12, ID13, ID14, ID15, ID16
      REAL*8 FEVL, G, FINEVL
      REAL*8 WK1(10000,N), WK2(10000,N), WK3(N,IWD1), WK4(NTD,IWD2)
      REAL*8 X(N), WK5(1), TINIT, TSTOP, H
      EXTERNAL FEVL, G, FINEVL
C
C This is merely an interfacing routine placed here in order to
C shorten and simplify the already long and complicated argument
C list. For a description of the variables, see the comments for
C subroutine DELA4 which follows.
C
C FEVL(T, X, XDEL, F)    Evaluates system of time delay equations
C   X(N)
C   XDEL(NTD x N)
C   F(N)
C
C G(T,I)                 Evaluates I'th time delay
C
C FINEVAL(T, FINIT)      Evaluates initial function
C   FINIT(N)
C
C N      Number of equations in time delay differential equations
C NTD    Number of time delays
C IWD1   Set equal to 6*(NTD+1)
C IWD2   Set equal to 3*N + 1
C
C T      Starting time
C TSTOP  Stopping time
C X(N)   Independent vector variable
C H      Stepsize of time T
C IDIG   Desired number of digits accuracy
C IND    Set to 1 for first call, 0 for subsequent calls
C
C WK1  dimensioned to (10000, N)
C WK2  dimensioned to (10000, N)
C WK3  dimensioned to (N, IWD1)  where IWD1 = 6*(NTD+1)
C WK4  dimensioned to (NTD,IWD2) where IWD2 = 3*N + 1
C WK5  dimensioned to (16*N)
C
      IC1 = N+2
      IC2 = IC1+N
      ID2 = N+1
      ID3 = ID2+N
      ID4 = ID3+N
      ID5 = ID4+N
      ID6 = ID5+N
      ID7 = ID6+N
```

```
      ID8 = ID7+N
      ID9 = ID8+N
      ID10 = ID9+N
      ID11 = ID10+N
      ID12 = ID11+N
      ID13 = ID12+N
      ID14 = ID13+N
      ID15 = ID14+N
      ID16 = ID15+N
C
C This interfacing routine simply relieves the user of a longer
C calling list than there already is via the splitting apart of
C the working storage array WK4. If this is not compatible with
C the compiler, call the subroutine DELA4 directly.
C
      CALL DELA4(FEVL, G, FINEVL, N, NTD, IWD1, TINIT, TSTOP,
     >       X, H, IDIG, IND, WK1, WK2, WK3, WK4(1,1), WK4(1,2),
     >       WK4(1,IC1), WK4(1,IC2), WK5(1), WK5(ID2), WK5(ID3),
     >       WK5(ID4), WK5(ID5), WK5(ID6), WK5(ID7), WK5(ID8),
     >       WK5(ID9), WK5(ID10), WK5(ID11), WK5(ID12),
     >       WK5(ID13), WK5(ID14), WK5(ID15), WK5(ID16) )
C
      RETURN
      END
      SUBROUTINE DELA4(FEVL, G, FINEVL, N, NTD, IWD1, TINIT, TSTOP,
     >           X, HINIT, IDIG, IND, XTAB, FXTAB, WK1,
     >           TDEL, XDEL, XDELP, WK2, WK3, F, FINIT, XINIT,
     >           XI, XP, XC, F1, F2, F3, F4, K1, K2, K3, K4,
     >           K5)
C
C Subroutine DELA4 (Adams-Moulton 4TH) uses the Adams-Moulton
C fourth order predictor-corrector method with varying stepsize
C to solve the first order nonautonomous delay differential equation
C X' = F(T,X(T),X(G(T))) where G(T) gives the time delay. The
C stepsize H is checked to ensure it is small enough for
C convergence. If not, the stepsize is cut in half.
C  A predicted value for X (XP) is computed, and using XP, a
C corrected value for X (XC) is next computed.
C  If XP and XC are equal and if there are already enough X values
C computed, stepsize H will be doubled to increase the speed of
C computation for succeeding X's if a convergence criterion is met.
C  However, if a second convergence criterion and an accuracy
C criterion are not met, stepsize H is halved, and computations
C from the present X are repeated with the smaller stepsize.
C
C PARAMETERS USED:
C   FEVL    Subroutine for calculating the N-dimensional array
C        X' = F(T,X,X(G(T))). FEVL must be declared EXTERNAL in
C        the calling routine.
C   G    Function subroutine to compute the delay values for T. The
C        time delays will then be given by T - G(T,I), I=1,...,NTD.
C        Needless to say, G must be positive, but G must also be
C        bounded away from zero, and must be finite.
C        G must be declared EXTERNAL in the calling routine.
C   FINEVL Subroutine for calculating the N-dimensional array FINIT
C        which contains the values of the N-dimensional initial
C        function at a given time T. FINEVL must be declared
```

```
C         EXTERNAL in the calling routine.
C   N     Number of equations in the system.
C   NTD   Number of time delays in the system.
C   IWD1  First dimension of WK1 array, must be equal to 6 + 8*NTD.
C   TINIT On INPUT, T value at the beginning of interval.
C         On OUTPUT, gives T value at end of interval.
C   TSTOP INPUT value of minimum T for which solution is given.
C   X(N)  On OUTPUT, gives approximation of X at end of interval.
C         Output value of T will be interpolated from TSTOP+H
C   H     On INPUT, next stepsize of T. Must be smaller than delay.
C         On OUTPUT, last stepsize used.
C   IDIG  INPUT value of number of digits accuracy required.
C   IND   INPUT value of 1 indicates first call to DELA4. Is reset
C         to 0 if integration was successful.
C         INPUT value of 0 indicates that this is not the first
C         call for the problem. Previous values of X are stored
C         from last call. IND is unchanged on output.
C
C VARIABLES AND ARRAYS (Carries an Nth dimension when appropriate):
C   WK1    Stores the present value of X in WK1(1), the values of
C          X(T-nH) in WK1(n+1), the values of X at G(T,1) in WK1(7),
C          and of X(G(T-nH,1)) in WK1(n+7), and so on, with the
C          values of X(G(T,NTD) in WK1(1+6*NTD), and of X(G(T-nH,NTD)
C          in WK1(1+n+6*NTD).  Here, n=1,...,5, and WK1(I) contains N
C          values, since X is a vector of length N. (N, 6*(NTD+1) )
C   WK2    Stores values of X at G(T,I) where I=1,...,NTD, for call
C          to FEVL.  Dimension (NTD, N).
C   WK3    Stores value of vector X for call to FEVL. Dimension N.
C   T      Intermediate values of T
C   TDEL   NTD dimensional vector containing values of retarded T;
C          G(T,I) where I=1,...,NTD.
C   TTAB   Table of values of T for which a value of X exists
C   PTTAB  Full table containing values less than TTAB(1) if the
C          a time value less than TTAB(1) may not be handled by the
C          initial function.
C   XI     N-dimensional intermediate values of X
C   XDEL   NTD by N dimensional intermediate values of X at retarded
C          times.  XDEL(I,K) = X(G(T,I)) for the Kth entry of X.
C   XDELP  NTD by N dimensional predicted values of X at times
C          G(T+H,I) where I=1,...,NTD.
C   XTAB   Table of previously computed or assigned X values
C   PXTAB  Full table of X values corresponding to time values less
C          than TTAB(1). Accessed only if X values for time T less
C          than TTAB(1) may not be defined by the initial function.
C   HINIT  Initial value of stepsize H
C   TOL    Tolerance: set to 1/IDIG
C   IXCNT  Number of previous X values stored in WK array.
C   XP     Predicted value for next value of X
C   XC     Corrected and final value for next value of X
C   FULL   .TRUE. only if time values less than TTAB(1) may not be
C          in the domain of definition of the initial function.
C   LINITL .TRUE. when tabels of previous values have been filled no
C          more than once, and the initial function may be referred
C          to for values not in the tables.
C   TABERR .TRUE. only if an attempt is being made to access a time
C          value which is not stored in the tables.
C   P      Parameter used in computing five-point interpolation for
```

```
C        X at TSTOP when solution goes past TSTOP.
C
C SUBROUTINES CALLED:
C  WKINIT(TINIT, TDEL, X, XDEL, WK1, IXCNT, N, NTD, IWD1, H, WK3)
C        Initializes the work array WK1 from which the
C        Adams-Moulton steps are taken.
C  UPDATD(FINEVL, G, N, NTD, IWD1, T, TDEL, XI, XDEL, FINIT, WK1,
C     IXCNT, H, XC, FULL, TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
C        Advances position along T - axis. To do this, T is reset
C        to T+H, X to XC, and WK is advanced along T axis. IXCNT
C        is incremented if it is less than 6. TTAB and XTAB are
C        also updated.
C  HDSTEP(H, N, NTD, IWD1, WK1, IXCNT)
C        Halves the stepsize H, interpolates new values for
C        WK1(1/2) and WK1(3/2), resets WK accordingly, and
C        reinitializes IXCNT to 5 if IXCNT is greater than 5.
C  XG(FINEVL, FINIT, TDEL, N, K, FULL, LINITL, TTAB, XTAB, PTTAB,
C   >                                      PXTAB, KHIGH, KPHIGH)
C        Interpolates the K'th value of X(G(T)) from the tables at
C        time TDEL.
C  APROX(TTABLE, XTABLE, N, K, NHIGH, TDEL, XVAL, DX)
C        Given a time value TDEL, APROX searches a table of time
C        values, and then interpolates a value for XVAL from a
C        corresponding table of X values to approximate X(TDEL).
C  STORE(FULL, N, TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
C        When the table of previous values becomes full, the table
C        is stored in an array of previous values, and a new table
C        is started. In this manner, we maximize the storage of
C        previous values without resorting to huge arrays. We will
C        never have less than 10000 previous values available to
C        us bearing in mind that we will have the initial function
C        at the start.
C  ERMSG1(H, HINIT, TINIT, TSTOP)
C        Gives appropriate error message if H is made too small,
C        H is set to zero or less, or if TINIT > TSTOP.
C  ERMSG2(TABERR)
C        Gives appropriate error message if an attempt is made to
C        access a time value less than what is in the tables.
C
C
   INTEGER N, NTD, IWD1
   INTEGER KHIGH, KPHIGH, IND, IDIG, I, K, IXCNT
   REAL*8 TTAB(10000), XTAB(10000,N), PTTAB(10000), PXTAB(10000,N)
   REAL*8 WK1(N,IWD1), WK2(NTD,N), WK3(N), TEMP, MINDEL
   REAL*8 F(N), FINIT(N), X(N), G, TINIT, TSTOP, H, HINIT, HMAX
   REAL*8 XDEL(NTD,N), XDELP(NTD,N), XINIT(N), XI(N), XP(N),XC(N)
   REAL*8 K1(N), K2(N), K3(N), K4(N), K5(N)
   REAL*8 TDEL(NTD), TOL, T, TMH, TPH, CONV, P, XABS, XG
   REAL*8 F1(N), F2(N), F3(N), F4(N)
   LOGICAL TABERR, FULL, LINITL
   EXTERNAL FEVL, G, FINEVL
   SAVE TTAB, PTTAB, T
C
C
C Initializations.  If first call to DELA4 initialize WK vector
C using call to WKINIT. Else use values left over from last call.
   H = HINIT
```

```
      IF (TINIT .GE. TSTOP)
     >                   CALL ERMSG1(H, HINIT, TINIT, TSTOP)
      IF (H .LE. 0)  CALL ERMSG1(H, HINIT, TINIT, TSTOP)
      TOL = 1.D0/(10.D0**(IDIG+2))
      HMAX = (TSTOP - TINIT)/10.D0
      IF (IND .EQ. 1)  THEN
        TABERR = .FALSE.
        FULL = .FALSE.
        LINITL = .TRUE.
        KHIGH = 0
        T = TINIT
C
C Evaluate initial value of X
        CALL FINEVL(TINIT, FINIT)
        DO 3020 K=1,N
          XINIT(K) = FINIT(K)
          X1(K) = XINIT(K)
          X(K) = XINIT(K)
 3020   CONTINUE
C
C Evaluate time delays at initial time with initial values of X
        DO 3050 I=1,NTD
          TDEL(I) = G(TINIT, XINIT, I)
 3050   CONTINUE
C
C Evaluate X at initial time delays determined by TINIT and XINIT
        DO 3070 K=1,N
          DO 3071 I=1,NTD
            XDEL(I,K) = XG(FINEVL, FINIT, TDEL(I), N, K, FULL,
     >              LINITL, TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
 3071     CONTINUE
 3070   CONTINUE
C
C Put the initial values of X and T into the tables. Include three
C values of T, namely TINIT - I*H, I=0,1,2 in TTAB and
C FINEVL(TINIT - I*H) in XTAB.
        TMH = T
        DO 3080 J=0,2
          TTAB(3-J) = TMH
          CALL FINEVL(TMH, WK3)
          DO 3085 K=1,N
            XTAB(3-J,K) = WK3(K)
 3085     CONTINUE
          TMH = TMH - H
 3080   CONTINUE
        KHIGH = 3
C
C Now we call subroutine WKINIT to fill the WK1 array at T=0 for the
C given stepsize H.
        DO 3090 K=1,N
          WK3(K) = XINIT(K)
 3090   CONTINUE
        CALL WKINIT(TINIT, TDEL, X, XDEL, WK1, IXCNT, N, NTD, IWD1,
     >              H, WK3)
      ENDIF
C
C Check to see if we are done, then proceed to check first
```

```
C convergence criterion. Halve stepsize H if necessary.
 3100 CONTINUE
      IF (T .GT. TSTOP)   GO TO 3500
C
C Evaluate F at time T: F1.
        DO 3110 K=1,N
          WK3(K) = WK1(K,1)
          DO 3111 I=1,NTD
            WK2(I,K) = WK1(K,6*I+1)
 3111     CONTINUE
 3110   CONTINUE
        CALL FEVL(T, WK3, WK2, F1)
C
C Evaluate F at time T-H: F2.
        DO 3120 K=1,N
          WK3(K) = WK1(K,2)
          DO 3121 I=1,NTD
            WK2(I,K) = WK1(K,6*I+2)
 3121     CONTINUE
 3120   CONTINUE
        TMH = T - H
        CALL FEVL(TMH, WK3, WK2, F2)
C
C  If H is too large, must halve the stepsize.
        MINDEL = 1.D75
        DO 3123 I=1,NTD
          TEMP = T - G(T, WK3, I)
          IF (TEMP .LT. MINDEL)  MINDEL = TEMP
 3123   CONTINUE
C
        DO 3130 K=1,N
          IF (WK1(K,1) .EQ. WK1(K,2))                          GO TO 3130
          IF (F1(K) .EQ. F2(K))                                GO TO 3130
          TEMP = 2.6D0/DABS((F2(K) -F1(K))/(WK1(K,2)-WK1(K,1)))
          IF ( (H .LT. TEMP) .AND. (2.D0*H .LT. MINDEL))  GO TO 3130
          IF (H .LT. (HINIT*(1.D0/256.D0)))
     >                            CALL ERMSG1(H, HINIT, TINIT, TSTOP)
          IF (T .EQ. TINIT)  THEN
            H = H/2.D0
            DO 3132 J=1,N
              WK3(K) = XINIT(K)
 3132       CONTINUE
            CALL WKINIT(TINIT, TDEL, X, XDEL, WK1, IXCNT, N, NTD,
     >                  IWD1, H, WK3)
          ELSE
            CALL HDSTEP(H, N, NTD, IWD1, WK1, IXCNT)
          ENDIF
        GO TO 3100
 3130   CONTINUE
C
C All is well with H. Compute XP for time T+H, and XDELP for time
C G(T+H). Next compute the corrected approximation XC for X at T+H.
C Then put these latest values for T and X(T) in the tables.
C
C Now calculate F at time T-2H:  F3.
        DO 3140 K=1,N
          WK3(K) = WK1(K,3)
```

```
          DO 3141 I=1,NTD
            WK2(I,K) = WK1(K,6*I+3)
 3141     CONTINUE
 3140   CONTINUE
        TMH = T - 2.D0*H
        CALL FEVL(TMH, WK3, WK2, F3)
C
C Then calculate F at time T-3H:  F4.
        DO 3150 K=1,N
          WK3(K) = WK1(K,4)
          DO 3151 I=1,NTD
            WK2(I,K) = WK1(K,6*I+4)
 3151     CONTINUE
 3150   CONTINUE
        TMH = T - 3.D0*H
        CALL FEVL(TMH, WK3, WK2, F4)
C
C Get XP by the Adams-Moulton fourth order method using F1 - F4.
        DO 3190  K=1,N
          XP(K) = WK1(K,1) + (H/24.D0)
     >       * (55.D0*F1(K)- 59.D0*F2(K) + 37.D0*F3(K) - 9.D0*F4(K))
          WK3(K) = XP(K)
 3190   CONTINUE
C
C Get each of the NTD time delays, TDEL.
        TPH = T + H
        DO 3200 I=1,NTD
          TDEL(I) = G(TPH,XP,I)
 3200   CONTINUE
C
C Get the values of X(i), i=1,N at each of the NTD time delays.
        DO 3205 K=1,N
          DO 3206 I=1,NTD
           XDELP(I,K) = XG(FINEVL, FINIT, TDEL(I), N, K, FULL,
     >             LINITL, TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
 3206     CONTINUE
 3205   CONTINUE
C
C Now compute the corrected values of X.
        DO 3210 K=1,N
          CALL FEVL(TPH, WK3, XDELP, F)
          XC(K) = WK1(K,1) + (H/24.D0)
     >         *(9.D0*F(K) + 19.D0*F1(K) - 5.D0*F2(K) + F3(K))
          WK3(K) = XC(K)
 3210   CONTINUE
C
C If we can get away with doubling the stepsize, do so for next X.
        DO 3300 K=1,N
          IF (DABS((XC(K) - XP(K))/XC(K)) .GE. TOL*5.D-1) GO TO 3301
 3300   CONTINUE
C
C Find the minimum time delay and be sure that H is no more than
C half that value. This prevents extrapolation from the history
C tables. Also make sure H is small in relation to the interval of
C integration to avoid integrating too far past TSTOP and forcing
C an extrapolation there as well.
        MINDEL = 1.D75
```

```
        DO 3303 I=1,NTD
          TEMP = TPH - G(TPH, XC, I)
          IF (TEMP .LT. MINDEL)  MINDEL = TEMP
 3303   CONTINUE
        IF ((2.D0*H .GE. HMAX) .OR. (4.D0*H) .GE. MINDEL) GO TO 3301
C
C All the relative errors for 1 to N are less than TOL/2. Can
C double H. To double H, we must have 6 previous X's stored in WK1.
C We then proceed as we would in subroutine UPDATE, except that we
C use 2H.
C
C If the main delay tables are already full, put them into the
C backup tables and start with fresh delay tables by calling STORE.
          IF (IXCNT .LT. 6)  GO TO 3310
            T = T+H
            DO 3305 I=1,NTD
              TDEL(I) = G(T,XC,I)
 3305       CONTINUE
C
            IF (KHIGH .GE. 10000)
     >        CALL STORE(FULL, LINITL, N, TTAB, XTAB, PTTAB, PXTAB,
     >                                        KHIGH, KPHIGH)
C
C Update the values of X and XDEL at present time T.
            DO 3315 K=1,N
              XI(K) = XC(K)
              DO 3316 I=1,NTD
                XDEL(I,K) = XG(FINEVL, FINIT, TDEL(I), N, K, FULL,
     >              LINITL, TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
 3316         CONTINUE
 3315       CONTINUE
C
C Now put the latest values into the delay tables.
            KHIGH = KHIGH + 1
            TTAB(KHIGH) = T
            DO 3317 K=1,N
              XTAB(KHIGH,K) = XC(K)
 3317       CONTINUE
C
C Update the work array WK1.
            H = 2.D0*H
            DO 3320 K=1,N
              WK1(K,1) = XC(K)
              WK1(K,2) = WK1(K,2)
              WK1(K,3) = WK1(K,4)
              WK1(K,4) = WK1(K,6)
              DO 3321 I=1,NTD
                WK1(K,6*I+1) = XDEL(I,K)
                WK1(K,6*I+2) = WK1(K,6*I+2)
                WK1(K,6*I+3) = WK1(K,6*I+4)
                WK1(K,6*I+4) = WK1(K,6*I+6)
 3321         CONTINUE
 3320       CONTINUE
            IXCNT = 4
          GO TO 3400
C
C We go here if we have less than six entries in the WK1 array.
```

```
C Fill up WK1 and forget trying to double the stepsize.
 3310       CONTINUE
            CALL UPDATD(FINEVL, G, N, NTD, IWD1, T, TDEL, X,
     >  XDEL, FINIT, WK1, IXCNT, H, XC, FULL, LINITL, TTAB, XTAB,
     >  PTTAB, PXTAB, KHIGH, KPHIGH)
          GO TO 3400
C
 3301     CONTINUE
C
C   We cannot double stepsize. Better check 2nd convergence
C   criterion and accuracy criterion.  Halve stepsize and do over
C   if needed.
C
C   Evaluate F at T and call it F.
          DO 3340 K=1,N
            WK3(K) = WK1(K,1)
            DO 3341 I=1,NTD
              WK2(I,K) = WK1(K,6*I+1)
 3341       CONTINUE
 3340     CONTINUE
          CALL FEVL(T, WK3, WK2, F)
C
          DO 3350 K=1,N
            XABS = DABS((XC(K) - XP(K))/TOL)
            CONV = 1.D75
            IF (F(K) .NE. 0.D0)   CONV = 2.6D0/(H*DABS(F(K)))
            IF ((XABS .GE.14.D0) .OR. (XABS .GE. CONV))   GO TO 3360
 3350     CONTINUE
C     Do not need to halve stepsize, so call UPDATE and go on to
C     the next step. All N X values are in specifications.
            CALL UPDATD(FINEVL, G, N, NTD, IWD1, T, TDEL, XI, XDEL,
     >  FINIT, WK1, IXCNT, H, XC, FULL, LINITL, TTAB, XTAB, PTTAB,
     >  PXTAB, KHIGH, KPHIGH)
            GO TO 3370
C
C Halve stepsize H.
 3360     CONTINUE
            IF (H .LT. HINIT*(1.D0/256.D0))
     >                          CALL ERMSG1(H, HINIT, TINIT, TSTOP)
          IF (T .EQ. TINIT)  THEN
            H = H/2.D0
            DO 3362 K=1,N
              WK3(K) = XINIT(K)
 3362       CONTINUE
            CALL WKINIT(TINIT, TDEL, X, XDEL, WK1, IXCNT, N, NTD,
     >                      IWD1, H, WK3)
          ELSE
            CALL HDSTEP(H, N, NTD, IWD1, WK1, IXCNT)
          ENDIF
 3370     CONTINUE
 3400   CONTINUE
        GO TO 3100
 3500 CONTINUE
C
C  We have a solution past TSTOP. Interpolate back to TSTOP using
C  the Lagrange five point interpolation formula.  WK1 array is
C  equally spaced.
```

```
C
      TINIT = TSTOP
      P = (2.D0*H + TSTOP - T)/H
      DO 3600 K=1,N
        X(K) = ((P*P-1.D0)*P*(P-2.D0)/24.D0)*WK1(K,5)
     1      - ((P-1.D0)*P*(P*P-4.D0)/6.D0)*WK1(K,4)
     2      + ((P*P-1.D0)*(P*P-4.D0)/4.D0)*WK1(K,3)
     3      - ((P+1.D0)*P*(P*P-4.D0)/6.D0)*WK1(K,2)
     4      + ((P*P-1.D0)*P*(P+2.D0)/24.D0)*WK1(K,1)
 3600 CONTINUE
      IND = 0
      RETURN
      END
      SUBROUTINE WKINIT(TINIT, TDEL, X, XDEL, WK1, IXCNT, N, NTD,
     >                  IWD1, H, F)
C
C Subroutine WKINIT initializes the work array WK1 when T = TINIT.
C
      INTEGER N, NTD, IWD1
      REAL*8 WK1(N, IWD1), XDEL(NTD, N), X(N), TDEL(NTD)
      REAL*8 F(N), TINIT, T, H, G
      INTEGER IXCNT
C
C First put the TINIT initial values of X and XDEL into their
C appropriate places in the WK1 array. See the comments for DELA4
C for an explanation of the structure of WK1.
      DO 3000 K=1,N
        WK1(K,1) = X(K)
        DO 3010 I=1,NTD
          WK1(K, 6*I+1) = XDEL(I,K)
 3010   CONTINUE
 3000 CONTINUE
C
C Then we take the values of X and XDEL at times T-H ,..., T-4*H
C and put them into the work array WK1.
      T = TINIT
      DO 3100 J=1,4
        T = T - H
C
C Evaluate X(TINIT - nH) and put these into the work array.
        DO 3110 K=1,N
          CALL FINEVL(T, F)
          WK1(K, 1+J) = F(K)
 3110   CONTINUE
C Evaluate the time delays for time T and X, where X is evaluated at
C F(T). Then evaluate X at those values TDEL, again by referring to
C the initial function.
        DO 3120 I=1,NTD
          TDEL(I) = G(T, F, I)
          CALL FINEVL(TDEL(I), F)
          DO 3121 K=1,N
            WK1(K, 6*I+1+J) = F(K)
 3121     CONTINUE
 3120   CONTINUE
 3100 CONTINUE
C
C Set the number of values in WK1 array to five.
```

```
      IXCNT = 5
      RETURN
      END
      SUBROUTINE UPDATD(FINEVL, G, N, NTD, IWD1, T, TDEL, XI, XDEL,
     >  FINIT, WK1, IXCNT, H, XC, FULL, LINITL, TTAB, XTAB, PTTAB,
     >  PXTAB, KHIGH, KPHIGH)
      INTEGER N, NTD, IWD1, J
      REAL*8 TTAB(10000), XTAB(10000,N), PTTAB(10000), PXTAB(10000,N)
      REAL*8 WK1(N,IWD1), XI(N), XDEL(NTD,N), XC(N), FINIT(N)
      REAL*8 G, T, TDEL(NTD), H, XG
      INTEGER KHIGH, KPHIGH, IXCNT, I, K, NTDP1, IKOUNT
      LOGICAL FULL, LINITL
      EXTERNAL FINEVL
C
C  Reset T, XI, and increment IXCNT if necessary.
      IXCNT = MIN0(IXCNT+1,6)
      T = T+H
C
      DO 3000 K=1,N
        XI(K) = XC(K)
 3000 CONTINUE
C
      DO 3100 I=1,NTD
        TDEL(I) = G(T,XI,I)
 3100 CONTINUE
C
      DO 3150 K=1,N
        DO 3155 I=1,NTD
          XDEL(I,K) = XG(FINEVL, FINIT, TDEL(I), N, K, FULL, LINITL,
     >                      TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
 3155   CONTINUE
 3150 CONTINUE
C
      KHIGH = KHIGH + 1
      IF (KHIGH .GT. 10000)  CALL STORE(FULL, LINITL, N, TTAB, XTAB,
     >                             PTTAB, PXTAB, KHIGH, KPHIGH)
C
      TTAB(KHIGH) = T
      DO 3200 K=1,N
        XTAB(KHIGH,K) = XI(K)
 3200 CONTINUE
C
C  Then update WK1 vector to advance X's one stepsize up T axis.
      DO 3300 K=1,N
        NTDP1 = NTD + 1
        I = 0
        DO 3310 IKOUNT=1,NTDP1
          DO 3315 J=1,5
            WK1(K, 6*I+7-J) = WK1(K,6*I+6-J)
 3315     CONTINUE
          I = I + 1
 3310   CONTINUE
        WK1(K,1) = XC(K)
        DO 3320 I=1,NTD
          WK1(K,6*I+1) = XDEL(I,K)
 3320   CONTINUE
 3300 CONTINUE
```

```
C
      RETURN
      END
      SUBROUTINE HDSTEP(H, N, NTD, IWD1, WK1, IXCNT)
      INTEGER IXCNT, IKOUNT, NTDP1, I, K
      REAL*8 WK1(N,IWD1), W1HALF, W3HALF, H
C
C  Divide H by two, and compute W(1/2) and W(3/2).
C  Interpolate using a five point formula for both X and the delay
C  values of X.
      H = H/2.D0
      DO 3000 K=1,N
        NTDP1 = NTD + 1
        I = 0
        DO 3100 IKOUNT=1,NTDP1
          W1HALF = (1.D0/128.D0) * (35.D0*WK1(K,6*I+1)
     >                 + 140.D0*WK1(K,6*I+2)- 70.D0*WK1(K,6*I+3)
     >                 + 28.D0*WK1(K,6*I+4) - 5.D0*WK1(K,6*I+5))
          W3HALF = (1.D0/64.D0) * (-WK1(K,6*I+1) +24.D0*WK1(K,6*I+2)
     >             + 54.D0*WK1(K,6*I+3)- 16.D0*WK1(K,6*I+4)
     >             + 3.D0*WK1(K,6*I+5) )
          WK1(K,6*I+5) = WK1(K,6*I+3)
          WK1(K,6*I+4) = W3HALF
          WK1(K,6*I+3) = WK1(K,6*I+2)
          WK1(K,6*I+2) = W1HALF
          WK1(K,6*I+1) = WK1(K,6*I+1)
          I = I + 1
 3100   CONTINUE
 3000 CONTINUE
C
C  Reset IXCNT to 5 or IXCNT, whichever is less.
      IXCNT = MIN0(IXCNT,5)
C
      RETURN
      END
      DOUBLE PRECISION FUNCTION XG(FINEVL, FINIT, TDEL, N, K, FULL,
     >             LINITL, TTAB, XTAB, PTTAB, PXTAB, KHIGH, KPHIGH)
      REAL*8 XTAB(10000,N), TTAB(10000), PXTAB(10000,N), PTTAB(10000)
      REAL*8 FINIT(N), TDEL, XVAL, DX, P
      INTEGER KHIGH, KPHIGH
      LOGICAL TABERR, FULL, LINITL
C
C For a specific index K, find a value for the function
C X(k)(T, X, X(G(T)) given an initial function FINIT. Call
C the routine APROX to approximate a value for X(G(T)) = XVAL if
C needed. Use the initial function to evaluate X(G(T)) only if
C values of TDEL = G(T) less than TTAB(1) are in the domain of
C definition of the initial function FINIT. Otherwise search the
C tables of previous values PTTAB for G(T).
      IF ((KHIGH .EQ. 0) .AND. (FULL))                  CALL ERROR
      IF ((KHIGH .EQ. 0) .AND. (.NOT. FULL))            GO TO 3210
      IF ((TDEL .LT. TTAB(1)) .AND. (.NOT. FULL))       GO TO 3210
      IF (TDEL .GT. TTAB(KHIGH))                        GO TO 3220
      IF (TDEL .GE. TTAB(1))                            GO TO 3230
      IF (TDEL .GE. PTTAB(1))                           GO TO 3240
      IF ((TDEL .LT. PTTAB(1)) .AND. LINITL)            GO TO 3210
      IF ((TDEL .LT. PTTAB(1)) .AND. (.NOT. LINITL))    GO TO 3250
```

```
      CALL ERROR
C
 3210 CONTINUE
        CALL FINEVL(TDEL, FINIT)
        XG = FINIT(K)
      GO TO 3300
C
 3220 CONTINUE
        P = (TDEL - TTAB(KHIGH-1))/(TTAB(KHIGH) - TTAB(KHIGH-1))
        XG = XTAB(KHIGH,K) + P*(XTAB(KHIGH,K) - XTAB(KHIGH-1,K))
      GO TO 3300
C
 3230 CONTINUE
        CALL APROX(TTAB, XTAB, N, K, KHIGH, TDEL, XVAL, DX)
        XG = XVAL
      GO TO 3300
C
 3240 CONTINUE
        CALL APROX(PTTAB, PXTAB, N, K, KPHIGH, TDEL, XVAL, DX)
        XG = XVAL
      GO TO 3300
C
 3250 CONTINUE
        TABERR = .TRUE.
        CALL ERMSG2(TABERR)
C
 3300 CONTINUE
C
      RETURN
      END
      SUBROUTINE APROX(TTABLE, XTABLE, N, K, NHIGH, TDEL, XVAL, DX)
      INTEGER N
      REAL*8 TTABLE(10000), XTABLE(10000,N), TDEL, XVAL, DX
      REAL*8 TA(4), XA(4), C(4), D(4), HO, HP, DEN, WK1, WK2
      INTEGER NHIGH, KBOT, KTOP, KMID, NS, I, M, NMM, K
C
C Use a binary search to compute the index to TTABLE(i) such that
C TTABLE(i) , TDEL < TTABLE(i+1), where T - TDEL is the time delay.
C NOTE that for T .LE. 0, the value of X(T) will be the initial
C function at that point.
C
C  TDEL      Present time value
C  XTABLE    Table of previously computed or assigned X values
C  TTABLE    Table of time values for which X has a value
C  NHIGH     The highest time value for which X has been computed
C  XVAL      Approximated value of X(k) at time TDEL
C  DX        Approximation of error
C
      KBOT = 1
      KTOP = NHIGH
      KMID = (KTOP + KBOT)/2
 3120 CONTINUE
      IF ((KTOP - KBOT) .LE. 1)    GO TO 3125
        KMID = (KTOP + KBOT)/2
        IF (TDEL .LE. TTABLE(KMID))  GO TO 3123
        IF (TDEL .GT. TTABLE(KMID))  GO TO 3124
 3123   CONTINUE
```

```
            KTOP = KMID
          GO TO 3120
 3124     CONTINUE
            KBOT = KMID
          GO TO 3120
 3125 CONTINUE
        KMID = KBOT
C
C Now compute the X(TDEL) value.  TTABLE(KMID) should be the highest
C entry in TTABLE that is lower than TDEL. Find the closest entry
C in TTABLE to TDEL. It is either at KMID or KMID+1. Approximation
C to X(TDEL) is made using an improved Neville's algorithm. We must
C remember that entries in XTABLE may not be equally spaced. See the
C reference NUMERICAL RECIPES, article 3.1 for the algorithm.
        WK1 = DABS(TTABLE(KMID+1) - TDEL)
        WK2 = DABS(TDEL - TTABLE(KMID))
        NS = KMID
        IF (WK1 .LT. WK2)  NS = KMID + 1
C
        IF (KMID .GE. NHIGH-1)  GO TO 3160
        IF (KMID .GE. 2)        GO TO 3170
        IF (KMID .EQ. 1)        GO TO 3200
C
C TDEL is between TTABLE(NHIGH-1) and TTABLE(NHIGH).
 3160 CONTINUE
          DO 3161 I=1,4
            TA(I) = TTABLE(NHIGH-4+I)
            XA(I) = XTABLE(NHIGH-4+I,K)
            C(I) = XA(I)
            D(I) = XA(I)
 3161     CONTINUE
          NS = NS - KMID+3
        GO TO 3190
C
C TDEL has at least two values of TTABLE both higher and lower than
C it.
 3170 CONTINUE
          DO 3171 I=1,4
            TA(I) = TTABLE(KMID-2+I)
            XA(I) = XTABLE(KMID-2+I,K)
            C(I) = XA(I)
            D(I) = XA(I)
 3171     CONTINUE
          NS = NS - KMID+2
        GO TO 3190
C
C TDEL is between TTABLE(1) and TTABLE(2)
 3200  CONTINUE
          DO 3201 I=1,4
            TA(I) = TTABLE(I)
            XA(I) = XTABLE(I,K)
            C(I) = XA(I)
            D(I) = XA(I)
 3201      CONTINUE
          NS = NS - KMID+1
        GO TO 3190
C
```

```
C We have the four values of XTABLE that we are going to use in XA.
C NS is the closest of these four values to TDEL. Now use the
C modified Neville's algorithm to approximate XVAL. DX approximates
C the error at the end of the process.
 3190 CONTINUE
      XVAL = XA(NS)
      NS = NS - 1
      DO 3192 M=1,3
        NMM = 4 - M
        DO 3193 I=1,NMM
          HO = TA(I) - TDEL
          HP = TA(I+M) - TDEL
          DEN = (C(I+1) - D(I))/(HO - HP)
          C(I) = HO*DEN
          D(I) = HP*DEN
 3193   CONTINUE
        IF (2*NS .LT. 4-M)  GO TO 3195
          DX = D(NS)
          NS = NS - 1
        GO TO 3196
C
 3195   CONTINUE
          DX = C(NS+1)
        GO TO 3196
C
 3196   CONTINUE
        XVAL = XVAL + DX
 3192 CONTINUE
      RETURN
      END
      SUBROUTINE STORE(FULL, LINITL, N, TTAB, XTAB, PTTAB, PXTAB,
     >                                                 KHIGH, KPHIGH)
      REAL*8 PTTAB(10000), TTAB(10000), PXTAB(10000,N), XTAB(10000,N)
      INTEGER KPHIGH, KHIGH, I, K
      LOGICAL FULL, LINITL
C
C Store the previous tables. Put tables TTAB and XTAB into tables
C of previous values, and initialize TTAB and XTAB from the values
C found in the last four values in that array. Note that there is
C no value in the tables corresponding to KHIGH, so decrement it.
      KHIGH = KHIGH - 1
C
      DO 3000 I=1,KHIGH
        PTTAB(I) = TTAB(I)
 3000 CONTINUE
C
      DO 3050 K=1,N
        DO 3051 I=1,KHIGH
          PXTAB(I,K) = XTAB(I,K)
 3051   CONTINUE
 3050 CONTINUE
C
      KPHIGH = KHIGH
C
C
C Now initialize the tables TTAB and XTAB so that the first four
C entries have values. If the previous table is already full we
```

```
C cannot go to the initial function in case we try to access a time
C previous to PTTAB(1), and we set LINITL = .TRUE. if this is the
C case. In any case we set FULL = .TRUE. to signal that the the
C table of previous values is active.
      DO 3200 I=1,4
        TTAB(I) = TTAB(KHIGH-4+I)
 3200 CONTINUE
C
      DO 3250 K=1,N
        DO 3251 I=1,4
          XTAB(I,K) = XTAB(KHIGH-4+I,K)
 3251   CONTINUE
 3250 CONTINUE
C
      KHIGH = 4
      IF (FULL)  LINITL = .FALSE.
      FULL = .TRUE.
      RETURN
      END
      SUBROUTINE ERMSG1(H, HINIT, TINIT, TSTOP)
      REAL*8 H, HINIT, TINIT, TSTOP
C
      IF (H .LE. 1.D-8)       GO TO 301
      IF (H .LE. 0)           GO TO 302
      IF (TINIT .GE. TSTOP)   GO TO 303
C
      WRITE(6,100) H
  100 FORMAT(' *** WARNING -- Stepsize H is set to ',1PD18.11,/
     >       ' and error or convergence criteria are not yet met.')
      HINIT = H
      GO TO 399
C
  301 CONTINUE
      WRITE(6,101) H
  101 FORMAT(' *** ERROR -- Stepsize H has been set to ',1PD18.11,/
     >       ' and error or convergence criteria are not met.')
      CALL ERROR
C
  302 CONTINUE
      WRITE(6,102)
  102 FORMAT(' *** ERROR -- Stepsize H has a value less than',
     >       ' or equal to zero')
      CALL ERROR
C
  303 CONTINUE
      WRITE(6,103) TINIT, TSTOP
  103 FORMAT(' *** ERROR -- Initial T value, ',1PD18.11,/
     >       ' is set greater than TSTOP, ',D18.11)
      CALL ERROR
C
  399 CONTINUE
      RETURN
      END
      SUBROUTINE ERMSG2(TABERR)
      LOGICAL TABERR
C
      IF (TABERR)             GO TO 300
```

```
C
 300  CONTINUE
      WRITE(6,100)
 100  FORMAT(' *** ERROR -- Attempt to access value of T smaller',/
     >       '              than smallest stored value in tables')
      CALL ERROR
      RETURN
      END
```