

Research Article

Dynamics of a Stage-Structured Leslie-Gower Predator-Prey Model

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A generalized version of the Leslie-Gower predator-prey model that incorporates the prey population structure is introduced. Our results show that the inclusion of (age) structure in the prey population does not alter the qualitative dynamics of the model; that is, we identify sufficient conditions for the “trapping” of the dynamics in a biological compact set—albeit the analysis is a bit more challenging. The focus is on the study of the boundedness of solutions and identification of sufficient conditions for permanence. Sufficient conditions for the local stability of the nonnegative equilibria of the model are also derived, and sufficient conditions for the global attractivity of positive equilibrium are obtained. Numerical simulations are used to illustrate our results.

1. Introduction

Lotka-Volterra predator-prey models have been extensively and deeply investigated [1–5]. In population biology, we are often interested in identifying potential mechanisms responsible for either fluctuations or the lack of fluctuations in predator-prey systems. If we let $x(t)$ denote the density of prey and let $y(t)$ be the density of predator, then the classical Lotka-Volterra predator-prey model is given by the following system:

$$\begin{aligned}x'(t) &= (r_1 - c_1 y - b_1 x)x, \\y'(t) &= (-\varepsilon_2 + \rho_2 x)y.\end{aligned}\tag{1.1}$$

It is known that these equations can support population fluctuations when $b_1 = 0$, but, because the model is not structurally stable, the results have been primarily used as

a metaphor and as an inspiration for mathematical and biological research on the mechanisms responsible for fluctuations (or their lack) in predator-prey systems. The equations in system (1.1) set no upper limit on the percapita growth rate of the predator (second term of Model (1.1)) which of course is unrealistic. For example, for mammals, such a limit will be determined in part by physiological factors (length of the gestation period, the shortest interval between litters, the maximum average number of daughters per litter, the age at which breeding first starts, and so on [6, 7]). Leslie modeled the effect of such limitations via a predator-prey model, where the "carrying capacity" of the predator's environment was assumed to be proportional to the number of prey. Hence, if $x(t)$ denotes the prey density and $y(t)$ the predators', then Leslie's model is given by the following system of nonlinear differential equations:

$$\begin{aligned}x'(t) &= (r_1 - c_1y - b_1x)x, \\y'(t) &= \left(r_2 - c_2\frac{y}{x}\right)y,\end{aligned}\tag{1.2}$$

where $r_i, c_i, i = 1, 2$, and b_1 are positive constants. The first equation of System (1.2) is standard, but the second is not because it contains the so-called Leslie-Gower term, namely, c_2y/x . The rationale behind this term is based on the view that as the prey becomes numerous ($x \rightarrow \infty$) then the percapita growth rate of the predator (dy/ydt) achieves its maximum r_2 . Conversely as the prey becomes scarce ($x \rightarrow 0$), the predator will go extinct since the percapita growth rate of the predator goes to $-\infty$. An alternative interpretation of the Leslie-Gower model concludes that the carrying capacity of the predators' environment is proportional to the number of prey available, that is,

$$y'(t) = r_2\left(1 - \frac{y}{Ax}\right)y = r_2\left(1 - \frac{y}{C}\right)y,\tag{1.3}$$

where $A = r_2/c_2$ can be interpreted as a prey predators' conversion factor and $C = Ax$ as the predators' carrying capacity (proportional to prey abundance). The Leslie-Gower term y/Ax has also been interpreted as a measure of the loss in percapita predator's reproduction rate due to the relative abundance (per capita y/x) of its "favorite" food (prey x). Model (1.2) is often referred to as a semi-ratio-dependent predator-prey model [8]. Model (1.2) is different from the ratio-dependent predator-prey models in the studies by Wang et al. [9] and Hsu et al. [10].

Scarcity of prey (x) could drive predators (y) to switch to alternative resources of food. In fact, there is an extensive literature on the evolutionary advantage of specialist versus generalist when it comes down to predators' diet [11–16]. Predator's growth may also be limited by nutritional factors. In fact, evolutionary forces may lead to the predators to specialize on the most nutritious prey. The possibility that a predator does not depend on a single prey type is modelled here in a rather simple way, that is, through the addition of a positive constant d in the denominator. In fact,

$$y'(t) = r_2\left(1 - \frac{y}{\alpha x + d}\right)y.\tag{1.4}$$

A modification of System (1.2) using a Holling-type II functional response for the prey population has led various researchers [11, 15] to consider the following model:

$$\begin{aligned}x'(t) &= \left(r_1 - \frac{c_1 y}{x + k_1} - b_1 x \right) x, \\y'(t) &= \left(r_2 - \frac{c_2 y}{x + k_2} \right) y,\end{aligned}\tag{1.5}$$

where r_1 is the percapita growth rate of the prey x , b_1 is a measure of the strength of prey (on prey) interference competition, c_1 is the maximum value of the per capita reduction rate of prey x due to predator y , k_1 measures the extent to which the environment provides protection to prey x (k_2 for predator y), r_2 gives the maximal percapita growth rate of predator y , and c_2 has a similar meaning to that of c_1 .

In Aziz-Alaoui [17], a preliminary analysis of a Leslie-Gower model (System (1.2)) is carried out. In the study by Korobeinikov [18], the global stability of the unique coexisting interior equilibrium of System (1.2) is established. In the study by Aziz-Alaoui and Daher Okiye [11], the existence and boundedness of solutions (including that of an attracting set) are established as well as the global stability of the coexisting interior equilibrium for Model (1.5). There have been additional extensions, for example, in the study by Letellier and Asis-Alaoui [13], the studies by Letellier et al. [14] and Upadhyay and Rai [19], a Leslie-Gower type tritrophic model was introduced and analyzed numerically.

Nindjina et al. considered the following extension of Leslie-Gower (modified with Holling-type II schemes and time delay τ):

$$\begin{aligned}x'(t) &= \left(r_1 - \frac{c_1 y}{x + k_1} - b_1 x \right) x, \\y'(t) &= \left(r_2 - \frac{c_2 y(t - \tau)}{x(t - \tau) + k_2} \right) y,\end{aligned}\tag{1.6}$$

that is, a single discrete delay $\tau > 0$ is introduced as a negative feedback in the predator's density. Some results associated with the global stability analysis of solutions to System (1.6) have been obtained including the impact of τ on the stability of positive equilibrium of System (1.6). In fact, researchers found out that the time delay can have a destabilizing effect on the positive equilibrium of System (1.6) [15].

Most prey species have a life history that includes multiple stages (juvenile and adults or immature and mature). In the study by Aiello and Freedman [20], the population dynamics of a single species with two identifiable stages was modeled by the following system:

$$\begin{aligned}x'_1(t) &= \alpha x_2(t) - \gamma x_1(t) - \alpha e^{-\gamma\tau} x_2(t - \tau), \\x'_2(t) &= \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t),\end{aligned}\tag{1.7}$$

where $x_1(t)$, $x_2(t)$ denote the immature and mature population densities, respectively. Here, $\alpha > 0$ represents the percapita birth rate, $\gamma > 0$ is the percapita immature death rate, $\beta > 0$

models death rate due to overcrowding and τ is the “fixed” time to maturity, and the term $\alpha e^{-\gamma\tau} x_2(t - \tau)$ models the immature individuals who were born at time $t - \tau$ (i.e., $\alpha x_2(t - \tau)$) and survive and mature at time t . The derivation and analysis of System (1.7) can be found in the study by Aiello and Freedman [20]. Several additional researchers ([21–23], and the references therein) have investigated versions of the above single species model under various stage-structure assumptions.

Liu and Beretta [24] reintroduced the impact of predators. They studied a predator-prey model with Beddington-DeAngelis functional response and stage-structure on the predator population. These researchers found that predator and prey coexist if and only if the predator’s recruitment rate at the peak of prey abundance is larger than its death rate. If the system is permanent, that is, if for any solution $x(t)$ of the system, there exist constants $M, m > 0$ such that $m \leq \liminf_{t \rightarrow \infty} x(t) \leq \limsup_{t \rightarrow \infty} x(t) \leq M$ then sufficiently “large” predators’ interference not only stabilizes the system but also guarantees its stability against increases in the carrying capacity of the prey and increases in the birth rate of the adult predator. Finally, it was shown (analytically and numerically in the study by Liu and Beretta [24]) that stability switches of interior equilibrium may occur as the maturation time delay increases. That is, stability may change from stable to unstable to finally stable, implying that “small” and “large” delays can be stabilizing. Song et al. [25] considered a ratio-dependent predator-prey system that incorporated “age” structure for the prey. Their analysis established boundedness of solutions, looked at the nature of equilibria and permanence as well as the local stability and global attractivity of the positive equilibrium of the model. Their results show that the inclusion of an “age” structure in the prey population does not change the qualitative dynamics of the model—albeit the analysis is more challenging.

A Leslie-Gower model that incorporates the prey’s stage structure is introduced here to study the combined effects of prey stage structure and within prey interference competitions. Following Song et al. [25], we assume that the immature prey cannot reproduce and the per capita birth rate of the mature prey is $\alpha > 0$, the per capita death rate of the immature prey is $\gamma > 0$, the per capita death rate of the mature prey is proportional to the current mature prey population with a proportionality constant $\beta > 0$, and immature individuals become mature at age τ . Predators only feed on the mature prey. Using these definitions, we formulate a modified Leslie-Gower and Holling-type II schemes with stage-structure for prey as follows:

$$\begin{aligned} x_1'(t) &= \alpha x_2(t) - \gamma x_1(t) - \alpha e^{-\gamma\tau} x_2(t - \tau), \\ x_2'(t) &= \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 y(t) x_2(t)}{x_2(t) + k_1}, \\ y'(t) &= y(t) \left(r_2 - \frac{c_2 y(t)}{x_2(t) + k_2} \right). \end{aligned} \tag{1.8}$$

The initial conditions are given by $x_2(\theta) \geq 0$, continuous on $\theta \in [-\tau, 0]$, and $x_1(0), x_2(0), y(0) > 0$, while $x_1(t), x_2(t)$, and $y(t)$ denote the densities of immature prey, mature prey and predator, respectively. Please note that our model (1.8) is different from the model in the study by Song et al. [25] which is based on standard ratio-dependent and symmetric cross term. Our model (1.8) includes the Leslie-Gower term. The differences between the standard ratio-dependent formulation and the Leslie-Gower formulation of the predator-prey system are listed in the following, standard ratio-dependent formulation can be interpreted as the effect of the predator-population on the prey population and the effect of the prey population

on the predator-population are both a function of the ratio between the two, however the Leslie-Gower formulation can be interpreted as the effect of the predator-population on the prey population is different from the effect of the prey population on the predator-population: both effects are inversely proportional to the (mature) prey population plus a constant.

From the first equation of system (1.8) we can see that

$$x_1(t) = \int_{t-\tau}^t \alpha e^{-\gamma(t-s)} x_2(s) ds, \quad (1.9)$$

$$x_1(0) = \int_{-\tau}^0 \alpha e^{\gamma s} x_2(s) ds. \quad (1.10)$$

The last two equations in (1.8) do not contain $x_1(t)$. Hence, if we know the properties of $x_2(t)$ then the properties of $x_1(t)$ can be easily obtained from (1.8) and (1.9). Hence, we only need to consider the following system:

$$\begin{aligned} x_2'(t) &= \alpha e^{-\gamma\tau} x_2(t-\tau) - \beta x_2^2(t) - \frac{c_1 y(t) x_2(t)}{x_2(t) + k_1}, \\ y'(t) &= y(t) \left(r_2 - \frac{c_2 y(t)}{x_2(t) + k_2} \right), \end{aligned} \quad (1.11)$$

with initial conditions $x_2(\theta) \geq 0$ (continuous on $\theta \in [-\tau, 0]$) and $x_2(0), y(0) > 0$.

The main purpose of this paper is to study the global dynamics of System (1.11). The paper is organized as follows. In Section 2, we establish the conditions that determine the permanence of the system and obtain positiveness and boundedness results. Section 3 focuses on the study of the local stability of the nonnegative equilibria. Section 4 derives sufficient conditions for the global asymptotic stability of boundary equilibrium and for the global attractivity of positive equilibrium, and in the Section 5, these results are illustrated through simulations and their relevance is briefly discussed.

2. Permanence of Solutions

To prove the permanence of System (1.11), we need the following lemma, which is a direct application of Theorem 4.9.1 in the study by Kuang [26], see also Song et al. [25] and Liu et al. [27].

Lemma 2.1. *Consider the following equation:*

$$x'(t) = ax(t-\tau) - bx(t) - cx^2(t), \quad (2.1)$$

where $a, b, c, \tau > 0$ and $x(t) > 0$, for $-\tau \leq t \leq 0$.

- (i) If $a > b$, then $\lim_{t \rightarrow \infty} x(t) = (a - b)/c$.
- (ii) If $a < b$, then $\lim_{t \rightarrow \infty} x(t) = 0$.

Following the proof of Song et al. [25] and Liu et al. [27], we can obtain the following lemma.

Lemma 2.2. *Suppose $x_2(\theta) \geq 0$ is continuous on $\theta \in [-\tau, 0]$, and $x_2(0), y(0) > 0$, then the solution of System (1.11) satisfies $x_2(t), y(t) > 0$ for all $t > 0$.*

First, we establish a condition for the boundedness of the solutions of System (1.11).

Theorem 2.3. *Suppose $x_2(\theta) \geq 0$ is continuous on $\theta \in [-\tau, 0]$, and $x_2(0), y(0) > 0$, then the solutions of (1.11) are bounded for all large t .*

Proof. From the first equation of (1.11), we have

$$x_2'(t) \leq \alpha e^{-\gamma t} x_2(t - \tau) - \beta x_2^2(t). \quad (2.2)$$

According to Lemma 2.1 and the standard comparison principle [28], there exists a $T_1 > 0$ and $\epsilon_1 > 0$ such that

$$x_2(t) \leq \frac{\alpha e^{-\gamma t}}{\beta} + \epsilon_1 = M_1, \quad \text{for } t > T_1 + \tau. \quad (2.3)$$

By the second equation of (1.11) and above inequality, we get

$$y'(t) \leq y(t) \left(r_2 - \frac{c_2 y(t)}{M_1 + k_2} \right), \quad \text{for } t > T_1 + \tau. \quad (2.4)$$

From the comparison principle, there exists a $T_2 > T_1$ such that, for any sufficiently small ϵ_2 ,

$$y(t) \leq \frac{(M_1 + k_2)r_2}{c_2} + \epsilon_2 = M_2, \quad \text{for } t > T_2 + \tau. \quad (2.5)$$

The proof is complete. □

Now, we show that System (1.11) is permanent.

Theorem 2.4. *Suppose that*

$$\alpha e^{-\gamma \tau} - \frac{c_1 M_2}{k_1} > 0, \quad (2.6)$$

where M_2 is defined by (2.5), then System (1.11) is permanent.

Remark 2.5. Comparing the above permanent result with that results for model in Nindjin et al. [15] and model in Song et al. [25], we see the inclusion of an extra term $e^{-\gamma \tau}$ in our permanence condition (2.6); that is, the surviving probability of each immature prey becomes mature must be taken into account.

Proof. From the second equation of system (1.11), we have

$$y'(t) \geq y(t) \left(r_2 - \frac{c_2 y(t)}{k_2} \right). \quad (2.7)$$

It then follows that

$$\liminf_{t \rightarrow \infty} y(t) \geq \frac{k_2 r_2}{c_2} = m_2 > 0. \quad (2.8)$$

Using the first equation of System (1.11) and Theorem 2.3, for sufficiently large T , we have

$$\begin{aligned} x_2'(t) &\geq \alpha e^{-\gamma t} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 y(t) x_2(t)}{k_1} \\ &\geq \alpha e^{-\gamma t} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 M_2 x_2(t)}{k_1}. \end{aligned} \quad (2.9)$$

By Lemma 2.1 and the comparison principle, we have that

$$\liminf_{t \rightarrow \infty} x_2(t) \geq \frac{\alpha e^{-\gamma \tau} - c_1 M_2 / k_1}{\beta} = m_1 > 0. \quad (2.10)$$

Therefore, the above calculations and Theorem 2.3 imply that there exist $M_i, m_i > 0, i = 1, 2$, such that

$$\begin{aligned} 0 < m_1 &\leq \liminf_{t \rightarrow \infty} x_2(t) \leq \limsup_{t \rightarrow \infty} x_2(t) \leq M_1, \\ 0 < m_2 &\leq \liminf_{t \rightarrow \infty} y(t) \leq \limsup_{t \rightarrow \infty} y(t) \leq M_2. \end{aligned} \quad (2.11)$$

The proof is complete. \square

3. Analysis of Equilibria

System (1.11) has the following nonnegative equilibria:

$$E_0 = (0, 0), \quad E_1 = \left(\frac{\alpha e^{-\gamma \tau}}{\beta}, 0 \right), \quad E_2 = \left(0, \frac{k_2 r_2}{c_2} \right), \quad E_3 = (x_2^*, y^*), \quad (3.1)$$

where

$$\begin{aligned} x_2^* &= \frac{(\alpha e^{-\gamma \tau} - \beta k_1 - c_1 r_2 / c_2) + \sqrt{(\alpha e^{-\gamma \tau} - \beta k_1 - c_1 r_2 / c_2)^2 - 4\beta((c_1 r_2 / c_2)k_2 - \alpha e^{-\gamma \tau} k_1)}}{2\beta}, \\ y^* &= \frac{k_2 r_2 + r_2 x_2^*}{c_2}. \end{aligned} \quad (3.2)$$

We see that the positive equilibrium E_3 exists if

$$\alpha e^{-\gamma\tau} > \frac{c_1 k_2 r_2}{c_2 k_1}. \quad (3.3)$$

The characteristic equation at equilibrium E_0 is

$$\left(\lambda - \alpha e^{-\gamma\tau} e^{-\lambda\tau}\right)(\lambda - r_2) = 0, \quad (3.4)$$

and, consequently, since it has a positive eigenvalue $\lambda = r_2$, E_0 is unstable.

The characteristic equation at equilibrium E_1 is given by the transcendental equation

$$\left(\lambda - \left(-2\alpha e^{-\gamma\tau} + \alpha e^{-\gamma\tau} e^{-\lambda\tau}\right)\right)(\lambda - r_2) = 0. \quad (3.5)$$

Again, $\lambda = r_2$ is a positive eigenvalue, so E_1 is also unstable.

The analysis of the stability of E_2 requires a little more work. We have the following results.

Theorem 3.1. *Let*

$$\mathfrak{R}_0 = \frac{c_2 k_1}{c_1 k_2 r_2} \alpha e^{-\gamma\tau}, \quad (3.6)$$

then equilibrium E_2 is

- (i) *unstable if $\mathfrak{R}_0 > 1$,*
- (ii) *linearly neutrally stable if $\mathfrak{R}_0 = 1$,*
- (iii) *locally asymptotically stable if $\mathfrak{R}_0 < 1$.*

Proof. (i) The characteristic equation of equilibrium E_2 is given by

$$\left(\lambda + \frac{c_1 k_2 r_2}{c_2 k_1} - \alpha e^{-\gamma\tau} e^{-\lambda\tau}\right)(\lambda + r_2) = 0, \quad (3.7)$$

clearly, one characteristic root is $\lambda = -r_2 < 0$, others are the roots of

$$F(\lambda) = \lambda + \frac{c_1 k_2 r_2}{c_2 k_1} - \alpha e^{-\gamma\tau} e^{-\lambda\tau} = 0. \quad (3.8)$$

Assume that $\mathfrak{R}_0 > 1$, therefore $< \alpha e^{-\gamma\tau}$ then $F(0) < 0$ and $F(+\infty) = +\infty$. Hence $F(\lambda)$ has at least one positive root and E_2 is unstable.

(ii) Since $\mathfrak{R}_0 = 1$, that is, $c_1 k_2 r_2 / c_2 k_1 = \alpha e^{-\gamma\tau}$, $F(0) = 0$, so $\lambda = 0$ is a root of $F(\lambda) = 0$. As $F'(\lambda) = \tau \alpha e^{-\gamma\tau} e^{-\lambda\tau} + 1$, we have $F'(0) > 0$. The root $\lambda = 0$ is simple. If other roots are of form $a + i\omega$, for some a and ω in \mathbb{R} , they satisfy

$$(a + \alpha e^{-\gamma\tau})^2 + \omega^2 = (\alpha e^{-\gamma\tau})^2 e^{-2a\tau}. \quad (3.9)$$

Then, we must have $a \leq 0$; that is, all other roots have nonpositive real parts. Hence E_2 is linearly neutrally stable.

(iii) If $\mathfrak{R}_0 < 1$, then $c_1 k_2 r_2 / c_2 k_1 > \alpha e^{-\gamma \tau}$. Assume that there exists an eigenvalue λ with $\text{Re } \lambda \geq 0$, then we have

$$\begin{aligned} \text{Re } \lambda &= -\frac{c_1 k_2 r_2}{c_2 k_1} + \alpha e^{-\gamma \tau} e^{-(\text{Re } \lambda) \tau} \cos(\tau \text{Im } \lambda) \\ &\leq \alpha e^{-\gamma \tau} e^{-(\text{Re } \lambda) \tau} - \frac{c_1 k_2 r_2}{c_2 k_1} < 0. \end{aligned} \quad (3.10)$$

It is a contradiction, so $\text{Re } \lambda < 0$. This shows that all roots of $F(\lambda) = 0$ must have negative real parts, hence, the equilibrium E_2 is locally asymptotically stable.

The proof of the theorem is complete. \square

Remark 3.2. Note that when the predator reaches its steady state $\hat{y} = k_2 r_2 / c_2$ in the absence of prey, $\alpha e^{-\gamma \tau}$ can be interpreted as the per capita recruitment rate of prey and $c_1 k_2 r_2 / c_2 k_1 = c_1 \hat{y} / k_1$ approximates the per capita death rate of the prey. Therefore, $\mathfrak{R}_0 = \alpha e^{-\gamma \tau} c_2 k_1 / c_1 k_2 r_2$ is the basic demographic number of prey when the predator's population size reaches its steady state \hat{y} in the absence of prey x . When $\mathfrak{R}_0 > 1$, the population size of prey will increase, thus E_2 is unstable. Similarly we can interpret (ii) and (iii) in Theorem 3.1.

Remark 3.3. The sufficient condition given by (2.6) for the permanence of System (1.11) can be rewritten in the following form

$$\mathfrak{R}_0 > 1 + \frac{\alpha e^{-\gamma \tau}}{k_2 \beta} \doteq p_0. \quad (3.11)$$

So a "large" basic demographic number ($\mathfrak{R}_0 > p_0 > 1$) for the prey when the predator's population size reaches its steady state in the absence of prey can guarantee the permanence of System (1.11).

Now, we consider the local stability of the interior equilibrium $E_3 = (x_2^*, y^*)$. Recall there exists E_3 when (3.3) holds, that is, when τ is in the interval $I = [0, \tau^*)$, where

$$\tau^* = \frac{1}{\gamma} \ln \frac{c_2 \alpha k_1}{c_1 r_2 k_2}. \quad (3.12)$$

The characteristic equation at E_3 is

$$\begin{aligned} D(\lambda, \tau) &= \lambda^2 + \left(r_2 + 2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right) \lambda + r_2 \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right) \\ &\quad + \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} + \left(r_2 - \lambda - \frac{2c_2 y^*}{k_2 + x_2^*} \right) \alpha e^{-\gamma \tau} e^{-\lambda \tau} = 0. \end{aligned} \quad (3.13)$$

Let

$$\begin{aligned} P(\lambda, \tau) &= \lambda^2 + P_1(\tau)\lambda + P_0(\tau), \\ Q(\lambda, \tau) &= \lambda Q_1(\tau) + Q_0(\tau), \end{aligned} \quad (3.14)$$

where

$$\begin{aligned} P_1(\tau) &= r_2 + 2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2}, \\ P_0(\tau) &= r_2 \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right) + \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2}, \\ Q_1(\tau) &= -\alpha e^{-\gamma\tau}, \quad Q_0(\tau) = -r_2 \alpha e^{-\gamma\tau}. \end{aligned} \quad (3.15)$$

Then the characteristic equation at E_3 becomes

$$D(\lambda, \tau) = P(\lambda, \tau) + Q(\lambda, \tau)e^{-\lambda\tau} = 0. \quad (3.16)$$

First, we will prove

$$P(0, \tau) + Q(0, \tau) \neq 0, \quad (3.17)$$

that is, $\lambda = 0$ cannot be a root of (3.16) for any $\tau \in I$.

In fact, by the definition of (x_2^*, y^*) , we have

$$\begin{aligned} D(0, \tau) &= P_0(\tau) + Q_0(\tau) = P(0, \tau) + Q(0, \tau) \\ &= r_2 \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right) + \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} - r_2 \alpha e^{-\gamma\tau} \\ &= r_2 \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} - \alpha e^{-\gamma\tau} \right) + \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} \\ &= r_2 \left(-\beta k_1 - \frac{c_1 r_2}{c_2} + \sqrt{\left(\alpha e^{-\gamma\tau} - \beta k_1 - \frac{c_1 r_2}{c_2} \right)^2 - 4\beta \left(\frac{c_1 r_2}{c_2} k_2 - \alpha e^{-\gamma\tau} k_1 \right)} \right) \\ &> 0. \end{aligned} \quad (3.18)$$

Therefore, $\lambda = 0$ is not a root of (3.16).

The characteristic equation (3.16) at $\tau = 0$ is

$$P(\lambda, 0) + Q(\lambda, 0) = 0, \quad (3.19)$$

that is,

$$\lambda^2 + (P_1(0) + Q_1(0))\lambda + P_0(0) + Q_0(0) = 0. \quad (3.20)$$

Then,

$$\lambda^2 + \left(r_2 + 2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} - \alpha \right) \lambda + r_2 \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} + \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} - \alpha \right) = 0. \quad (3.21)$$

Since $P_0(\tau) + Q_0(\tau) > 0$ for all $\tau \in [0, \tau^*)$, then $P_0(0) + Q_0(0) > 0$. Notice that

$$P_1(0) + Q_1(0) = r_2 + 2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} - \alpha. \quad (3.22)$$

If $P_1(0) + Q_1(0) > 0$, then (3.20) has two solutions with negative real parts. Hence, E_3 is locally asymptotically stable at $\tau = 0$. If $P_1(0) + Q_1(0) < 0$, then E_3 is unstable at $\tau = 0$.

To determine the local stability of the interior equilibrium $E_3 = (x_2^*, y^*)$, we proceed as follows [29].

Assume that $\lambda = \pm i\omega(\tau)$, $\omega(\tau) > 0$ satisfy (3.16), we have

$$\begin{aligned} P(i\omega, \tau) &= -\omega^2 + i\omega P_1(\tau) + P_0(\tau), \\ P_R(i\omega, \tau) &= P_0(\tau) - \omega^2, \quad P_I(i\omega, \tau) = \omega P_1(\tau), \\ Q(i\omega, \tau) &= i\omega Q_1(\tau) + Q_0(\tau), \\ Q_R(i\omega, \tau) &= Q_0(\tau), \quad Q_I(i\omega, \tau) = \omega Q_1(\tau). \end{aligned} \quad (3.23)$$

The first step is to look for the positive roots $\omega(\tau) > 0$ of

$$F(\omega, \tau) = |P(i\omega, \tau)|^2 - |Q(i\omega, \tau)|^2 = 0 \quad (3.24)$$

in $I = [0, \tau^*)$. Since

$$F(\omega, \tau) = \omega^4 + \omega^2 \left(-2P_0(\tau) + P_1^2(\tau) - Q_1^2(\tau) \right) + P_0^2(\tau) - Q_0^2(\tau), \quad (3.25)$$

we have

$$\begin{aligned} F(\omega, \tau) &= \omega^4 + b(\tau)\omega^2 + c(\tau) = 0, \\ b(\tau) &= -2P_0(\tau) + P_1^2(\tau) - Q_1^2(\tau), \\ c(\tau) &= P_0^2(\tau) - Q_0^2(\tau). \end{aligned} \quad (3.26)$$

Depending on the signs of $b(\tau)$ and $c(\tau)$, System (3.26) may have no positive real roots, or the root

$$\omega_+(\tau) = \left[\frac{1}{2} \left(-b(\tau) + \sqrt{b(\tau)^2 - 4c(\tau)} \right) \right]^{1/2}, \quad \tau \in I_+ \subseteq I, \quad (3.27)$$

or otherwise the root

$$\omega_-(\tau) = \left[\frac{1}{2} \left(-b(\tau) - \sqrt{b(\tau)^2 - 4c(\tau)} \right) \right]^{1/2}, \quad \tau \in I_- \subseteq I, \quad (3.28)$$

or, as the last case, both $\omega_+(\tau)$ and $\omega_-(\tau)$. Note that if System (3.26) has no positive roots $\omega(\tau)$ in I , then no stability switches can occur.

From the structure of $P_1(0) + Q_1(0)$, a sufficient condition for E_3 at $\tau = 0$ to be locally asymptotically stable is given by

$$\alpha - 2\beta k_1 - 2c_1 \frac{r_2}{c_2} > 0, \quad (3.29)$$

which implies $P_1(0) + Q_1(0) > 0$. Stability switches for increasing τ in $I = [0, \tau^*)$ may occur only with a pair of roots $\lambda = \pm i\omega(\tau)$ ($\omega(\tau)$ real positive) that cross the imaginary axis.

Next, we state the following theorem on the local asymptotic stability of equilibrium E_3 .

Theorem 3.4. *The positive equilibrium E_3 of System (1.11) is locally asymptotically stable if*

$$\alpha - 2\beta k_1 - 2c_1 \frac{r_2}{c_2} > 0, \quad c_2 - 2c_1 > 0. \quad (3.30)$$

Remark 3.5. From (3.30), we know that if the birth rate of immature prey (α) is sufficiently large and the maximum value of the per capita reduction rate of x due to y is smaller than the maximum value of the per capita reduction rate of y due to x then the positive equilibrium E_3 is locally asymptotically stable.

Proof. We only need to prove that E_3 has no stability switches as τ increases and that E_3 is stable at $\tau = 0$. Consider the roots of (3.20), by the above discussion, we know if (3.30) holds then

$$P_1(0) + Q_1(0) = r_2 + 2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} - \alpha > 0. \quad (3.31)$$

So the roots of (3.20) must have negative real parts, hence E_3 is stable at $\tau = 0$. Next, we prove that E_3 has no stability switches as τ increases in $[0, \tau^*)$. We only need to prove that System (3.26) has no positive roots $\omega(\tau)$ in I .

From (3.26), we have

$$c(\tau) = P_0^2(\tau) - Q_0^2(\tau) = (P_0(\tau) + Q_0(\tau))(P_0(\tau) - Q_0(\tau)). \quad (3.32)$$

We know that $P_0(\tau) + Q_0(\tau) > 0$ and

$$P_0(\tau) - Q_0(\tau) = r_2 \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} + \alpha e^{-\gamma\tau} \right) > 0. \quad (3.33)$$

So $c(\tau) > 0$.

By (3.26), we also have

$$\begin{aligned} b(\tau) &= -2P_0(\tau) + P_1^2(\tau) - Q_1^2(\tau) \\ &= -2 \left(\frac{2c_2 y^*}{k_2 + x_2^*} - r_2 \right) \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right) - 2 \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} \\ &\quad + \left(-r_2 + \frac{2c_2 y^*}{k_2 + x_2^*} + 2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right)^2 - \alpha^2 e^{-2\gamma\tau} \\ &= \left(\frac{2c_2 y^*}{k_2 + x_2^*} - r_2 \right)^2 + \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} \right)^2 - 2 \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} - \alpha^2 e^{-2\gamma\tau} \\ &= \left(\frac{c_2 y^*}{k_2 + x_2^*} \right)^2 - 2 \frac{c_1 c_2 x_2^* y^{*2}}{(k_1 + x_2^*)(k_2 + x_2^*)^2} \\ &\quad + \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} + \alpha e^{-\gamma\tau} \right) \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} - \alpha e^{-\gamma\tau} \right) \\ &> \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} + \alpha e^{-\gamma\tau} \right) \left(2\beta x_2^* + \frac{c_1 k_1 y^*}{(k_1 + x_2^*)^2} - \alpha e^{-\gamma\tau} \right) + \frac{c_2^2 y^{*2}}{(k_2 + x_2^*)^2} - \frac{2c_1 c_2 y^{*2}}{(k_2 + x_2^*)^2} \\ &> 0, \end{aligned} \quad (3.34)$$

the last inequality holds because (3.30) and therefore we have that $b(\tau) > 0$ and $c(\tau) > 0$. Hence $F(\omega, \tau) \neq 0$ for all $\tau \in I = [0, \tau^*)$, that is, there are no stability switches for $\tau \in I = [0, \tau^*)$. The proof is complete. \square

4. Global Stability and Attractiveness

In this section, we establish conditions for the global stability of equilibria $E_2 = (0, k_2 r_2 / c_2)$ and $E_3 = (x_2^*, y^*)$ of System (1.11). The following theorems hold.

Theorem 4.1. *Suppose that*

$$\frac{M_1 + k_1}{c_1 m_2} \alpha e^{-\gamma\tau} < 1, \quad (4.1)$$

where $m_2 = k_2 r_2 / c_2$, $M_1 = \alpha e^{-\gamma\tau} / \beta + \epsilon_1$, then the equilibrium $E_2 = (0, k_2 r_2 / c_2)$ of System (1.11) is globally asymptotically stable.

Remark 4.2. From (4.1), we also find that $\gamma\tau$ has a positive effect on the extinction of prey in that a proper increase of $\gamma\tau$ (which is defines as the “degree of stage structure” by Liu et al. [27]) can drive the prey into extinction, regardless of how large other coefficients were.

Remark 4.3. Inequality (4.1) is equivalent to

$$\mathfrak{R}_0 < \frac{1}{1 + \alpha e^{-\gamma\tau} / \beta k_1} \doteq p_1. \quad (4.2)$$

That is, a small basic demographic number ($\mathfrak{R}_0 < p_1 < 1$) for the prey (when the predator’s population size reaches its steady state in the absence of prey) can guarantee the prey’s extinction (E_2 is globally stable).

Proof. From Theorem 3.1, we know that E_2 is locally asymptotically stable. Now, we only need to prove global attractiveness of E_2 . By the first equation of System (1.11), the proof of Theorems 2.3 and 2.4, and $x_2(t)$ is nonnegative, we have that

$$\begin{aligned} x_2'(t) &= \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 y(t) x_2(t)}{x_2(t) + k_1} \\ &\leq \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 m_2 x_2(t)}{M_1 + k_1}. \end{aligned} \quad (4.3)$$

From Lemma 2.1 and (4.1), we obtain that

$$\lim_{t \rightarrow \infty} x_2(t) = 0. \quad (4.4)$$

Then, there is a T_0 such that, for $t > T_0$, we have $-\epsilon < x_2(t) < \epsilon$, where ϵ is sufficiently small. From the second equation of System (1.11), we have that

$$y'(t) \leq y(t) \left(r_2 - \frac{c_2 y(t)}{\epsilon + k_2} \right), \quad (4.5)$$

and, by the comparison principle, we conclude that

$$y(t) \leq \frac{(k_2 + \epsilon)r_2}{c_2}, \quad (4.6)$$

and consequently $\lim_{t \rightarrow \infty} \inf y(t) \geq k_2 r_2 / c_2$. Hence, we have that

$$\lim_{t \rightarrow \infty} y(t) = \frac{k_2 r_2}{c_2}. \quad (4.7)$$

The proof is complete. \square

Next, we study the global attractivity of the interior equilibrium E_3 of System (1.11). Consider the following system:

$$\begin{aligned} v'(t) &= a_4 v(t - \tau) - a_3 v^2(t) - \frac{a_1 v(t)}{v(t) + a_2}, \\ v(t) &= \varphi(t) \geq 0, \quad \text{for } t \in [-\tau, 0], \\ v(0) &> 0, \end{aligned} \tag{4.8}$$

where $a_i > 0$, $i = 1, 2, 3, 4$. A similar reasoning using Lemma 2.2 gives that $v(t) > 0$ for all $t \geq 0$. From Theorem 4.9.1 in Kuang [26] we conclude by the following lemma.

Lemma 4.4. *System (4.8) has a unique positive equilibrium*

$$v^* = \frac{\left(a_4 - a_2 a_3 + \sqrt{(a_4 - a_2 a_3)^2 + 4a_3(a_2 a_4 - a_1)} \right)}{2a_3} \tag{4.9}$$

which is globally asymptotically stable if $a_2 a_4 - a_1 > 0$.

Finally, we have the following result.

Theorem 4.5. *Suppose that*

$$\begin{aligned} \alpha e^{-\gamma\tau} k_1 - r_2 \left(\frac{c_1(k_2\beta + \alpha e^{-\gamma\tau})}{c_2\beta} \right) &> 0, \quad \beta > 1, \\ \alpha e^{-\gamma\tau} - \beta k_1 - c_1 \frac{r_2}{c_2} &> 0, \end{aligned} \tag{4.10}$$

then the positive equilibrium E_3 in System (1.11) is globally attractive.

Remark 4.6. From (4.10), we know that $\gamma\tau$ has a negative effect on the global attractivity of positive equilibrium; that is, an increase in the value of $\gamma\tau$ can destroy Condition (4.10).

Remark 4.7. Comparing Theorems 4.1 and 4.2 with Theorems 4.1 and 4.2 in Song et al. [25], we also see the inclusion of an extra term $e^{-\gamma\tau}$ in our condition, that is, the surviving probability of each immature prey becomes mature must be taken into account.

Proof. By the first equation of System (1.11), we have

$$x_2'(t) \leq \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t), \tag{4.11}$$

then by Lemma 2.1 and the comparison principle, for sufficiently small $\epsilon > 0$, there is a $T_1 > 0$ such that

$$x_2(t) < \frac{\alpha e^{-\gamma\tau}}{\beta} + \epsilon = \bar{u}_1 \tag{4.12}$$

for $t \geq T_1 + \tau$. Replacing this inequality into the second equation of (1.11), we have

$$y'(t) \leq y(t) \left(r_2 - \frac{c_2 y(t)}{\bar{u}_1 + k_2} \right), \quad t \geq T_1. \quad (4.13)$$

Again by the comparison principle, there is a $T_2 > T_1 + \tau > 0$ such that

$$y(t) < \frac{(\bar{u}_1 + k_2)r_2}{c_2} + \varepsilon = \bar{v}_1, \quad t \geq T_2. \quad (4.14)$$

Substituting (4.14) into the first equation of (1.11), we have

$$x_2'(t) \geq \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 \bar{v}_1 x_2(t)}{x_2(t) + k_1}. \quad (4.15)$$

Consider the following equation:

$$z'(t) = \alpha e^{-\gamma\tau} z(t - \tau) - \beta z^2(t) - \frac{c_1 \bar{v}_1 z(t)}{z(t) + k_1}. \quad (4.16)$$

From the first inequality of (4.14) and Lemma 4.4, we see that (4.16) has a unique positive equilibrium $z^* = (\alpha e^{-\gamma\tau} - \beta k_1 + \sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4\beta(\alpha e^{-\gamma\tau} k_1 - c_1 \bar{v}_1)})/2\beta$ which is globally asymptotically stable. Using the comparison principle, for sufficiently small $\varepsilon > 0$, we see that there is a $T_3 > T_2 + \tau$ such that

$$x_2(t) > z^* - \varepsilon = \underline{u}_1 > 0. \quad (4.17)$$

Plugging (4.17) into the second equation of (1.11), we have that

$$y'(t) \geq y(t) \left(r_2 - \frac{c_2 y(t)}{\underline{u}_1 + k_2} \right), \quad t \geq T_3. \quad (4.18)$$

By the comparison principle, there is $T_4 > T_3$ such that

$$y(t) > \frac{(\underline{u}_1 + k_2)r_2}{c_2} - \varepsilon = \underline{v}_1, \quad t \geq T_4. \quad (4.19)$$

Hence, we have

$$\underline{u}_1 < x(t) < \bar{u}_1, \quad \underline{v}_1 < y(t) < \bar{v}_1, \quad t \geq T_4. \quad (4.20)$$

By replacing (4.19) in the first equation of (1.11) we see that

$$x_2'(t) \leq \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 \underline{v}_1 x_2(t)}{x_2(t) + k_1}. \quad (4.21)$$

From a similar use of the comparison principle, we conclude that there is $T_5 > T_4 + \tau$ such that

$$x_2(t) < z_1^* + \epsilon = \bar{u}_2 > 0, \quad t \geq T_5, \quad (4.22)$$

where $z_1^* = (\alpha e^{-\gamma\tau} - \beta k_1 + \sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4(\alpha e^{-\gamma\tau} k_1 - c_1 \underline{v}_1)\beta})/2\beta > 0$ is the positive equilibrium for the equation

$$z'(t) = \alpha e^{-\gamma\tau} z(t) - \beta z^2(t) - \frac{c_1 \underline{v}_1 z(t)}{z(t) + k_1}. \quad (4.23)$$

From (4.10), we have

$$\bar{u}_2 < \bar{u}_1. \quad (4.24)$$

Substituting (4.22) into the second equation in (1.11), we have that

$$y'(t) \leq y(t) \left(r_2 - \frac{c_2 y(t)}{\bar{u}_2 + k_2} \right), \quad t \geq T_5. \quad (4.25)$$

A similar discussion (as above) implies that for sufficiently small $\epsilon > 0$, there is a $T_6 > T_5$ such that

$$y(t) < \frac{(\bar{u}_2 + k_2)r_2}{c_2} + \epsilon = \bar{v}_2. \quad (4.26)$$

Since $\bar{u}_2 < \bar{u}_1$, we get

$$\bar{v}_2 < \bar{v}_1. \quad (4.27)$$

Plugging (4.26) into the first equation of (1.11) leads to

$$x_2'(t) > \alpha e^{-\gamma\tau} x_2(t - \tau) - \beta x_2^2(t) - \frac{c_1 \bar{v}_2 x_2(t)}{x_2(t) + k_1}, \quad t \geq T_6. \quad (4.28)$$

From (4.10), Lemma 4.4 and the comparison principle, we see that for sufficiently small $\epsilon > 0$, there is a $T_7 > T_6 + \tau$ such that

$$x_2(t) > z_2^* - \epsilon = \underline{u}_2 > 0, \quad t \geq T_7, \quad (4.29)$$

where $z_2^* = (\alpha e^{-\gamma\tau} - \beta k_1 + \sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4(\alpha e^{-\gamma\tau} k_1 - c_1 \bar{v}_2)\beta})/2\beta > 0$ is the positive equilibrium for the equation

$$z'(t) = \alpha e^{-\gamma t} z(t) - \beta z^2(t) - \frac{c_1 \bar{v}_2 z(t)}{z(t) + k_1}. \quad (4.30)$$

Moreover, since $\bar{v}_2 < \bar{v}_1$ we have that $\underline{u}_2 > \underline{u}_1$.

Replacing (4.22) in the second equation of (1.11) leads to

$$y'(t) \geq y(t) \left(r_2 - \frac{c_2 y(t)}{\underline{u}_2 + k_2} \right), \quad t \geq T_7. \quad (4.31)$$

Arguments similar to those used above guarantee the existence of a $T_8 > T_7$ such that

$$y(t) > \frac{(\underline{u}_2 + k_2)r_2}{c_2} - \epsilon = \underline{v}_2, \quad t \geq T_8, \quad (4.32)$$

from which we get that $\underline{v}_2 > \underline{v}_1$.

Repeating the above process leads to the construction of the sequences $(\bar{u}_n)_{n=1}^\infty$, $(\underline{u}_n)_{n=1}^\infty$, $(\bar{v}_n)_{n=1}^\infty$, $(\underline{v}_n)_{n=1}^\infty$, and $T_{4n} > 0$. For $t \geq T_{4n}$, we have that

$$\begin{aligned} 0 < \underline{u}_1 < \underline{u}_2 < \cdots < \underline{u}_n < x_2(t) < \bar{u}_n < \cdots < \bar{u}_2 < \bar{u}_1, \\ 0 < \underline{v}_1 < \underline{v}_2 < \cdots < \underline{v}_n < y(t) < \bar{v}_n < \cdots < \bar{v}_2 < \bar{v}_1. \end{aligned} \quad (4.33)$$

Hence, the limits of $(\bar{u}_n)_{n=1}^\infty$, $(\underline{u}_n)_{n=1}^\infty$, $(\bar{v}_n)_{n=1}^\infty$, $(\underline{v}_n)_{n=1}^\infty$ exist. Denote that

$$\bar{u} = \lim_{t \rightarrow \infty} \bar{u}_n, \quad \bar{v} = \lim_{t \rightarrow \infty} \bar{v}_n, \quad \underline{u} = \lim_{t \rightarrow \infty} \underline{u}_n, \quad \underline{v} = \lim_{t \rightarrow \infty} \underline{v}_n, \quad (4.34)$$

then $\bar{u} \geq \underline{u}$, $\bar{v} \geq \underline{v}$. To complete the proof, we only need to show $\bar{u} = \underline{u}$, $\bar{v} = \underline{v}$.

By the definition of \bar{v}_n and \underline{v}_n , we have

$$\underline{v}_n = \frac{(\underline{u}_n + k_2)r_2}{c_2} - \epsilon, \quad \bar{v}_n = \frac{(\bar{u}_n + k_2)r_2}{c_2} + \epsilon, \quad (4.35)$$

thus

$$\bar{v}_n - \underline{v}_n = \frac{r_2}{c_2} (\bar{u}_n - \underline{u}_n) + 2\epsilon. \quad (4.36)$$

According to the definitions of $\bar{u}_n, \underline{u}_n$ and (4.36), we have

$$\begin{aligned}
& \bar{u}_n - \underline{u}_n \\
&= \frac{\alpha e^{-\gamma\tau} - \beta k_1 + \sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4\beta(\alpha e^{-\gamma\tau} k_1 - c_1 \underline{v}_n)}}{2\beta} \\
&\quad - \frac{\alpha e^{-\gamma\tau} - \beta k_1 + \sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4\beta(\alpha e^{-\gamma\tau} k_1 - c_1 \bar{v}_n)}}{2\beta} + 2\epsilon \\
&= - \frac{4c_1(\underline{v}_n - \bar{v}_n)\beta}{2\beta \left(\sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4\beta(\alpha e^{-\gamma\tau} k_1 - c_1 \underline{v}_n)} + \sqrt{(\alpha e^{-\gamma\tau} - \beta k_1)^2 + 4\beta(\alpha e^{-\gamma\tau} k_1 - c_1 \bar{v}_n)} \right)} \\
&\quad + 2\epsilon \\
&< - \frac{c_1(\underline{v}_n - \bar{v}_n)}{(\alpha e^{-\gamma\tau} - \beta k_1)} + 2\epsilon.
\end{aligned} \tag{4.37}$$

Let $n \rightarrow \infty$, we have

$$(\bar{u} - \underline{u}) \leq \frac{c_1(r_2/c_2)(\bar{u} - \underline{u}) + 2\epsilon}{\alpha e^{-\gamma\tau} - \beta k_1} + 2\epsilon, \tag{4.38}$$

hence

$$\left(\alpha e^{-\gamma\tau} - \beta k_1 - c_1 \frac{r_2}{c_2} \right) (\bar{u} - \underline{u}) \leq (1 + \alpha e^{-\gamma\tau} - \beta k_1) 2\epsilon. \tag{4.39}$$

By (4.10), we know that $\alpha e^{-\gamma\tau} - \beta k_1 - (c_1 r_2)/c_2 > 0$ and $(1 + \alpha e^{-\gamma\tau} - \beta k_1) > 0$. Note that ϵ can be arbitrarily small, that is, letting $\epsilon \rightarrow 0$ leads to the conclusion that $\bar{u} = \underline{u}$. From (4.36) and letting $n \rightarrow \infty$, we also conclude that $\bar{v} = \underline{v}$. The proof is complete. \square

5. Discussion

In this paper, we consider a Leslie-Gower predator-prey type model that incorporates the prey "age" structure (an extension of the ODE model in the study by Aziz-Alaoui and Daher Okiye [11]). We derive the "conditional" basic demographic number (\mathfrak{R}_0) for the prey, that is the value of \mathfrak{R}_0 when the predator's population size has reached its steady state in the absence of prey. We obtain sufficient conditions that ensure the boundedness of solutions as well as permanence of System (1.11) ($\mathfrak{R}_0 > p_0 > 1$). Second, we derive sufficient conditions for the local stability of nonnegative equilibria of Model (1.11). We show that $E_0 = (0, 0)$ and $E_1 = (\alpha e^{-\gamma\tau}/\beta, 0)$ are unstable, $E_2 = (0, k_2 r_2/c_2)$ is unstable if $\mathfrak{R}_0 > 1$ (stable if $\mathfrak{R}_0 < 1$), and the positive equilibrium E_3 exists when $\mathfrak{R}_0 > 1$. Finally, through the application

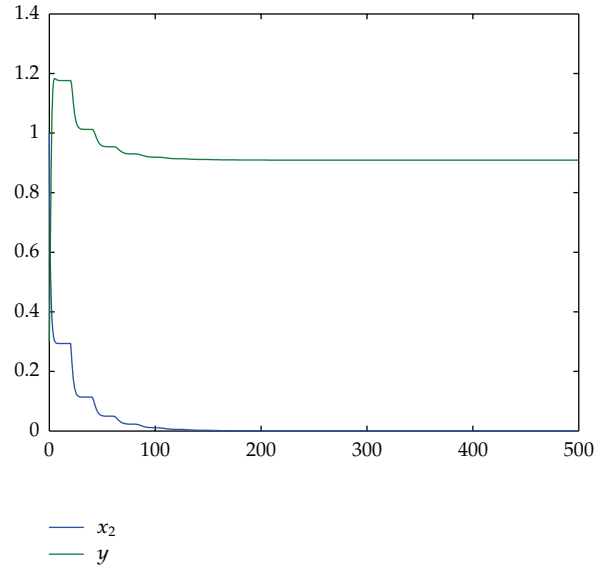


Figure 1: The boundary equilibrium $E_2 = (0, k_2 r_2 / c_2)$ of System (1.11) is globally asymptotically stable.

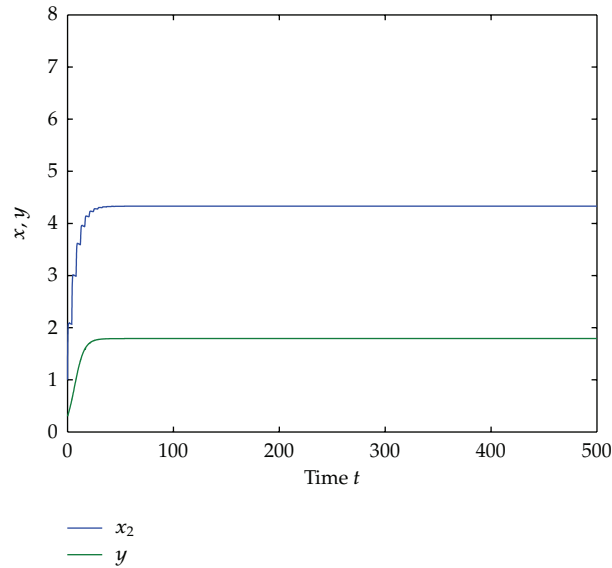


Figure 2: The positive equilibrium E_3 of System (1.11) is globally attractive.

of the comparison principle, sufficient conditions for the global attractivity of nonnegative equilibria are obtained. We prove that E_2 is globally asymptotically stable when $\mathfrak{R}_0 < p_1 < 1$. We conclude that the incorporation of a delay (“age” structure in the prey) does not change the asymptotic behavior of the model when some restrictions are imposed on the effect of such delay. Here we provide two numerical examples to illustrate our main results.

Example 5.1. If $\alpha = 12$, $\gamma = 0.2$, $\beta = 1$, $c_1 = 0.5$, $c_2 = 1.1$, $k_1 = 1$, $k_2 = 1$, $r_2 = 1$, and $\tau = 20$ then the conditions of Theorem 4.1 are satisfied and the equilibrium $E_2 = (0, k_2 r_2 / c_2)$ of System (1.11) is globally asymptotically stable (see Figure 1).

Example 5.2. If $\alpha = 12$, $\gamma = 0.2$, $\beta = 1.2$, $c_1 = 0.5$, $c_2 = 2$, $k_1 = 0.25$, $k_2 = 10$, $r_2 = 0.25$, and $\tau = 4$ then the conditions of Theorem 4.5 are satisfied and the positive equilibrium E_3 of system (1.11) is globally attractive (see Figure 2).

The length of the time delay τ plays an important role on the stability of the positive equilibrium of System (1.11). Since the delay also appears in the coefficient of the variable $x_2(t - \tau)$ in the second equation of (1.8) linearization at the positive equilibrium is algebraically complicated. This complication prevents us from analytically computing the precise parameter regimes where the positive equilibrium switches its stability as the delay τ is increased. Furthermore, because the positive equilibrium depends on τ then some of the existing stability switch methods are unapplicable (see [26]). Recently Beretta and Kuang [29] have introduced a systematic method for the study of associated characteristic equations. However, their approach is computer assisted and consequently, requires the identification of suitable choices for the model parameters. We hope to apply their method to Model (1.8) in near future.

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