Chapter-IV
Chapter - IV

A PREDATOR-SPECIFIC DEFENSE MODEL WITH AGE-STRUCTURE

4.1 Introduction

In this chapter, we enlarge the scope of the model of Chapter-II by introducing age-structure in the dynamics of one of the predator populations. This allows us to incorporate delay effects (possibly) for the first time in a prey defensive switching model.

It has been a generally held tenet in population biology that a time delay in the growth rate response to environmental changes (including changes in the population's own size) will, if long enough, lead to instabilities or at least to destabilization of equilibrium population levels. Delay causing mechanisms most frequently mentioned by population biologists are those related to age-specific fecundity or to other parameters closely connected with it. The existence of an equilibrium (or stationary) age distribution, its stability properties and the occurrence of regular or even chaotic oscillations in population size, all have been related to age specific fecundity or to other parameters closely connected with it, such as maturation time, mean gestation time, age of maximum fecundity or with the "reproductive window" (see e.g. [26,29,79,97,107,131] and references therein).

The type of delay we are interested in the present model system is that due to age-specific maturation periods [27]. For this purpose, we
assume that one of the predator populations has an age-structure that significantly affects its fecundity. The mathematical goal of this study is to analyze two special but equally important cases of the main model (4.7) of this chapter called Model A and Model B with a view to study the effects of the maturation periods on the equilibrium stability.

We derive the model equations in section 4.2 under several basic biological assumptions with certain types of predator and prey populations in mind which we now describe.

We assume that the populations of both predators and their common prey are closed to immigration and emigration and that they interact in a constant environment. We consider two types of predators, one with age-structure and the other without it. We ignore any age-structure in the prey population. For ignoring age-structure in a population, we suppose that either such a population's vital parameters are not age-specific or that their dependence on age-structure is insignificant as far as their effect on age-structured population's fecundity and death rates is concerned. Examples of populations without age-structure might include those populations whose life cycles are either simple as to render age-structure within them insignificant or whose life cycles are significantly longer (or shorter) than that of the age-structured population.

As mentioned earlier also we are primarily concerned here with maturation periods as delay and instability causing mechanism, and therefore we concentrate on age-specific differentials in reproductive
output (fecundity rate) of the age-structured predator population at the expense of ignoring age differentials in its death rate. We also assume the death rate of a second non age-structured predator population to be constant. Such an assumption may well be justified for various reasons such as (i) delays in death rate responses are generally supposed to be of less importance [106] and (ii) the survivorship curve of a population may be of type II i.e. exponentially decreasing [59].

Finally, we assume that each of the non age-structured predator and the prey population grows under self-inhibition in the absence of other species. We also assume that prey defends itself against predators by being vigilant against relatively abundant predators and switching (in defense) to a relatively low density predator species. More specifically, we assume that prey displays defensive switching behavior against predators.

Under these assumptions, we derive the model equations (4.7) in section 4.2. In section 4.3. we analyze Model A using the construction of Liapunov functionals method and give the sufficient conditions for the asymptotic stability of its positive equilibrium. In section 4.4, we analyze Model B using Krasovskii method. Section 4.5 contains the main conclusions of this chapter.

4.2 Model Equations

Let \( x(t) \) denote the total number of individuals at time \( t \) of an age-structured predator population. Let \( \rho(a,t) \) denote the density of individuals of age \( a \) at time \( t \) of this population, thus
\[ x(t) = \int_0^\infty \rho(a,t) \, da \]

Following general theory of age-structured populations essentially due to McKendrick [85] and Foerster [130] (also see [26,61] and section 1.3.2 of Chapter-I), we assume that the dynamics of the predator population \( x \) is governed by (see model (1.7) in Chapter-I)

\[
\frac{\partial \rho}{\partial a} + \frac{\partial \rho}{\partial t} = -\alpha \rho, \quad a > 0, \, -\infty < t < \infty
\]

\[
\rho(0,t) = \int_0^\infty f(a,t) \rho(a,t) da , \quad (4.1)
\]

where

\( \alpha \) is the death rate of the population \( x \). As discussed in section 4.1, \( \alpha \) is taken to be a positive constant independent of \( a, t \) and \( \rho \).

\( f(a,t) \) is the age-specific fecundity rate of the population \( x \).

We assume the function \( f \) to be a function of time \( t \) only implicitly through its dependence on the population size \( x \), population size \( y \) (of a second non age-structured predator population) and the population size \( z \) (of the prey). More specifically, we assume that \( f \) has the form

\[
f = \gamma \beta(a) R(x,y) z \quad (4.2)
\]

The positive constant \( \gamma > 0 \) is called the birth modulus and the function \( \beta \) is the maturation function. The maturation function \( \beta \) which obviously describes the effects of age on fecundity is assumed to satisfy
\( \beta(a) > 0, \beta(0) = 0 \) and \( \beta^*(s) = \int_0^\infty e^{-as} \beta(a) \, da < +\infty \) (4.3)

for all \( s > 0 \). Here \( \beta^*(s) \) is the Laplace transform of \( \beta(a) \). Function \( R \) represents a fraction of the prey available to the population \( x \) against its defensive switching behavior to be explained shortly.

Before considering the dynamical equations for populations \( y \) and \( z \), we integrate (see [26,28,29]) equations (4.1) under the assumptions (4.2), (4.3) and \( \rho(+\infty,t)=0 \) and obtain the dynamical equation for the population \( x \) as under (also see the derivation of equation (1.12) in Chapter-1)

\[
\frac{dx}{dt} = -\alpha_1 x + \gamma_1 Rz \int_{-\infty}^t \beta'(t-s) e^{-\alpha_1(t-s)} x(s) \, ds
\] (4.4)

One can derive similar equations for populations \( y \) and \( z \). But since the present study is the first attempt (to the best of our knowledge) to introduce delays in a defensive switching model, we restrict ourselves to a simpler model in this chapter. Thus we consider some special types of predator-prey interactions with some specific assumptions in mind as have been cited in section 4.1. Under one such assumption, we ignore any age-structure in populations \( y \) and \( z \) and consider their dynamics to be governed by the Lotka-Volterra type equations as follows :

\[
\frac{dy}{dt} = y \left[ -\alpha_2 - f(y) + \gamma_2 (1 - R)z \right]
\]

\[
\frac{dz}{dt} = z \left[ \alpha_3 - g(z) - \delta_1 R \int_{-\infty}^t \beta'(t-s) e^{-\alpha_1(t-s)} x(s) \, ds - \delta_2 (1 - R)y \right]
\] (4.5)
Various entities in (4.5) are explained in the following:

\( \alpha_2 > 0 \) is the death rate of the predator \( y \).

\( f(y) > 0 \) is the self-inhibition rate of the predator \( y \).

\( \gamma_2 \) is the rate of conversion of the prey eaten by the predator \( y \) into newborns. \( (1-R) \) is the fraction of the prey available to the predator \( y \).

\( \alpha_3 > 0 \) is the intrinsic growth rate of the prey \( z \).

\( g(z) \) is the self-inhibition rate of the prey \( z \).

\( \delta_1 > 0 \) is the rate of consumption of the prey \( z \) by the predator \( x \).

\( \delta_2 > 0 \) is the rate of consumption of the prey \( z \) by the predator \( y \).

To be specific for the defensive switching strategy of the prey, we assume (see equations (2.2) in Chapter-II) the following simple form for the function \( R \).

\[
R = \frac{1}{1 + x/y}
\]  

(4.6)

This particular form of the function \( R \) implies that the availability of the prey to a predator population diminishes if its population becomes large compared to population of the other predator. Obviously \( R \) represents the prey defensive switching behavior and thus it may also be called as defensive switching function.

Substitution of (4.6) into (4.4) and (4.5) gives the main model
equations of this chapter as under

\[ \frac{dx}{dt} = -\alpha_1 x + \gamma_1 \frac{yz}{x+y} \int_0^t \beta'(t-s) e^{-\alpha_3(t-s)} x(s) \, ds \]

\[ \frac{dy}{dt} = -\alpha_2 y - yf(y) + \frac{xyz}{x+y} \]

\[ \frac{dz}{dt} = \alpha_3 z - zg(z) - \delta_1 \frac{yz}{x+y} \int_0^t \beta'(t-s) e^{-\alpha_3(t-s)} x(s) \, ds - \delta_2 \frac{xyz}{x+y} \]  

For the purpose of simplicity in our subsequent analysis, we concentrate on two special but equally generalised cases of the model (4.7) and denote them Model A and Model B

**Case I**

We assume here that \( f(y) = 0 \) (i.e. the predator \( y \) has no self-inhibition effect).

Under this assumption, the model (4.7) is reduced to

\[ \frac{dx}{dt} = -\alpha_1 x + \gamma_1 \frac{yz}{x+y} \int_0^t \beta'(t-s) e^{-\alpha_3(t-s)} x(s) \, ds, \]

\[ \frac{dy}{dt} = -\alpha_2 y + \frac{xyz}{x+y}, \quad \text{Model A} \]

\[ \frac{dz}{dt} = \alpha_3 z - zg(z) - \delta_1 \frac{yz}{x+y} \int_0^t \beta'(t-s) e^{-\alpha_3(t-s)} x(s) \, ds - \delta_2 \frac{xyz}{x+y} \]

It can be verified that Model A has a unique positive equilibrium \( e_A = (x^*, y^*, z^*) \) given by
\[ z^* = \frac{1}{\gamma_1 \beta'(\alpha_1)} + \frac{\alpha_2}{\gamma_2} \]

\[
x^* = \frac{[\alpha_3 - g(z')] [\gamma_2 + \gamma_2 \alpha_2 \beta'(\alpha_1)]}{\gamma_2 [\delta_2 + \delta_2 \alpha_2 \beta'(\alpha_1)]}
\]

and

\[
y^* = \frac{[\alpha_3 - g(z')] [\gamma_2 + \gamma_2 \alpha_2 \beta'(\alpha_1)]}{\gamma_2 \alpha_2 \beta'(\alpha_1) [\delta_2 + \delta_2 \alpha_2 \beta'(\alpha_1) + \delta_2]}
\]

provided,

\[ \alpha_3 > g(z^*) \]

This condition implies that Model A has a positive equilibrium \( x^* \) only when the intrinsic growth rate of the prey \( z \) is greater than its unit abundance self-inhibition rate.

**Case II**

It is assumed here that the prey \( z \) has no self-inhibition effect (i.e. \( g(z) = 0 \)). Thus the model (4.7) takes the form

\[
\frac{dx}{dt} = -\alpha_1 x + \frac{\gamma_1 y z}{x+y} \int_{-\infty}^{t} \beta (t-s)e^{-\alpha_1(t-s)}x(s)ds,
\]

\[
\frac{dy}{dt} = -\alpha_2 y - yf(y) + \gamma_2 \frac{xyz}{x+y},
\]

**Model B**

\[
\frac{dz}{dt} = \alpha_3 z - \delta_1 yz \int_{-\infty}^{t} \beta'(t-s)e^{-\alpha_1(t-s)}x(s)ds - \delta_2 \frac{xyz}{x+y}
\]
This model indeed differs from Model A in that here the predator $y$ is assumed to have self-inhibition (crowding) effect whereas the prey $z$ is assumed to grow exponentially in the absence of both predators $x$ and $y$. Model B is thus another model with prey defensive switching behavior.

Model B has a positive equilibrium $e^* = (x^*, y^*, z^*)$

where $y^*$ is a solution of

$$f(y) = -\alpha_s \frac{y - C}{y - D},$$

such that

$$D < y^* < C,$$

with

$$C = \frac{[\gamma_s, \alpha_s, \beta^*(\alpha_1) + \gamma_s]}{\gamma_s, \alpha_s, \beta^*(\alpha_1) [\delta_s, \alpha_s, \beta^*(\alpha_1) + \delta_s]},$$

and

$$D = \frac{1}{[\delta_s, \alpha_s, \beta^*(\alpha_1) + \delta_s]}$$

$x^*$ and $z^*$ can now be obtained in terms of $y^*$ as

$$x^* = \frac{\gamma_s, \beta^*(\alpha_1)[\alpha_s + f(y^*)]}{\gamma_s}$$

and

$$z^* = \frac{\gamma_s + \gamma_s, \beta^*(\alpha_1)[\alpha_s + f(y^*)]}{\gamma_s, \gamma_s, \beta^*(\alpha_1)}$$
We determine sufficient conditions for asymptotic stability of the positive equilibrium of Model A and Model B in sections 4.3 and section 4.4 employing the construction of Liapunov functionals and Krasovskii methods respectively.

4.3 Linear System (Model A)

Under the transformations

\[ x(t) = x^* + u(t), \quad y(t) = y^* + v(t) \text{ and } z(t) = z^* + w(t), \]

the linearized system corresponding to Model A takes the form

\[
\begin{align*}
\frac{du(t)}{dt} &= a_{11}(t)u(t) + a_{12}v(t) + a_{13}w(t) + \frac{1}{\beta^*(\alpha_1)} \int_{-\infty}^{t} \beta'(t-s)e^{-\alpha_1(t-s)}u(s)ds \\
\frac{dv(t)}{dt} &= a_{21}(t)u(t) + a_{22}v(t) + a_{23}w(t) \\
\frac{dw(t)}{dt} &= a_{31}(t)u(t) + a_{32}v(t) + a_{33}w(t) - \frac{\delta_1}{\gamma_1^*(\alpha_1)} \int_{-\infty}^{t} \beta'(t-s)e^{-\alpha_1(t-s)}u(s)ds,
\end{align*}
\]

where

\[
\begin{align*}
a_{11} &= -\alpha_1 \left(1 + \frac{x^*}{(x^* + y^*)}\right), \quad a_{12} = \frac{\alpha_1 x^*}{y^*(x^* + y^*)}, \quad a_{13} = \frac{\alpha_1 x^*}{z^*} \\
a_{21} &= \frac{\alpha_2 y^*}{x^*(x^* + y^*)}, \quad a_{22} = -\frac{\alpha_2 y^*}{(x^* + y^*)}, \quad a_{23} = \frac{\alpha_2 y^*}{z^*} \\
a_{31} &= \frac{\alpha_1 \delta_1 x^*}{\gamma_1^* (x^* + y^*)} - \frac{\alpha_2 \delta_2 y^*}{\gamma_2^* x^*(x^* + y^*)},
\end{align*}
\]
In order to study the asymptotic stability of the solution \((u, v, w) = (0, 0, 0)\) of (4.9), we use the method of construction of Liapunov functionals (see [18, 103] and section 1.4.6 in Chapter-I). To this end, we introduce the Liapunov functional \(W\) as

\[
W(u(.), v(.), w(.)) = m_1 |u(t)| + m_2 |v(t)| + |w(t)|
\]  

(4.10)

where,

\[
m_1 = \frac{\delta_1}{\gamma_1} > 0
\]  

(4.11)

It is obvious that \(W\) is a positive definite functional on \(\mathbb{R}^3\). Further, it has continuous first order partial derivatives with respect to all variables \(((u, v, w) \neq (0, 0, 0))\). The time derivative of (4.10) along a solution \(((u, v, w) \neq (0,0,0))\) of (4.9) yields

\[
\frac{dW}{dt} = m_1 \frac{d}{dt} |u(t)| + m_2 \frac{d}{dt} |v(t)| + \frac{d}{dt} |w(t)|
\]

\[
= \left[ -m_1 \alpha_1 \left( 1 + \frac{x^*}{(x^* + y^*)} \right) + m_2 \frac{\alpha_3 y^*}{x^*(x^* + y^*)} + \frac{\alpha_3 x^*}{\gamma_1 (x^* + y^*)} - \frac{\alpha_3 x^*}{\gamma_2 (x^* + y^*)} \right] |u(t)|
\]

\[
+ \left[ \frac{m_1 \alpha_2 x^*}{y^*(x^* + y^*)} - \frac{m_2 \alpha_2 y^*}{(x^* + y^*)} - \frac{\alpha_3 \delta_1 x^*}{\gamma_1 y^* (x^* + y^*)} - \frac{\delta_2 \alpha_3 x^*}{\gamma_2 (x^* + y^*)} \right] |v(t)|
\]

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The right hand side expression of (4.12) has been obtained after using (4.9). It follows from (4.8) and (4.11) that the coefficients of \(|u(t)|\) and \(|v(t)|\) are negative. The coefficient of \(|w(t)|\) is negative and hence by construction of Liapunov functionals method, the linear system (4.9) is asymptotically stable if

\[
g(z^*) < \alpha_3 < \left. \frac{d}{dz} (zg(z)) \right|_{z=z^*} \tag{4.13}
\]

This condition implies that all the three species (predators x, y and prey z) with prey defending itself against predators by defensive switching may coexist at their equilibrium values (4.8) provided the intrinsic growth rate of the prey z is greater than its per unit abundance self-inhibition rate but less than the rate of growth of total inhibition at the equilibrium. The condition (4.13) also emphasizes that at the equilibrium, the total inhibition of the prey z should be increasing.

The question now arises what happens if the rate of growth of total inhibition of the prey at the equilibrium is less than its intrinsic growth rate, i.e.

\[
\left. \frac{d}{dz} (zg(z)) \right|_{z=z^*} < \alpha_3 \tag{4.14}
\]

To answer this question, we apply the construction of Liapunov
functionals method again using another functional as

\[ L(u(.), v(.), w(.)) = n_1 |u(t)| + n_2 |v(t)| + |w(t)|, \quad (4.15) \]

where,

\[ n_1 = \frac{\delta_1}{\gamma_1} \quad \text{and} \quad n_2 = \frac{\delta_2}{2\gamma_2} \]

The time derivative of (4.15) along a solution \((u, v, w) \neq (0, 0, 0)\) of (4.9) yields

\[
\frac{dL}{dt} = \left[ -n_1 \alpha_1 \left(1 + \frac{x^*}{(x^* + y^*)}\right) + \frac{n_1 \alpha_2 y^*}{x^*(x^* + y^*)} + \frac{\delta_1 \alpha_1 x^*}{\gamma_1 (x^* + y^*)} - \frac{\delta_2 \alpha_2 y^*}{\gamma_2 x^*(x^* + y^*)} \right] |u(t)|
\]

\[
+ \left[ \frac{n_1 \alpha_1 x^*}{y^* (x^* + y^*)} + \frac{n_1 \alpha_2 y^*}{(x^* + y^*)} - \frac{\delta_1 \alpha_1 x^*}{\gamma_1 y^* (x^* + y^*)} - \frac{\delta_2 \alpha_2 y^*}{\gamma_2 x^*(x^* + y^*)} \right] |v(t)|
\]

\[
+ \left[ \frac{n_1 \alpha_1 x^*}{z^*} + \frac{n_1 \alpha_2 y^*}{z^*} + \alpha_3 (g(z^*) + z^* g'(z^*)) - \frac{\delta_1 \alpha_1 x^*}{\gamma_1 z^*} - \frac{\delta_2 \alpha_2 y^*}{\gamma_2 z^*} \right] |w(t)|
\]

From \(n_1 = \frac{\delta_1}{\gamma_1}\) and \(n_2 = \frac{\delta_2}{2\gamma_2}\), it follows that the coefficients of \(|u(t)|\) and \(|v(t)|\) are negative. The coefficient of \(|w(t)|\) is negative if

\[
\alpha_3 - \frac{d}{dz} (g(z)) \bigg|_{z = z^*} < \frac{\delta_2 \alpha_2 y^*}{2\gamma_2 z^*} \quad (4.16)
\]

Substituting for \(y^*\) and \(z^*\) from (4.8) into (4.16), it becomes
Thus it follows that the linear system (4.9) (and hence the positive equilibrium \( e_A \) of Model A) is asymptotically stable provided condition (4.17) holds. Obviously this condition holds true if \( \alpha_3 \frac{d}{dz}(zg(z)) \bigg|_{z=z^*} < 0 \) as expected. On the other hand, although condition (4.17) turns out to be too complex in reference to its biological interpretation but at the same time it seems to be interesting for its dependence on the maturation function \( \beta \). With a view to elaborate (4.17) in biological terms, we suppose that (in the absence of predators \( x \) and \( y \)) the prey \( z \) grows logistically and hence we assume a linear form of the function \( g \) such that \( g(z) = \alpha_4 z \). This assumption reduces the inequality (4.17) to

\[
a \beta^2(\alpha_4/\alpha_3) + b \beta^*(\alpha_4) + c > 0 \tag{4.18}
\]

where,

\[
a = 2 \delta_1 \alpha_1 \gamma_1 (2 \alpha_4 \alpha_2 - \alpha_3 \gamma_2)
\]
\[
b = 4 \delta_1 \alpha_1 \alpha_4 \gamma_2 + \delta_2 \gamma_1 (3 \alpha_2 \alpha_4 - \alpha_3 \gamma_2)
\]

and

\[
c = 3 \delta_2 \alpha_4 \gamma_2
\]

It can be seen that under the condition

\[
\frac{\alpha_4}{\alpha_3} < \frac{\gamma_2}{2 \alpha_2} \tag{4.19}
\]
(which may hold true for large $\alpha_3$, intrinsic growth rate of the prey or large $\gamma_2$, rate of conversion of the prey eaten by the predator $y$ into its newborns),

inequality (4.19) is satisfied provided

$$\beta^*(\alpha_1) < \eta^* \quad (4.20)$$

where $\eta^*$ is the positive root of the quadratic

$$a\eta^2 + b\eta + c = 0 \quad (4.21)$$

We now summarize the results of this section in the following:

Theorem 1

(a) Positive equilibrium $e_A$ of Model A is asymptotically stable if

$$g^*(z) < \alpha_3 < \frac{d}{dz}[zg(z)] \bigg|_{z = z^*}.$$ 

(b) Positive equilibrium $e_A$ of Model A is asymptotically stable if

$$C < \alpha_3 - \frac{d}{dz}(zg(z)) \bigg|_{z = z^*} < \frac{\delta_2 \left[\alpha_3 - g(z^*)\right]}{2 \left[\delta_1, \beta^*(\alpha_1) + \delta_2\right]}.$$ 

(c) Supposing a linear function $g(z) = \alpha_4z$ in Model A and denoting the positive root of (4.21) as $\eta^*$, the positive equilibrium $e_A$ of Model A is asymptotically stable if

$$\frac{\alpha_4}{\alpha_3} < \frac{\gamma_2}{2\alpha_2}.$$ 

and
\[ \beta^* (a_1) < \eta^* \]

Condition (4.20) involves the maturation function \( \beta \) and hence it may explain what effects delays may have on equilibrium stability. To see it, we consider the following form for the maturation function

\[ \beta(a) = \frac{1}{m^2} a e^{-a/m}, \]  

(4.22)

This choice of \( \beta \) implies that fecundity of the predator \( x \) peaks at age \( a = m \) (although it is rather broadly distributed around \( a = m \) ) which might be taken as a measure of a biological maturation period.

Substitution of (4.22) into (4.20) yields

\[ m > \frac{1}{\alpha_1} \left( \frac{1}{\sqrt{\eta^*}} - 1 \right) \]

This condition suggests that the maturation period of the predator \( x \) should be large to ensure the coexistence of two predators that share a common prey which displays defensive switching behavior against predators.

For the purpose of stability results (maturation versus no-maturation periods), we consider the following model which corresponds to a non age-structured version of Model A.

\[
\begin{align*}
\frac{dx}{dt} &= -\alpha_1 x + \frac{\gamma_1 xyz}{x+y} \\
\frac{dy}{dt} &= -\alpha_2 y + \frac{\gamma_2 xyz}{x+y}
\end{align*}
\]
\[
\frac{dz}{dt} = \alpha_z z - zg(z) - \frac{(\delta_1 + \delta_2)xyz}{x + y} \tag{4.23}
\]

Taking the transformations
\[x(t) = x^* + u_1(t), \quad y(t) = y^* + v_1(t) \text{ and } z(t) = z^* + w_1(t),\]
the linearized system corresponding to (4.23) turns out to be

\[
\frac{dY(t)}{dt} = BY(t) \tag{4.24}
\]

where,
\[
Y = \begin{bmatrix}
u_1 \\ v_1 \\ w_1
\end{bmatrix}
\]

and
\[
B = \begin{bmatrix}
-\frac{\alpha_1 x^*}{(x^* + y^*)} & \frac{\alpha_1 y^*}{y^*(x^* + y^*)} & \frac{\alpha_1 z^*}{z^*} \\
\frac{\alpha_2 y^*}{x^*(x^* + y^*)} & -\frac{\alpha_2 y^*}{x^* + y^*} & \frac{\alpha_2 y^*}{z^*} \\
-\frac{(\delta_1 + \delta_2)\alpha_1 y^*}{\gamma_1 (x^* + y^*)} & \frac{(\delta_1 + \delta_2)\alpha_1 x^*}{\gamma_2 (x^* + y^*)} & -z^* g'(z^*)
\end{bmatrix}
\]

It can be seen using Hurwitz criteria (see section 1.4.4 in Chapter-I) that all the roots of the characteristic equation associated with (4.24) have negative real parts. Thus the positive equilibrium of (4.23) is asymptotically stable. On the other hand, one may verify that with no-self-inhibition effect in the prey population (i.e. \( g(z) = 0 \)), the positive
equilibrium of (4.23) is asymptotically stable if the death rates of both predators $x$ and $y$ are different (i.e. $\alpha_1 \neq \alpha_2$). One may consult Chapter-II for this result. This leads to the well known fact that the self-inhibition effects enhance stability. Furthermore, comparing the results of Model A and model (4.23), it may be concluded that even with the self-inhibition effects, the age-structure makes the system less stable.

4.4 Nonlinear System [Model B]

In this section, we assume (as in [23]) that all the positive solutions of Model B exist and are bounded for all $t \in [0, \infty]$ and are such that

$$K_1 \leq x(t) \leq K_2, \quad L_1 \leq y(t) \leq L_2, \quad M_1 \leq z(t) \leq M_2$$  \hspace{1cm} (4.25)

where $K_i$, $L_i$ and $M_i$ are positive real numbers.

Invoking the transformations

$$p_1 = \log \frac{x(t)}{x}, \quad q_1 = \log \frac{y(t)}{y}, \quad \text{and} \quad r_1 = \log \frac{z(t)}{z},$$

the Model B takes the form

$$\frac{dZ}{dt} = \tilde{f}(z, t)$$  \hspace{1cm} (4.26)

where,
\[
Z = \begin{bmatrix}
p_1 \\
q_1 \\
r_1
\end{bmatrix}
\]

and

\[
\tilde{f}(Z,t) = \begin{bmatrix}
F_1(p_1, q_1, r_1) \\
G_1(p_1, q_1, r_1) \\
H_1(p_1, q_1, r_1)
\end{bmatrix}
\]

with

\[
F_i \overset{\text{def}}{=} -\alpha_i + \frac{\gamma_i y^* Z e^{\theta_i t} - p_i}{x^* e^{p_i} + y^* e^{q_i}} \int_0^t \beta'(t-s)e^{-\alpha_i(t-s)} e^{p_i(s)} ds
\]

\[
G_i \overset{\text{def}}{=} -\alpha_2 - f(y^* e^{q_1}) + \frac{\gamma_2 x^* Z e^{\theta_1}}{x^* e^{p_1} + y^* e^{q_1}}
\]

\[
H_i \overset{\text{def}}{=} \alpha_3 - \frac{\delta_1 x^* y^* e^{q_1}}{x^* e^{p_1} + y^* e^{q_1}} \int_0^t \beta'(t-s)e^{-\alpha_i(t-s)} e^{p_i(s)} ds - \frac{\delta_2 x^* y^* e^{\theta_1}}{x^* e^{p_1} + y^* e^{q_1}}
\]

It can be seen that \( \tilde{f}(0,t) \equiv 0 \) for all \( t \in (-\infty, \infty) \).

Now following the analysis steps as in [51,103,104] (also see section 1.4.7 in Chapter-I), it yields that the positive equilibrium \( \bar{e}_B \) of Model B is asymptotically stable if

\[
\frac{\partial F_i}{\partial p_1} < 0,
\]
\[ \frac{\partial F_i}{\partial p_i, \partial q_i} > \frac{1}{4} \left[ \frac{\partial F_i}{\partial q_i} + \frac{\partial G_i}{\partial p_i} \right]^2, \]

and

\[ \left[ \frac{\partial F_i}{\partial r_i} + \frac{\partial H_i}{\partial p_i} \right] \left[ \frac{\partial G_i}{\partial q_i} + \frac{\partial H_i}{\partial p_i} \right] \left[ \frac{\partial F_i}{\partial q_i} + \frac{\partial G_i}{\partial p_i} \right] < \frac{\partial F_i}{\partial p_i} \left[ \frac{\partial G_i}{\partial q_i} + \frac{\partial H_i}{\partial q_i} \right]^2 \]

\[ + \frac{\partial G_i}{\partial q_i} \left[ \frac{\partial F_i}{\partial r_i} + \frac{\partial H_i}{\partial p_i} \right]^2 \]

(4.27)

Various first order partial derivatives of \( F_i, G_i \) and \( H_i \) involved in (4.27) are

\[ \frac{\partial F_i}{\partial p_i} = -\frac{\gamma_1 x^* y^* z^* e^{q_i + r_i}}{(x^* e^{p_i} + y^* e^{q_i})^2} \int_{-\infty}^{t} \beta'(t-s) e^{-a_i(t-s)} e^{b_i(s)} \, ds \]

\[ \frac{\partial F_i}{\partial q_i} = \frac{\gamma_1 x^* y^* z^* e^{q_i + r_i}}{(x^* e^{p_i} + y^* e^{q_i})^2} \int_{-\infty}^{t} \beta'(t-s) e^{-a_i(t-s)} e^{b_i(s)} \, ds \]

\[ \frac{\partial F_i}{\partial r_i} = \frac{\gamma_1 y^* z^* e^{q_i + r_i} - p_i}{(x^* e^{p_i} + y^* e^{q_i})^2} \int_{-\infty}^{t} \beta'(t-s) e^{-a_i(t-s)} e^{b_i(s)} \, ds \]

\[ \frac{\partial G_i}{\partial p_i} = \frac{\gamma_2 x^* y^* z^* e^{p_i + q_i + r_i}}{(x^* e^{p_i} + y^* e^{q_i})^2} \]

\[ \frac{\partial G_i}{\partial q_i} = -f'(y^* e^{q_i}) y^* e^{q_i} - \frac{\gamma_2 x^* y^* z^* e^{p_i + q_i + r_i}}{(x^* e^{p_i} + y^* e^{q_i})^2} \]

\[ \frac{\partial G_i}{\partial r_i} = \frac{\gamma_2 x^* z^* e^{p_i + r_i}}{(x^* e^{p_i} + y^* e^{q_i})} \]
\[
\frac{\partial H_1}{\partial p_i} = -\frac{\delta_1 x' y' e^{2q}}{(x'e^n + y'e^n)^2} \int_0^t \beta'(t-s) e^{-\alpha(t-s)} e^{p_i(s)} \, ds
\]
\[
\frac{\delta_2 x'y' e^{n+2q}}{(x'e^n + y'e^n)^2}
\]
\[
\frac{\partial H_1}{\partial q_1} = -\frac{\delta_1 x'y' e^{p+q}}{(x'e^n + y'e^n)^2} \int_0^t \beta'(t-s) e^{-\alpha(t-s)} e^{p(s)} \, ds
\]
\[
\frac{\delta_2 x'y' e^{2p+q}}{(x'e^n + y'e^n)^2}
\]

Denoting
\[
P = P(t) = \int_0^t \beta'(t-s) e^{-\alpha(t-s)} x(s) \, ds
\]

the stability conditions (4.27) can be written as

\[
P > 0
\]
\[
\gamma_1 f'(y)(x+y)^2 P > z/4 \quad [\gamma_1 P - \gamma_2 x]^2
\]

and

\[
\left[ \left( \frac{\gamma_1 yz}{x(x+y)} - \frac{\delta_1 y^2}{(x+y)^2} \right) P - \frac{\delta_2 x'y^2}{(x+y)^2} \right] \text{ product}
\]
\[
\left[ \frac{\gamma_2 xz}{x+y} - \frac{\delta_2 x^2 y}{(x+y)^2} - \frac{\delta_1 xy}{(x+y)^2} P \right] \text{ product}
\]
It is clear that for asymptotic stability of the positive equilibrium $e_B$ of Model B, conditions (4.28) must hold true for all $t > 0$. These conditions are too complicated to make any meaningful interpretation. It is for this reason that we further simplify our assumptions and assume that $\gamma_2$ and $\delta_2$ (the two parameters concerning the population $y$ (see section 4.2)) are so small that $\gamma_2 = 0$ and $\delta_2^2 = 0$. Under these assumptions, stability conditions (4.28) reduce to

$$0 < P < \frac{4f'(y)(x+y)^2}{\gamma_1 z}$$

and

$$G(P) > 0 \tag{4.29}$$

where,

$$G(P) = a_1 P^2 + b_1 P + c_1,$$

with
\[ a_1 = \gamma_1 \delta_1 z \left[ \frac{\gamma_1}{\delta_1} - \frac{x}{z} \right], \]

\[ b_1 = \gamma_1 \delta_2 x z \left[ \frac{\gamma_1}{\delta_1} - \frac{2x}{z} \right] - \frac{f'(y) \delta_1 z(x+y)^3}{x^2} \left[ \frac{\gamma_1}{\delta_1} - \frac{y}{z} \right], \]

and

\[ c_1 = 2f'(y) \delta_2 (x+y)^2 \left[ \frac{\gamma_1}{\delta_1} - \frac{xy}{z(x+y)} \right]. \]

Conditions (4.29) must be satisfied for all \( t > 0 \) for \( e_b \) to be asymptotically stable. For any fixed \( t > 0 \), let

\[ \frac{xy}{z(x+y)} < \frac{\gamma_1}{\delta_1} < \frac{x}{z}, \]

\[ P^* = \frac{4f'(y) (x+y)^2}{\gamma_1 z} \]

and \( P^{**} \) denote the positive real root of \( G(P) = 0 \) i.e.

\[ P^{**} = \frac{-b_1 - \sqrt{b_1^2 - 4a_1 c_1}}{2a_1}, \]

where \( a_1 < 0 \), \( b_1 < 0 \) and \( c_1 > 0 \)

Thus conditions (4.29) are satisfied for any fixed \( t > 0 \), if

\[ 0 < P < \min (P^*, P^{**}) \]

Using (4.25) and supposing that
\[
\frac{K_2 L_2}{M_1 (K_1 + L_1)} < \frac{\gamma_1}{\delta_1} < \frac{K_1}{M_2},
\]

\[
\xi_1 = \frac{4f'(L_1)(K_1 + L_1)^2}{\gamma_1 M_2},
\]

and

\[
\xi_2 = \frac{-b'_1 - \sqrt{b'^2_1 - 4a_1 c_1}}{2a_1},
\]  
(4.30)

where,

\[
a_1' = \gamma_1 \delta_1 M_2 \left[ \frac{\gamma_1}{\delta_1} - \frac{K_1}{M_2} \right],
\]

\[
b_1' = \gamma_1 \delta_1 K_2 M_2 \left[ \frac{\gamma_1}{\delta_1} - \frac{2K_1}{M_2} \right] - \frac{f'(L_1)\delta_1 M_2 (K_2 + L_2)^3}{K_1^2} \text{ product}
\]

\[
\left[ \frac{\gamma_1}{\delta_1} - \frac{K_2 L_2}{M_1 (K_1 + L_1)} \right]^2
\]

and

\[
c_1' = 2f'(L_1)L_1 \delta_2 (K_1 + L_1)^2 \left[ \frac{\gamma_1}{\delta_1} - \frac{K_2 L_2}{M_1 (K_1 + L_1)} \right]
\]

it turns out that the positive equilibrium \( e_B \) of Model B is asymptotically stable provided

\[
0 < P < \min (\xi_1, \xi_2)
\]  
(4.31)

for all \( t > 0 \) Assuming (without losing generality) that there exists \( m > 0 \) such that

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\[ P'(a) > 0 \text{ for } a \leq m \text{ and } P'(a) < 0 \text{ for } a > m, \quad (4.32) \]

the condition (4.31) is reduced to

\[ 0 < K_1 \int_0^m \beta'(a)e^{-a}da + K_2 \int_m^\infty \beta'(a)e^{-a}da < \min(\xi_1, \xi_2) \]

We now summarize the results of this section in the following theorem.

**Theorem 4.2**

(a) The positive equilibrium \( e_b \) of Model B is asymptotically stable provided the conditions (4.27) hold.

(b) Assume that \( \gamma = 0, \delta = 0 \) and conditions (4.25), (4.30a) and (4.32) hold. The positive equilibrium \( e_b \) of Model B is asymptotically stable if

\[ 0 < K_1 \int_0^m \beta'(a)e^{-a}da + K_2 \int_m^\infty \beta'(a)e^{-a}da < \min(\xi_1, \xi_2) \]

where \( \xi_1, \xi_2 \) are given in (4.30b,c)

In order to have some insight into the result of (Theorem 4.2(b)), we consider the specialized form (4.22) for the distribution function \( \beta(a) \) for which

\[ \beta'(a) = \frac{1}{m^2} e^{-a/m} \left[ 1 - \frac{a}{m} \right] \]

and
\[ K_1 \int_0^\alpha \beta'(a)e^{-a}da + K_2 \int_\alpha^\infty \beta'(a)e^{-a}da \]

\[ = \frac{K_1}{m^2} \int_0^\infty \left(1 - \frac{a}{m}\right)e^{-\left(\frac{a}{m}\right)}da + \frac{K_2}{m^2} \int_\infty^\alpha \left(1 - \frac{a}{m}\right)e^{-\left(\frac{a}{m}\right)}da \]

\[ = \frac{K_1 \alpha_1}{\alpha(m+1)^2} + \frac{(K_1 - K_2)e^{\alpha m-1}}{m(\alpha,m+1)^2} \quad (4.33) \]

It implies from (4.33) that large \( m \) facilitates the condition of Theorem 4.2(b) to be satisfied. This result further confirms the contention of section 4.3 that large maturation periods may promote the coexistence of two predators and a single prey with prey adopting defensive switching behavior. This result strengthens the view that the generally held tenet in population biology that large delays cause instabilities may not hold true even for some nonlinear model systems.

4.5 Conclusions

Many authors in mathematical ecology have studied one-predator-two-prey models with predator switching behavior emphasizing predator preference for relatively abundant prey items. Conclusions from the results of these models have been very much model dependent [5,76,101,124,125]. Prey switching behavior has also been studied in recent years (see e.g. [34,62,64,122]). This is called predator-specific defense. These studies mainly concern those situations where a single prey is eaten by two or three predators (such as scale eaters in Lake Tanganyika [62]) and this prey has predator-specific defense (each prey behavior is effective against one predator species). Here again different models have produced different results varying from coexistence of species to permanent fluctuations (see e.g. [62,77,122]).
We consider in this chapter a new two-predator-one-prey model with prey defensive switching behavior. We introduce delays for the first time in such a model through age-structure in one of the predator populations with a purpose to study the effects of maturation periods (as delays) on the equilibrium stability. Main result of this chapter can be summarized as "although maturation periods result in the weakening of equilibrium stability (or weakening of resilience), large maturation periods can promote the coexistence of two predators and a single prey when prey displays defensive switching behavior. This result is very much in contrast to the usually held tenet in population biology that large delays cause instabilities. It is interesting to note that same contrasting result holds true even for a nonlinear model."