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Abstract

In this article we study the behavior of a nonlinear age-structured predator-prey model that is a generalization of Lotka-Volterra equations. We prove global existence, uniqueness and positivity of the solution using a semigroup approach. We make some analytically explicit thresholds that ensure, or not depending of their values, the boundedness of the solution and time asymptotic stability of equilibria. The latter theoretical results and their limits are enlightened by simulations.

1 Introduction

The relationships between a predator and its prey are subject of numerous studies in ecology. Since the first mathematical model describing over time such trophic interactions was introduced (see [23], [44]), the

2010 *Mathematics subject classification.* (35B35) 35B40 65M08 (65M25) 92D40 92D50 (92D25)
Key words and phrases. Lotka Volterra, nonlinear EDP, stability, bifurcation, semigroup theory.

so-called Lotka Volterra equations, predator-prey models are still a wide subject of study in population dynamics. Most of them are described using ODEs and sometimes using PDEs when adding a diffusive part to model spatial dispersion properties (see for instance [15], [17] and more generally the book of Murray [28]).

Furthermore, it can be important to take into account an age-structure in the dynamics of the considered interacting species, the prey size being recognized as a key factor of a selective predation [39]. The literature about predator-prey models with age-structure offers several compartmental ODE models (see [1], [11], [12], [21] and references therein), but to our knowledge very few articles take into account a continuous age variable: the first model was proposed in [13] by Gurtin and Levine, in which they prove that under some specific assumptions on the demographic parameters, the model can be transformed into a more classical ODE problem. Then most of the following articles on this subject used the same kind of assumptions on the parameters and consequently get some stability results through the ODE models (see Levine [18], Thompson [42], Coleman and Frauenthal [4], Saleem [35, 36] for the specific case of egg-eating predator models, also Cushing and Saleem [5], [37] and Luo, He and Li [24] for more general models). Two articles focused on some qualitative properties of the solutions, that are the existence of a time-periodic solution when assuming a constant mortality rate for the prey by Levine in [19], and boundedness results by Venturino in [43]. In the case where the predation depends only on the total quantity of prey, Li studied in [20] the existence and stability of three biologically meaningful equilibria corresponding to the extinction and the coexistence of both species and the persistence of the prey specie only. However, it is more realistic and relevant to assume that the predation depends on the age of the prey. More recently, based on the model of Cushing and Saleem where the predator is age-structured, two articles analyzed the effect of a maturation period and a delay for a birth process (see Liu [22, 40]). Finally, one can also note that some age-structured predator-prey models were also used in epidemiology, coupled with SI models (see Arino, Delgado and Molina-Becerra [2, 6]).

The goal of the present work is to study predator-prey interactions by incorporating a continuous age-structure in the prey densities, leading to a PDE predator-prey model that would generalize the Lotka Volterra equations. Then we exhibit some time asymptotic properties of the solutions through a stability analysis of the PDE problem. These latter properties then allow us to study how the age-structure may alter the dynamics of the classical Lotka Volterra equations (i.e. with linear reponse) described by ODEs.

As introduced by Sharpe and Lotka in [38] and by McKendrick in [26], structuring individuals by a continuous age variable leads to the formulation of a linear PDE of transport type. This single PDE model has been extensively studied by Gurtin and MacCamy [14], Webb [45], Metz and Diekmann [27], Thieme [41], Perthame [33] and Magal [25]. In our case, the interactions between species due to predation induce a nonlinear part in the PDE problem as described in the following predator-prey system:

$$\left\{\begin{array}{rcl} \frac{\partial x}{\partial t}(t,a)+\frac{\partial x}{\partial a}(t,a) & = & -\mu(a)x(t,a)-y(t)\gamma(a)x(t,a), \\ \frac{dy}{dt}(t) & = & \alpha y(t)\int_0^\infty \gamma(a)x(t,a)\mathrm{d}a-\delta y(t), \\ x(t,0) & = & \int_0^\infty \beta(a)x(t,a)da \ \forall t\geq 0, \\ x(0,a) & = & x_0(a)\ \forall a\geq 0 \text{ and } y(0)=y_0, \end{array}\right. \tag{1}$$

with $x(t,a)$ and $y(t)$ that are respectively the density of preys at age $a \geq 0$ and time $t \geq 0$ and the density of predators at time t where:

- $\alpha \in (0,1)$, $\delta > 0$ are constant parameters that respectively denote the assimilation coefficient of ingested preys and the basic mortality rate of the predator;
- $\mu, \gamma, \beta \in L^\infty_+(\mathbb{R}_+)$ are age-dependent functions that represent the basic mortality rate of the preys, the predation rate and the birth rate for the preys.

In all that follows, we assume the following on parameter μ:

$$\exists\, \mu_0 > 0 \text{ such that } \mu(a) \geq \mu_0 \text{ f.a.e. } a \geq 0. \tag{H1}$$

A consequence of (H1) is that $\int^\infty \mu(a)\mathrm{d}a = \infty$, implying that $a \mapsto e^{-\int_0^a \mu(l)dl}$ is a probability function, this latter describing the survival until age a.

Note that, linked to Problem (1), the total population at time t is given by

$$y(t) + \int_0^\infty x(t,a)\ \mathrm{d}a$$

and the total ingested preys by the predators by

$$\alpha \int_0^\infty \gamma(a)x(t,a)\ \mathrm{d}a.$$

To study nonlinear problems with an age-structure, the main approaches that have been developped are the use of Volterra formulation (see [16], [45]), the use of suns and stars spaces (see [8]) and by semigroup theory (see [45]). In the present work, we focus on semigroup theory, that is a useful tool to study the well-posedness of the problem and also the asymptotic properties of the solution in the nonlinear case.

This article is structured as follows: in Section 2 we tackle the well posedness of the PDE problem and prove that the solution is global in time. These results are obtained by considering model (1) as a semilinear abstract Cauchy Problem and using semigroup theory. Section 3 is devoted to the main results of the article: one can exhibits an explicit formulation of a threshold for the extinction of the total population, by performing a stability analysis of equilibria of Problem (1). The use of spectral theory for the differential operator of the PDE problem, and some compactness properties of the nonlinear part of the problem are the main arguments to achieve that goal. Results about boundedness and persistence are also proved, using upper bounds of the characteristics of the PDE equation. Some numerical computations that enlighten the theoretical results are performed in Section 4. Finally, some remarks are postponed in Section 4.3.

The reader will find in Appendix a brief reminder about Lotka Volterra model and the link with the age-structured predator-prey model studied in this article.

2 Well Posedness and Positivity

2.1 Notations

In all that follows, consider the Banach Spaces $X = L^1(\mathbb{R}_+) \times \mathbb{R}$ with the product norm and his nonnegative cone defined by $X_+ = L^1_+(\mathbb{R}_+) \times \mathbb{R}_+$.

We consider the following differential operator $A : D(A) \subset X \to X$,

$$D(A) = \{(\phi, z) \in X, \phi \in W^{1,1}(\mathbb{R}_+) \text{ and } \phi(0) = \int_0^\infty \beta(a)\phi(a)da\},$$

$$A = \begin{pmatrix} \mathcal{D} & 0 \\ 0 & -\delta \end{pmatrix}$$

with

$$\mathcal{D}\phi = -\frac{d\phi}{da} - \mu\phi$$

and the function $f : X \to X$ given by

$$f(\phi, z) = \begin{pmatrix} -z\gamma(.)\phi(.) \\ \alpha z \int_0^\infty \gamma(a)\phi(a)\mathrm{d}a \end{pmatrix},$$

so that Problem (1) rewrites as the following abstract Cauchy Problem:

$$\begin{cases} \dfrac{d}{dt}\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = A\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} + f(x(t), y(t)), \\ (x(0), y(0)) = (x_0(.), y_0) \in X. \end{cases} \tag{2}$$

2.2 Linear Part

To perform an analysis of Problem (2), we start by a study of the differential operator $(A, D(A))$. The same arguments that developped in [3] prove that $D(A)$ is a dense subset of X. Furthermore, as proved in [45] and [30] for such an operator, there exists real values λ_0 and ω_0 satisfying $\min(\lambda_0, \omega_0) \geq \|\beta\|_{L^\infty(\mathbb{R}_+)} - \mu_0$ such that $A - \lambda_0 I$ is dissipative and $(\lambda I - A)$ is surjective for every $\lambda \geq \omega_0$. Then the classical Lumer-Phillips theorem implies that A is the infinitesimal generator of a positive C_0-semigroup $(T_A(t))_{t\geq 0}$ that is quasicontractive: $\|T_A(t)\|_X \leq e^{\omega t}$ for all $t \geq 0$ and $\omega \geq \|\beta\|_{L^\infty(\mathbb{R}_+)} - \mu_0$.

2.3 Local existence, Uniqueness and Positivity

Since the nonlinear part f of Problem (2) is quadratic, it is clearly a locally Lipschitz continuous function on X. A consequence of [29] is that for every $(x_0, y_0) \in X$, there exists $t_{\max} \leq +\infty$ such that Problem (2) has a unique mild solution $u \in C([0, t_{\max}(x_0, y_0)), X)$ where $t_{\max}(x_0, y_0) \leq \infty$. Furthermore, this solution is defined in a classical sense whenever $(x_0, y_0) \in D(A)$.

We now prove that for any initial condition $(x_0, y_0) \in X_+$, the corresponding solution remains non-negative on $[0, t_{\max})$. To achieve that goal, we need the two following lemmas. Their proof can be found in the articles [31, 32].

Let us define $B_m = \{(\phi, z) \in X : \|(\phi, z)\|_X \leq m\}$ for $m > 0$.

Lemma 2.1. *$\exists K > 0$ such that $\forall m > 0$ and $\forall((\phi_1, z_1), (\phi_2, z_2)) \in B_m^2$, we have $\|f(\phi_1, z_1) - f(\phi_2, z_2)\|_X \leq m\, K\|(\phi_1, z_1) - (\phi_2, z_2)\|_X$.*

Lemma 2.2. *$\forall m > 0, \exists \lambda_m \in \mathbb{R}$ such that $(\phi, z) \in B_m \cap X_+ \Rightarrow f(\phi, z) + \lambda_m(\phi, z) \in X_+$. In fact, it is sufficient to take $\lambda_m > m\|\gamma\|_{L^\infty(\mathbb{R}_+)}$.*

Proposition 2.1. *$\forall (x_0, y_0) \in X_+, \exists t_{\max}(x_0, y_0) \leq \infty$ such that Problem (2) has a unique mild solution $u \in C([0, t_{\max}(x_0, y_0)), X_+)$.*

Proof. Let $m > 0$ and $\lambda_m \geq m\|\gamma\|_{L^\infty(\mathbb{R}_+)}$. Let us define the differential operator $A_m = A - \lambda_m I$ and the function $f_m = f + \lambda_m I$. Then A_m is the infinitesimal generator of a positive C_0-semigroup $(T_{A_m}(t))_{t\geq 0}$ on X_+ that satisfies $\|T_{A_m}(t)\|_X \leq e^{-(\lambda_m+\omega)t}$ for every $t \geq 0$.

We then define $r_m = 2\|(x_0, y_0)\|_X \sup_{s\in[0,1]} \|T_{A_m}(s)\| > 0$, suppose m large enough to have $r_m \leq m$ and we denote $X_+^{r_m} = X_+ \cap B_{r_m} \subset B_m$. Then considering $\tau > 0$ such that:

$$\tau \leq \min\left(1, \frac{1}{2(Kr_m + \lambda_m) \times \sup\limits_{s\in[0,1]} \|T_{A_m}(s)\|_X}\right),$$

a consequence of lemmas 2.1 and 2.2 is that the linear operator $G : C([0,\tau], X) \to C([0,\tau], X)$ defined by

$$G(x(t,\cdot), y(t)) = T_{A_m}(t).\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} + \int_0^t T_{A_m}(t-s) f_m \begin{pmatrix} x(s,\cdot) \\ y(s) \end{pmatrix} ds$$

is a $1/2$-shrinking operator on $C([0,\tau], X_+^{r_m})$ that preserves this latter space. The Banach-Picard theorem and some classical time extending properties of the solution then yield the proposition. □

2.4 Global existence

Theorem 2.3. *For all $(x_0, y_0) \in X_+$, Problem (2) has a unique mild solution $(x, y) \in C(\mathbb{R}_+, X_+)$.*

Proof. Consider $(x, y) \in C([0, t_{\max}), X_+)$ the solution of (2) and suppose by contradiction that $t_{\max} < \infty$. Let us first prove that for every $t \geq 0$, $\|x(t,\cdot)\|_{L^1(\mathbb{R}_+)} < \infty$.

A direct consequence of the positivity is that $\partial_t x(t,a) + \partial_a x(t,a) \leq -\mu(a)x(t,a)$. It is classical, using the characteristics of the PDE equation, that an implicit formulation of the solution of $\partial_t x(t,a) + \partial_a x(t,a) = -\mu(a)x(t,a)$ that satisfies the loopback boundary condition in (1) is given by:

$$x(t,a) = \begin{cases} x_0(a-t)e^{-\int_{a-t}^a \mu(s)\mathrm{d}s} & \text{if } a \geq t, \\ \psi(t-a)e^{-\int_0^a \mu(s)\mathrm{d}s} & \text{if } a < t, \end{cases} \tag{3}$$

where $\psi(t) = x(t, 0)$ satisfies:

$$\begin{aligned} \psi(t) &= \textstyle\int_0^t \beta(u)\psi(t-u)e^{-\int_0^u \mu(s)\mathrm{d}s}\mathrm{d}u + \int_t^\infty \beta(u)x_0(u-t)e^{-\int_{u-t}^u \mu(s)\mathrm{d}s}\mathrm{d}u \\ &= \textstyle\int_0^t \psi(u)\beta(t-u)e^{-\int_0^{t-u} \mu(s)\mathrm{d}s}\mathrm{d}u + \int_0^\infty \beta(u+t)x_0(u)e^{-\int_u^{u+t} \mu(s)\mathrm{d}s}\mathrm{d}u. \end{aligned} \tag{4}$$

From equation (4) we define two operators $S_1 : L^1(0,t) \to L^1(0,t)$ and $S_2 : L^1(\mathbb{R}_+) \to L^1(0,t)$ for every $\psi \in L^1(0,t)$, $\phi \in L^1(\mathbb{R}_+)$ and $\xi \in [0,t]$ by:

$$\begin{aligned} S_1\psi(\xi) &= \textstyle\int_0^\xi \psi(y)\beta(\xi-y)e^{-\int_0^{\xi-y}\mu(s)\mathrm{d}s}dy, \\ S_2\phi(\xi) &= \textstyle\int_0^\infty \phi(y)\beta(y+\xi)e^{-\int_y^{\xi+y}\mu(s)ds}\mathrm{d}y, \end{aligned}$$

so we formally get the following representation:

$$x(t,a) = \begin{cases} x_0(a-t)e^{-\int_{a-t}^a \mu(s)\mathrm{d}s} & \text{if } a \geq t, \\ (I-S_1)^{-1}S_2x_0(t-a)e^{-\int_0^a \mu(s)\mathrm{d}s} & \text{if } a < t. \end{cases}$$

This latter equality is well defined. Indeed, as proved in [2], S_1 is a Volterra operator, then for all $\lambda \in \mathbb{C} \setminus \{0\}$ and $\psi \in L^1(0,t)$ fixed, we have a unique function $\varphi \in L^1(0,t)$ such as $(\lambda I - S_1)\varphi = \psi$. Thus $(I-S_1)^{-1}$ is well defined from $L^1(0,t)$ to $L^1(0,t)$.
Since $x_0 \in L^1(\mathbb{R}_+)$ then $(I-S_1)^{-1}S_2x_0 \in L^1(0,t)$. So for all $t \geq 0$ we have:

$$\|x(t,\cdot)\|_{L^1(\mathbb{R}_+)} \leq \int_t^\infty x_0(a-t)\mathrm{d}a + \int_0^t (I-S_1)^{-1}S_2x_0(t-a)\mathrm{d}a < \infty.$$

Moreover, straightforward upper bounds imply that for every $t \geq 0$, $y'(t) \leq \alpha M y(t)\|\gamma\|_{L^\infty(\mathbb{R}_+)}$ where $M = \max_{s\in[0,t_{\max}]}\|x(s,\cdot)\|_{L^1(\mathbb{R}_+)} < \infty$. Thus, if $t_{\max} < \infty$, an integration of the differential inequality would lead to $y(t) \leq y_0 e^{\alpha M t_{\max}\|\gamma\|_{L^\infty}} < \infty$, implying a contradiction with the fact that we have either $\lim_{t\to t_{\max}}\|x(t,\cdot)\|_{L^1(\mathbb{R}^+)} = \infty$ or $\lim_{t\to t_{\max}}|y(t)| = \infty$. Finally $t_{\max} = \infty$ and the solution is global in time. □

We finally get existence and uniqueness of a global nonnegative solution. The goal is now to analyze the asymptotic behavior of the solutions.

3 Stability, persistence and boundedness

Suppose that we have a positive initial condition $(x_0, y_0) \in X_+^*$, where $X_+^* = \{(x_0,y_0) \in X_+ : \int_0^\infty x_0(a)\mathrm{d}a > 0 \text{ and } y_0 > 0\}$. Let us define a_1 by:

$$a_1 = \sup\{a \geq 0 : |\mathrm{supp}(\gamma) \cap (0,a)| = 0\} < \infty. \tag{5}$$

Remark 1. *This definition implies that there exists $\gamma_- > 0$ and $a_2 > a_1$ such that $\int_{a_1}^{a_2} \gamma(a)\mathrm{d}a \geq \gamma_-$. The case $a_1 > 0$ translates the fact that the youngest preys are not considered as a resource availability for the predators.*

In all that follows, let us consider the following thresholds:

$$R_0 = \int_0^\infty \beta(a) e^{-\int_0^a \mu(s)\mathrm{d}s} \mathrm{d}a, \tag{6}$$

$$R_- = \int_0^{a_1} \beta(a) e^{-\int_0^a \mu(s)\mathrm{d}s} \mathrm{d}a. \tag{7}$$

Note that, similarly to the basic reproductive number in the epidemiological case (see [7]), the R_0 value represents the average number of offspring that is produced over the lifetime by one prey and in a context with no predation. This threshold will give a characterization of extinction of the total population.
In the same idea, the R_- value represents the offspring produced by one prey from his birth, until it begins to be hunted by the predator. We will get an unboundedness result from this threshold.

3.1 Equilibria

We first look for steady points of problem (1).
The point $(x^*, y^*) \in X$ will be an equilibrium if it is a solution of the following system:

$$\begin{cases} (x^*)'(a) &= -\mu(a)x^*(a) - y^*\gamma(a)x^*(a), \\ 0 &= \alpha y^* \int_0^\infty \gamma(a)x^*(a)da - \delta y^*, \\ x^*(0) &= \int_0^\infty x^*(a)\beta(a)da. \end{cases}$$

An integration then gives:

$$\begin{cases} x^*(a) = x^*(0)e^{-\int_0^a \mu(s)\mathrm{d}s - y^*\int_0^a \gamma(s)\mathrm{d}s}, \\ x^*(0)\left[1 - \int_0^\infty \beta(a)e^{-\int_0^a \mu(s)\mathrm{d}s - y^*\int_0^a \gamma(s)\mathrm{d}s}\mathrm{d}a\right] = 0, \\ y^*\left[\alpha\int_0^\infty \gamma(a)x^*(a)\mathrm{d}a - \delta\right] = 0. \end{cases}$$

Note that $R_- \leq R_0$ and we get the following proposition:

Proposition 3.1.

1. *If $R_0 < 1$ or if ($R_0 > 1$ and $R_- \geq 1$) then there is a unique equilibrium that is $E_0 = (0, 0)$;*

2. *If $R_0 = 1$ and $R_- < 1$ then for all $\xi \in [0, \infty)$, $E_{1,\xi} = (x^*_{1,\xi}, 0)$ is an equilibrium, where $x_{1,\xi}$ is defined by $x^*_{1,\xi}(a) = \xi e^{-\int_0^a \mu(s)\mathrm{d}s}$. In particular $E_{1,0} = E_0$;*

3. *If $R_0 = 1$ and $R_- = 1$ then $\forall \xi \geq 0$, $E_{1,\xi}$ is an equilibrium and $E_{2,\xi} = (x^*_{2,\xi}, \xi)$ also, where:*

$$x^*_{2,\xi}(a) = x^*_{2,\xi}(0) e^{-\int_0^a \mu(s)\mathrm{d}s - \xi \int_0^a \gamma(s)\mathrm{d}s},$$
$$x^*_{2,\xi}(0) = \frac{\delta}{\alpha}\left[\int_0^\infty \gamma(a) e^{-\int_0^a \mu(s)\mathrm{d}s - \xi \int_0^a \gamma(s)\mathrm{d}s} \mathrm{d}a\right]^{-1};$$

4. *If $R_0 > 1$ and $R_- < 1$ then there are the trivial equilibrium E_0 and the positive equilibrium $E_2 = (x^*_2, y^*) = (x_{2,y^*}, y^*)$ with y^* that satisfies:*

$$\int_0^\infty \beta(a) e^{-\int_0^a \mu(s)\mathrm{d}s - y^* \int_0^a \gamma(s)\mathrm{d}s} da = 1. \tag{8}$$

3.2 Stability

To perform the stability analysis, we exhibit some spectral properties of the differential operator A and of the semigroup $\{T_A(t)\}_{t\geq 0}$. Before proceeding, we introduce some notations and recall some definitions of spectral theory.

Denoting $\rho(A)$ the resolvent set of $A : D(A) \subset X \to X$, we define the *spectrum* $\sigma(A)$, the *point spectrum* $\sigma_p(A)$ and the *spectral bound* $s(A)$ by:

$$\sigma(A) = \mathbb{C} \backslash \rho(A),$$
$$\sigma_p(A) = \{\lambda \in \mathbb{C},\ \lambda I - A \text{ is not injective}\},$$
$$s(A) = \sup\{\mathrm{Re}\,\lambda,\ \lambda \in \sigma(A)\}.$$

Denoting $\mathcal{L}(X)$ the set of bounded linear operators on X and $\mathcal{K}(X)$ the subset of compact operators on X, we then define the *essential norm* $\|L\|_{\text{ess}}$ of $L \in \mathcal{L}(X)$ by:

$$\|L\|_{\text{ess}} = \inf_{K \in \mathcal{K}(X)} \|L - K\|_X.$$

We recall that the quotient $\mathcal{L}(X)/_{\mathcal{K}(X)}$ is called the Calkin algebra which, when providing the norm

$$\|\hat{L}\| = \|L\|_{\text{ess}},$$

where $\hat{L} = L + \mathcal{K}(X)$, is a Banach algebra with unit (see [10] and references cited in for details). The growth bound $\omega_0(A) \in [-\infty, \infty)$ of A is defined by:

$$\omega_0(A) = \lim_{t\to\infty} \frac{1}{t} \ln\left(\|T_A(t)\|_X\right),$$

and the essential growth bound $\omega_{\text{ess}}(A) \in [-\infty, \infty)$ of A is:

$$\omega_{\text{ess}}(A) = \lim_{t\to\infty} \frac{1}{t} \ln\left(\|T_A(t)\|_{\text{ess}}\right).$$

The following theorem that gives a characterization of the growth bound using the spectrum of A was proved by Engel and Nagel [10].

Theorem 3.1. *The growth bound of A satisfies*

$$\omega_0(A) = \max\{\omega_{\text{ess}}(A), s(A)\},$$

and for every $\omega > \omega_{\text{ess}}(A)$ the set $\sigma_\omega = \{\lambda \in \sigma(A),\ Re(\lambda) > \omega\}$ is finite and composed of finite algebraic multiplicity elements.

A classical result states that (see [46]):

$$\omega > \omega_{\text{ess}}(A) \Rightarrow \sigma_\omega \subset \sigma_p(A).$$

Remark 2. *Due to the quotient defined previously, the use of the Calkin algebra shows well why the compact operators do not affect the growth bound values. More specifically, one gets $\omega_{\text{ess}}(A+K) = \omega_{\text{ess}}(A)$ for every $K \in \mathcal{K}(X)$.*

The following theorem (see [34] or [45]), gives some conditions for an equilibrium to be stable.

Theorem 3.2. *Consider E an equilibrium of Problem (2). Then the following assertions hold:*

1. *If $\omega_0(A + D_E f) < 0$ then E is locally exponentially asymptotically stable for Problem (2);*
2. *If $\omega_0(A + D_E f) > 0$ and $\omega_{\text{ess}}(A + D_E f) \leq 0$ then E is unstable for Problem (2).*

In the context of Problem (1), the following result holds:

Theorem 3.3. *We have $\omega_{\text{ess}}(A + D_E f) \leq -\mu_0 < 0$.*

To prove Theorem 3.3, we start by a lemma dealing with some compactness properties about the differential of f. One can note that for every $E = (x^*, y^*) \in X$, the differential of f at an equilibrium E can be written as:

$$D_E f = (D_E f)_1 + (D_E f)_2 = \begin{pmatrix} -y^*\gamma & 0 \\ 0 & 0 \end{pmatrix} + \begin{pmatrix} 0 & -\gamma x^* \\ \alpha y^* L_\gamma(\cdot) & \alpha \int_0^\infty \gamma(a) x^*(a) da \end{pmatrix},$$

where L_γ is the operator defined for some integrable function h on $\mathbb{R}_+$ by:

$$L_\gamma : h \mapsto \int_0^\infty \gamma(a)h(a)\mathrm{d}a. \tag{9}$$

Here is the compactness result:

Lemma 3.4. *The function f is in $C^1(X)$ and the operator $(D_E f)_2$ is compact.*

Proof. Since function $D_E f : X \to X$ is Lipschitz continuous, it is a bounded operator on the Banach space X and so $D_E f$ is continuous and f is in $C^1(X)$.
We now prove that $(D_E f)_2$ is compact.
Denoting $(D_E f)_2 = (G_1, G_2)^\top$ where $G_1 : X \to L^1(\mathbb{R}_+)$ and $G_2 : X \to \mathbb{R}$, we can easily check that G_2 has a finite dimensional range and is consequently compact. To prove the compactness of G_1 we use the classical Riesz-Fréchet-Kolmogorov (RFK) criterion in L^1 (see for instance Yosida [46]).
Let $h \in \mathbb{R}_+$ and $S \subset X$ be a bounded subset of X. Then there exists $M \in \mathbb{R}_+$ such that $\|(\phi, z)\|_X \leq M$ for every $(\phi, z) \in S$. Denoting by $\tau_h(\phi) = \phi(\cdot + h)$ the translation operator in L^1 we then have:

$$\begin{array}{rcl} \|\tau_h G_1(\phi, z) - G_1(\phi, z)\|_{L^1(\mathbb{R}^+)} & \leq & |z| \int_0^\infty |\gamma(a)x^*(a) - \gamma(a+h)x^*(a+h)|da \\ & \leq & M\|\tau_h(\gamma x^*) - (\gamma x^*)\|_{L^1(\mathbb{R}^+)}. \end{array}$$

Since $\gamma \in L^\infty(\mathbb{R}_+)$ and $x^* \in L^1(\mathbb{R}_+)$ then $\gamma x^* \in L^1(\mathbb{R}_+)$ and consequently we have:

$$\|\tau_h(\gamma x^*) - (\gamma x^*)\|_{L^1(\mathbb{R}_+)} \underset{h\to 0}{\to} 0.$$

It implies that:

$$\sup_{(\phi,z)\in S} \|\tau_h G_1(\phi, z) - G_1(\phi, z)\|_{L^1(\mathbb{R}_+)} \underset{h\to 0}{\to} 0. \tag{10}$$

Furthermore we can similarly prove, using the Lebesgue theorem, that

$$\sup_{(\phi,z)\in S} \int_r^\infty |G_1(\phi(a), z)|\mathrm{d}a \underset{r\to\infty}{\to} 0. \tag{11}$$

The consequence of (10)-(11) and the RFK criterion is the relative compactness of $G_1(S)$ in $L^1(\mathbb{R}_+)$. Finally, G_1 is compact and so is $(D_E f)_2$. □

We can now prove Theorem 3.3:

Proof. (Theorem 3.3)

Lemma 3.4 implies that for every equilibrium E, $\omega_{\text{ess}}(A + D_E f) = \omega_{\text{ess}}(A + (D_E f)_1)$, so we have to prove that $\omega_{\text{ess}}(A + (D_E f)_1) \le -\mu_0$.

Similarly to the proof of Theorem 2.3, we can calculate the concrete expression of the semigroup generated by $A + (D_E f)_1$ that is:

$$T_{A+(D_E f)_1}(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} = \begin{pmatrix} x_0(a-t)e^{-\int_{a-t}^{a}(\mu(s)+y^*\gamma(s))\mathrm{d}s}\mathbb{1}_{\{a\ge t\}} + \psi(t-a)e^{-\int_0^a(\mu(s)+y^*\gamma(s))\mathrm{d}s}\ \mathbb{1}_{\{a<t\}} \\ y_0 e^{-\delta t} \end{pmatrix},$$

where $\psi(t) = x(t,0)$.

We decompose the operator $T_{A+(D_E f)_1}$ in:

$$T_{A+(D_E f)_1}(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) = T_1(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) + T_2(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) + T_3(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a), \text{ with :}$$

$$\begin{aligned}
T_1(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) &= \begin{cases} (x_0(a-t)e^{-\int_{a-t}^{a}(\mu(s)+y^*\gamma(s))\mathrm{d}s}, 0) & \text{if } a \ge t, \\ (0,0) & \text{if } a < t. \end{cases} \\
T_2(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) &= \begin{cases} (0,0) & \text{if } a \ge t, \\ (\psi(t-a)e^{-\int_0^a(\mu(s)+y^*\gamma(s))\mathrm{d}s}, 0) & \text{if } a < t. \end{cases} \\
T_3(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) &= (0, y_0 e^{-\delta t}), \forall t \ge 0, a \ge 0.
\end{aligned}$$

The operator T_3 is compact because its range is a finite dimensional space.

For the operator T_1, we get the following upper bound:

$$\left\| T_1(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} \right\|_X \le \int_t^\infty x_0(a-t)e^{-\int_{a-t}^{a}\mu(s)\mathrm{d}s}\mathrm{d}a \le e^{-\mu_0 t}\int_0^\infty x_0(u)\mathrm{d}u$$

and consequently we get:

$$\|T_1(t)\|_X \le e^{-\mu_0 t}. \tag{12}$$

Let us define $\hat{S}_1 : L^1(0,t) \to L^1(0,t)$ and $\hat{S}_2 : L^1(\mathbb{R}_+) \to L^1(0,t)$ by:

$$\begin{aligned}
\hat{S}_1\psi(\xi) &= \int_0^\xi \psi(y)\beta(\xi - y)e^{-\int_0^{\xi-y}[\mu(s)+y^*\gamma(s)]\mathrm{d}s}\mathrm{d}y, \\
\hat{S}_2\phi(\xi) &= \int_0^\infty \phi(y)\beta(y+\xi)e^{-\int_y^{\xi+y}[\mu(s)+y^*\gamma(s)]\mathrm{d}s}\mathrm{d}y.
\end{aligned}$$

Thus we get the following expression for the operator T_2:

$$T_2(t)\begin{pmatrix} x_0 \\ y_0 \end{pmatrix}(a) = \begin{cases} (0,0) & \text{if } a \geq t, \\ \left(\left((I-\hat{S}_1)^{-1}\hat{S}_2 x_0(t-a)\right) e^{-\int_0^a (\mu(s)+y^*\gamma(s)\mathrm{d}s)}, 0\right) & \text{if } a < t. \end{cases}$$

We can show that $\hat{S}_1$ is bounded, so as $I-\hat{S}_1$. Since $(I-\hat{S}_1)^{-1}$ is well defined and $(I-\hat{S}_1)$ is bijective from $L^1(0,t)$ in itself, which is a Banach space, then $(I-\hat{S}_1)^{-1}$ is bounded.

Let us define the operator $\overline{S_2} : L^1(\mathbb{R}_+) \to L^1(0,t)$ by:

$$\overline{S_2}\phi(\xi) = \int_0^\infty \phi(y) c e^{-\int_y^{\xi+y}[\mu(s)+y^*\gamma(s)]\mathrm{d}s}\mathrm{d}y,$$

where c is a positive constant. Using the RFK criterion (see Lemma 3.4), we can prove that $\overline{S_2}$ is compact for every $c > 0$. Indeed, setting $h > 0$ and taking B a bounded subset of $L^1(\mathbb{R}_+)$ we get, for $\phi \in B$:

$$\begin{aligned} \|\tau_h\left(\overline{S_2}\phi\right) - \overline{S_2}\phi\|_{L^1(0,t)} &\leq c\int_0^t\int_0^\infty \phi(y)\left(e^{-\int_y^{\xi+y}[\mu(s)+y^*\gamma(s)]\mathrm{d}s} - e^{-\int_y^{\xi+y+h}[\mu(s)+y^*\gamma(s)]\mathrm{d}s}\right)\mathrm{d}y\mathrm{d}\xi \\ &\leq c\int_0^t\int_0^\infty \phi(y) e^{-\int_y^{\xi+y}[\mu(s)+y^*\gamma(s)]\mathrm{d}s}\left(1 - e^{-\int_{\xi+y}^{\xi+y+h}[\mu(s)+y^*\gamma(s)]\mathrm{d}s}\right)\mathrm{d}y\mathrm{d}\xi \\ &\leq c\int_0^t\int_0^\infty \phi(y)\left(1-e^{-h\|\mu\|_{L^\infty}}\right)\mathrm{d}y\mathrm{d}\xi \\ &\leq ct\left(1-e^{-h\|\mu\|_{L^\infty}}\right)\int_0^\infty \phi(y)\mathrm{d}y, \end{aligned}$$

which converges to 0 uniformly on B when h tends to 0 since B is bounded.
Therefore $\overline{S_2}$ is compact. Since for $c = \|\beta\|_{L^\infty}$ we have $\hat{S}_2\phi(x) \leq \overline{S_2}\phi(x)$ for all $\phi \in L^1(\mathbb{R}_+)$ and $x \in [0,t]$, then $\hat{S}_2$ is also compact and so is the operator T_2.
Finally since T_2 and T_3 are compact,

$$\begin{aligned} \|T_{A+(D_Ef)_1}(t)\|_{\mathrm{ess}} &= \|T_1(t)+T_2(t)+T_3(t)\|_{\mathrm{ess}} \\ &= \|T_1(t)\|_{\mathrm{ess}} \leq \|T_1(t)\|_X, \end{aligned}$$

and consequently to (12),

$$\omega_{\mathrm{ess}}(A+(D_Ef)_1) \leq -\mu_0.$$

□

3.2.1 Equilibrium E_0

The differential of f at the point E_0 is the null matrix. So the linearized system to study is $u'(t) = Au(t)$. Using Theorem 3.1 and since $\omega_{\mathrm{ess}}(A) < 0$, we just need to study eigenvalues of A. We thus try to solve the following system:

$$\begin{cases} \dfrac{\partial x}{\partial t}(t,a) &= -\dfrac{\partial x}{\partial a}(t,a) - \mu(a)x(t,a), \\ y'(t) &= -\delta y(t), \\ x(t,0) &= \int_0^\infty x(t,a)\beta(a)da. \end{cases} \tag{13}$$

We are looking for solutions of the form $x(t,a) = \bar{x}(a)e^{\lambda t}$ and $y(t) = \bar{y}e^{\lambda t}$, $\lambda \in \mathbb{C}$. So, after replacing the latter expressions in the first equation of the system (13) then resolving the system, we get:

$$\begin{cases} \bar{x}(a) &= \bar{x}(0)e^{-\int_0^a [\lambda+\mu(s)]ds}, \\ \lambda\bar{y} &= -\delta\bar{y}, \\ \bar{x}(0) &= \int_0^\infty \bar{x}(a)\beta(a)\mathrm{d}a. \end{cases}$$

The second equation only admits $-\delta$ as eigenvalue, which is real and negative. Then, using the third equation, we obtain the following characteristic equation:

$$\int_0^\infty \beta(a)e^{-\int_0^a [\lambda+\mu(s)]\mathrm{d}s}\mathrm{d}a = 1.$$

We thus can show the following theorem, where R_0 is defined in (6):

Theorem 3.5.

1. *If $R_0 < 1$ then E_0 is globally stable.*

2. *If $R_0 > 1$ then E_0 is unstable.*

Proof. 1. Suppose that $R_0 < 1$. The real part of the characteristic equation gives:

$$\int_0^\infty \beta(a)e^{-\mathrm{Re}\,(\lambda)a}\cos(-\mathrm{Im}\,(\lambda)a)e^{-\int_0^a \mu(s)\mathrm{d}s}\mathrm{d}a = 1.$$

Then, if $\mathrm{Re}\,(\lambda) \geq 0$ we get $R_0 \geq 1$ that is absurd, so $\omega_0(A) < 0$ and E_0 is locally exponentially asymptotically stable from Theorem 3.2.

Now we prove the global stability. Using characteristics we get for $t \geq 0$:

$$x(t,a) \leq \begin{cases} x_0(a-t)e^{-\mu_0 t} & \text{if } a \geq t, \\ x(t-a,0)e^{-\int_0^a \mu(s)\mathrm{d}s} & \text{if } a < t. \end{cases}$$

Then $\psi(t) \leq \int_0^t \beta(u)\psi(t-u)e^{-\int_0^u \mu(s)\mathrm{d}s}\mathrm{d}u + \int_t^\infty \beta(u)x_0(u-t)e^{-\mu_0 t}\mathrm{d}u$.

Some standard upper bounds give: $\psi(t) \leq R_0 \max_{z\in[0,t]} \psi(z) + \|\beta\|_{L^\infty}\|x_0\|_{L^1}e^{-\mu_0 t}$.

Since $R_0 < 1$, we can consider $C \in]R_0, 1[$.

Then for $t = t^\star$ big enough, we get $\psi(t^\star) \le C\psi(\bar{t})$, where $\psi(\bar{t}) = \max_{z\in[0,t^\star]} \psi(z)$.

Moreover, $\forall h > 0, \psi(t^\star + h) \le C \max_{z\in[0,t^\star+h]} \psi(z)$ so $\psi(t^\star + h) \le C\psi(\bar{t})$, consequently $\psi(\bar{t}) = \max_{z\in[0,\infty[} \psi(z)$ and ψ is bounded.

For every $h > 0$, we get, by separating the integral, the following upper bound:

$$\psi(t^\star + h) \le \max_{u\in[0,t^\star]} \psi(u)\|\beta\|_{L^\infty} \frac{e^{-\mu_0 h}}{\mu_0} + R_0 \max_{u\in[t^\star,t^\star+h]} \psi(u) + \|\beta\|_{L^\infty}\|x_0\|_{L^1} e^{-\mu_0(t^\star+h)}.$$

Since the first and the third terms go to 0 when h tends to ∞, then we can find $h_1 > 0$ such that $\forall h \ge h_1, \psi(t^\star + h) \le C^2\psi(\bar{t})$.

Using the same method, we can find $h_2 > h_1$ such that $\forall h \ge h_2 : \psi(t^\star + h) \le C^3\psi(\bar{t})$.

Then by induction we get: $\forall n \in \mathbb{N}, \exists h_n > 0$ such that $\forall h \ge h_n : \psi(t^\star + h) \le C^{n+1}\psi(\bar{t})$.

Since $C < 1$, we have $\lim_{n\to\infty} C^{n+1} = 0$ and $\lim_{t\to\infty} \psi(t) = 0$.

Then using the implicit formulation (3) of $x(t, a)$ along the characteristics and some basical upper bounds we get:

$$\|x(t, .)\|_{L^1(\mathbb{R}_+)} \le e^{-\mu_0 t}\|x_0\|_{L^1(\mathbb{R}_+)} + e^{-\mu_0 t} \int_0^t \psi(u)e^{\mu_0 u}\mathrm{d}u.$$

Moreover, for every $\kappa > 0$, there exists $T > 0$ such that $\psi(t) \le \kappa,\ \forall t \ge T$ and consequently:

$$\begin{aligned} \|x(t, .)\|_{L^1(\mathbb{R}_+)} &\le e^{-\mu_0 t}\|x_0\|_{L^1(\mathbb{R}_+)} + e^{-\mu_0 t} \int_0^T \psi(u)e^{u\mu_0}\mathrm{d}u + \kappa e^{-\mu_0 t} \int_T^t e^{u\mu_0}\mathrm{d}u \\ &\le e^{-\mu_0 t}\|x_0\|_{L^1(\mathbb{R}_+)} + e^{-\mu_0 t} \int_0^T \psi(u)e^{u\mu_0}\mathrm{d}u + \frac{\kappa}{\mu_0}. \end{aligned}$$

We know that for every $\kappa_2 > 0$, there exists $T_2 > T$ such that $e^{-\mu_0 t} \le \kappa_2, \forall t \ge T_2$. Then we get:

$$\|x(t, .)\|_{L^1(\mathbb{R}_+)} \le \kappa_2\|x_0\|_{L^1(\mathbb{R}_+)} + \kappa_2 \int_0^T \psi(u)e^{u\mu_0}\mathrm{d}u + \frac{\kappa}{\mu_0}.$$

Now, take $\varepsilon > 0$ and define:

$$\kappa = \frac{\varepsilon\mu_0}{3}, \qquad \kappa_2 = \frac{\kappa}{\mu_0} \min\left(\frac{1}{\|x_0\|_{L^1(\mathbb{R}_+)}}, \frac{1}{\int_0^T \psi(u)e^{u\mu_0}\mathrm{d}u}\right).$$

Then for every $t \ge T_2$ we have $\|x(t, .)\|_{L^1(\mathbb{R}_+)} \le \varepsilon$. Consequently $\lim_{t\to\infty} \|x(t, .)\|_{L^1(\mathbb{R}_+)} = 0$.

Finally, with the second equation of (1), we get $\lim_{t\to\infty} y(t) = 0$ and the global stability of E_0 follows.

2. Suppose that $R_0 > 1$ and define the function g by:

$$g : \lambda \mapsto \int_0^{\infty} \beta(a) e^{-\lambda a} e^{-\int_0^a \mu(s)\mathrm{d}s} \mathrm{d}a.$$

   Then g is strictly decreasing, with $g(0) = R_0 > 1$. There consequently exists $\lambda > 0$ such that $g(\lambda) = 1$, so $\omega_0(A) > 0$ and since $\omega_{\mathrm{ess}}(A) \leq 0$, Theorem 3.2 implies that E_0 is unstable.

□

Remark 3. *We can see that in the case $R_0 < 1$, the total population is bounded.*

3.2.2 Equilibria $E_{1,\xi}$

Let $\xi > 0$ and consider the equilibrium $E_{1,\xi}$. Then the differential of f at the point $E_{1,\xi}$ is given by:

$$D_{E_{1,\xi}} f = \begin{pmatrix} 0 & -\gamma x^*_{1,\xi} \\ 0 & \alpha \int_0^{\infty} \gamma(a) x^*_{1,\xi}(a)\mathrm{d}a \end{pmatrix}.$$

The linearized system is thus:

$$\frac{\mathrm{d}u}{\mathrm{d}t}(t) = (A + D_{E_{1,\xi}} f) u(t).$$

Once again we just need to study eigenvalues of the operator $A + D_{E_{1,\xi}}$, so we study the following system:

$$\begin{cases} \bar{x}(a) &= \bar{x}(0) e^{-\int_0^a [\lambda + \mu(s)]\mathrm{d}s} - \gamma(a) x^*_{1,\xi}(a) \bar{y}, \\ \lambda \bar{y} &= -\delta \bar{y} + \alpha \bar{y} \int_0^{\infty} \gamma(a) x^*_{1,\xi}(a)\mathrm{d}a, \\ \bar{x}(0) &= \int_0^{\infty} \bar{x}(a) \beta(a)\mathrm{d}a. \end{cases} \tag{14}$$

Let us denote :

$$S = \frac{\delta}{\alpha} \left[\int_0^{\infty} \gamma(a) e^{-\int_0^a \mu(s)\mathrm{d}s} \mathrm{d}a \right]^{-1}.$$

Then we get the following instability theorem:

Theorem 3.6.

1. *If $\xi > S$ then the equilibrium $E_{1,\xi}$ is unstable.*

2. *If $\xi > 0$ then for every $\epsilon > 0$ there exists $\bar{\xi}(\epsilon)$ such that $E_{1,\bar{\xi}} \in B(E_{1,\xi}, \epsilon)$.*

Proof.

1. Let $\xi > S$. The second equation of (14) and the definition of $x^*_{1,\xi}$ given in Proposition 3.1 imply:
$$\lambda \bar{y} = \left(-\delta + \alpha \int_0^\infty \gamma(a) \xi e^{-\int_0^a \mu(s) \mathrm{d}s} \mathrm{d}a \right) \bar{y}.$$
Then defining $\bar{\lambda} = -\delta + \alpha \int_0^\infty \gamma(a)\xi e^{-\int_0^a \mu(s)\mathrm{d}s}\mathrm{d}a$, we get $\bar{\lambda} > 0$ since $\xi > S$.
The first and third equations of (14) give us:
$$\left(1 - \int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\bar{\lambda})\mathrm{d}s} \mathrm{d}a \right) \bar{x}(0) + \xi \bar{y} \int_0^\infty \beta(a)\gamma(a) e^{-\int_0^a \mu(s)\mathrm{d}s} \mathrm{d}a = 0.$$
Since $\bar{\lambda} > 0$, we get $\int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\bar{\lambda})\mathrm{d}s}\mathrm{d}a < R_0$. We know by definition of $E_{1,\xi}$ that $R_0 = 1$. Consequently $(1 - \int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\bar{\lambda})\mathrm{d}s}\mathrm{d}a) > 0$. Let $\bar{y} = 1$ and define:
$$\bar{x}(0) = \frac{-\xi \int_0^\infty \beta(a)\gamma(a) e^{-\int_0^a \mu(s)\mathrm{d}s}\mathrm{d}a}{1 - \int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\bar{\lambda})\mathrm{d}s}\mathrm{d}a}.$$
Then, defining $\bar{x}(a) = \bar{x}(0) e^{-\int_0^a [\bar{\lambda}+\mu(s)]\mathrm{d}s} - \gamma(a) x^*_{1,\xi}(a)$, we finally find $(\bar{x}, \bar{y}) \neq (0,0)$ verifying the system (14), so we find a positive eigenvalue and the equilibrium $E_{1,\xi}$ is unstable by using Theorem 3.2.

2. Let $\xi > 0$ and let $\epsilon > 0$. Then, by defining $\bar{\xi} = \xi + \epsilon\mu_0$ we get $E_{1,\bar{\xi}} \in B(E_{1,\xi}, \epsilon)$.
Indeed $\|E_{1,\bar{\xi}} - E_{1,\xi}\|_X = \|x^*_{1,\bar{\xi}} - x^*_{1,\xi}\|_{L^1(\mathbb{R}_+)} = |\bar{\xi} - \xi| \int_0^\infty e^{-\int_0^a \mu(s)\mathrm{d}s}\mathrm{d}a \leq \epsilon\mu_0 \int_0^\infty e^{-\mu_0 a}\mathrm{d}a \leq \epsilon$.

$\square$

The latter assertion prevents all equilibria $E_{1,\xi}, \xi \geq 0$ to be locally asymptotically stable.

3.2.3 Equilibrium E_2

We now focus on the equilibrium $E_2 = (x^*_2, y^*)$ that exists if and only if $R_0 > 1$ and $R_- < 1$. Then the differential of f at the point E_2 is given by:
$$D_{E_2} f = \begin{pmatrix} -y^*\gamma & -\gamma x^*_2 \\ \alpha y^* L_\gamma(\cdot) & \delta \end{pmatrix}$$
where L_γ is defined in (9). Since the linearized system is $u'(t) = (A + D_{E_2} f) u(t)$ we thus have to study the following system:
$$\begin{cases} \bar{x}'(a) &=& -\left[\lambda + \mu(a) + y^*\gamma(a)\right] \bar{x}(a) - \gamma(a) x^*_2(a) \bar{y}, \\ \lambda \bar{y} &=& \alpha y^* \int_0^\infty \gamma(a) \bar{x}(a) \mathrm{d}a, \\ \bar{x}(0) &=& \int_0^\infty \bar{x}(a) \beta(a) \mathrm{d}a. \end{cases}$$

We finally have to solve the system $BX = C$, where:

$$B = \begin{pmatrix} b_1 & b_2 \\ b_3 & b_4 \end{pmatrix}, C = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \text{ and } X = \begin{pmatrix} \bar{x}(0) \\ \bar{y} \end{pmatrix}, \text{ with :}$$

$$\begin{cases} b_1 &= 1 - \int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\lambda+y^*\gamma(s))\mathrm{d}s} \mathrm{d}a, \\ b_2 &= \dfrac{\delta}{\alpha\Gamma} \int_0^\infty \beta(a) e^{-\int_0^a [\mu(s)+y^*\gamma(s)]\mathrm{d}s} \int_0^a \gamma(u) e^{-\lambda(a-u)} \mathrm{d}u\mathrm{d}a, \\ b_3 &= \alpha y^* \int_0^\infty \gamma(a) e^{-\int_0^a (\mu(s)+\lambda+\gamma(s)y^*)\mathrm{d}s} \mathrm{d}a, \\ b_4 &= -\lambda - \dfrac{\delta y^*}{\Gamma} \int_0^\infty \gamma(a) e^{-\int_0^a [\mu(s)+\gamma(s)y^*]\mathrm{d}s} \int_0^a \gamma(u) e^{-\lambda(a-u)} \mathrm{d}u\mathrm{d}a, \end{cases}$$

and $\Gamma = \int_0^\infty \gamma(a) e^{-\int_0^a [\mu(s)+y^*\gamma(s)]\mathrm{d}s} \mathrm{d}a$.

In the specific case where γ is constant, we can compute the eigenvalues.

Theorem 3.7. *If $\gamma(a) = \gamma_0, \ \forall a \geq 0$, then $\lambda = \pm i\sqrt{y^*\gamma_0\delta}$.*

Proof. By solving $BX = C$, we need to have $\det(B) = 0$ to get a non zero solution X. So, if and only if we have $b_1 b_4 = b_2 b_3$. But we see that:

$$b_2 = \frac{\delta\gamma_0}{\alpha\Gamma\lambda} \left(\int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+y^*\gamma(s))\mathrm{d}s} \mathrm{d}a - \int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\lambda+y^*\gamma(s))\mathrm{d}s} \mathrm{d}a \right).$$

Then, with (8) we get:

$$b_2 = \frac{\delta\gamma_0}{\alpha\Gamma\lambda} \left(1 - \int_0^\infty \beta(a) e^{-\int_0^a (\mu(s)+\lambda+y^*\gamma(s))\mathrm{d}s} \mathrm{d}a \right) = \frac{\delta\gamma_0 b_1}{\alpha\Gamma\lambda}.$$

This implies that:

$$\begin{aligned} b_1 b_4 = b_2 b_3 \Leftrightarrow b_4 = \frac{\delta\gamma_0 b_3}{\alpha\Gamma\lambda} \Leftrightarrow -\lambda - \frac{\delta y^* \gamma_0^2}{\lambda\Gamma} \left(\int_0^\infty e^{-\int_0^a (\mu(s)+\gamma_0 y^*)\mathrm{d}s} \mathrm{d}a - \int_0^\infty e^{-\int_0^a (\mu(s)+\gamma_0 y^*+\lambda)\mathrm{d}s} \mathrm{d}a \right) \\ = \frac{\delta y^* \gamma_0^2}{\lambda\Gamma} \int_0^\infty e^{-\int_0^a (\mu(s)+\gamma_0 y^*+\lambda)\mathrm{d}s} \mathrm{d}a. \end{aligned}$$

With the expression of Γ, we finally get:

$$-\lambda = \frac{\delta y^* \gamma_0}{\lambda}$$

and the proof is completed. $\square$

Note that similarly to the ODE Lotka Volterra system, we get the existence of imaginary eigenvalues. In the case where γ is not constant, the analysis is much more complicate to perform. However, we will perform some simulations in the next section to exhibit the different possible behaviors.

3.3 Persistence

In this subsection we express some standard notions from mathematical ecology by formulating, in the context of Problem (1), the definition of persistence. First, let us give a proposition, whose arguments of the proof can be found in [32].

Proposition 3.2. *Problem (1) induces a continuous semiflow via*

$$\begin{aligned} \phi_t : \mathbb{R}_+ \times X_+ &\to X_+ \\ (t, z_0) &\mapsto \phi_t(z_0) = (x(t), y(t)), \end{aligned}$$

where $(x(t), y(t))$ is the unique solution that satisfies $(x(0), y(0)) = z_0$.

Let $\rho : X \to \mathbb{R}_+$ be a nonnegative uniformly continuous function on X and consider the composition $\sigma_\rho(t, x) = \rho(\phi_t(x))$, where ϕ_t is the semiflow defined in Proposition 3.2. Remark that this latter proposition implies that σ_ρ is a continuous map from $\mathbb{R}_+ \times X_+$ to $\mathbb{R}_+$. Let us introduce the following notations, that will be used in all the sequel:

$$\sigma_\rho^+(x) = \limsup_{t\to\infty} \sigma_\rho(t, x), \qquad \sigma_\rho^-(x) = \liminf_{t\to\infty} \sigma_\rho(t, x).$$

Let us suppose the following assumption on parameter β:

$$\exists\, \eta_1 > 0, \exists\, 0 < \underline{a} < \overline{a} < \infty \text{ such that } \beta(a) \geq \eta_1 \text{ for almost every (f.a.e) } a \in (\underline{a}, \overline{a}) \tag{H2}$$

and consider the following property that will ensure persistence:

$$\exists\, \eta_2 > 0, \exists\, 0 \leq t_1 < t_2 < \underline{a} : \int_{t_1}^{t_2} x_0(a)\mathrm{d}a \geq \eta_2. \tag{P}$$

Without lost of generality, we assume that $|t_2 - t_1| < |\overline{a} - \underline{a}|$ even if we reduce η_2.

Remark 4.

1. *Assumption (H2) means that preys of a certain range of age have a high ability to reproduce.*

2. *Assumption (P) together with property (H2) means that there is initially a high enough quantity of young preys that will be able to reproduce later.*

Let us consider in all that follows the set $X_{\mathrm{P}} = \{(x_0, y_0) \in X_+^* \text{ that satisfies (P)}\}$. Here is the definition of persistence for our system.

Definition 1. *Considering the mapping $\rho_1 : (x, y) \in X \mapsto \|x\|_{L^1(\mathbb{R}_+)}$, we say that:*

1. *The prey population is* ***uniformly strongly persistent*** *if*

$$\exists \varepsilon > 0 : \forall (x_0, y_0) \in X_{\mathrm{P}}, \quad \rho_1(x_0, y_0) > 0 \Rightarrow \sigma^-_{\rho_1}(x_0, y_0) \geq \varepsilon.$$

2. *The prey population is* ***uniformly weakly persistent*** *when considering $\sigma^+_{\rho_1}(x)$ instead of $\sigma^-_{\rho_1}(x)$.*

This definition can be naturally extended to the case of persistence of the predator population, by considering the map $\rho_2 : (x, y) \in X \mapsto y$ instead of ρ_1.

We thus can prove the following theorem, where R_- is defined in (7).

Theorem 3.8. *Suppose that the initial condition $(x_0, y_0) \in X_{\mathrm{P}}$. If $R_- > 1$ then prey population and predator population are unbounded functions.*

Proof. We know that:

$$\partial_t x(t, a) + \partial_a x(t, a) = -(\mu(a) + y(t)\gamma(a))x(t, a), \forall t \geq 0, \forall a \geq 0.$$

This latter equation leads to:

$$x(t, a) \geq \begin{cases} x_0(a - t)e^{-\int_{a-t}^{a}(\mu(s)+y(t-a+s)\gamma(s))\mathrm{d}s} & \text{if } a \geq t, \\ \psi(t - a)e^{-\int_0^a(\mu(s)+y(t-a+s)\gamma(s))\mathrm{d}s} & \text{if } a < t. \end{cases}$$

1. First we prove that $\exists t^\star$ such that $\forall t \in [t^\star, t^\star + a_1]$, $\psi(t) > 0$ with a_1 defined by (5).
   We know that $\forall t \in [\underline{a} - t_1, \overline{a} - t_2] : \psi(t) \geq \int_{t_1}^{t_2} \beta(u + t)x_0(u)e^{-(\|\mu\|_{L^\infty}+M\|\gamma\|_{L^\infty})t}\mathrm{d}u$, where $M = \max_{u\in[0,\overline{a}-t_2]} y(u) < \infty$ so $\psi(t) \geq \sigma_1 := \eta_1\eta_2 e^{-(\|\mu\|_{L^\infty}+M\|\gamma\|_{L^\infty})(\overline{a}-t_2)} > 0$ by Hypotheses (P) and (H2).
   Either $\overline{a} - t_2 - (\underline{a} - t_1) \geq a_1$ and this step is done, or we continue by defining $\varepsilon \in]0, \overline{a} - t_2 - (\underline{a} - t_1)[$.
   Then we prove that $\forall t \in [2\underline{a} - t_1 + \varepsilon, 2\overline{a} - t_2 - \varepsilon]$ we have:
   $\psi(t) \geq \sigma_2 := \eta_1\sigma_1(t_2 - t_1)e^{-\|\mu\|_{L^\infty}+\tilde{M}\|\gamma\|_{L^\infty}(2\overline{a}-t_2-\varepsilon)} > 0$, where $\tilde{M} = \max_{u\in[0,2\overline{a}-t_2-\varepsilon]} y(u) < \infty$.
   If $\overline{a} - t_2 - (\underline{a} - t_1) + (\overline{a} - \underline{a} - \varepsilon) \geq a_1$ we stop, else we continue.
   Since we get each time a bigger interval on which ψ is positive then we get what we wanted.

2. With this suitable $t^\star$, we can even prove that $\forall t \geq t^\star, \psi(t) > 0$.
   Indeed, since $R_- > 0$, there exists $\epsilon \in]0, a_1[$ such that $\int_\epsilon^{a_1} \beta(u)\mathrm{d}u > 0$.

Then $\forall \bar{\epsilon} \in [0, \epsilon]$ we get:

$$\psi(t^* + a_1 + \bar{\epsilon}) \geq \int_{t^\star+\bar{\epsilon}}^{t^\star+a_1} \psi(u)\beta(t^\star + \bar{\epsilon} + a_1 - u)e^{-(t^\star+\bar{\epsilon}+a_1-u)\|\mu\|_{L^\infty}}\mathrm{d}u > 0.$$

Doing this step by step, we finally prove that $\forall t \geq t^\star, \psi(t) > 0$.

3. Now we prove that $\lim_{t\to\infty} \psi(t) = \infty$.

   We have $\psi(t^\star + a_1) \geq \psi(\underline{t})R_-$ where $\psi(\underline{t}) = \min_{u\in[t^\star,t^\star+a_1]} \psi(u)$.

   Moreover $\forall h > 0 : \psi(t^\star + a_1 + h) \geq R_- \min_{u\in[t^\star+h,t^\star+a_1+h]} \psi(u) \geq \psi(\underline{t})R_-$.

   Then $\forall h > 0, \psi(t^* + 2a_1 + h) \geq R_- \min_{u\in[t^\star+a_1+h,t^\star+2a_1+h]} \psi(u) \geq \psi(\underline{t})R_-^2$.

   Once again, by induction and since $R_- > 1$ we prove that $\lim_{t\to\infty} \psi(t) = \infty$.

4. Since $\forall a \in [0, a_1]$ and $\forall t > a : x(t, a) = \psi(t - a)e^{-\int_0^a \mu(s)\mathrm{d}s}$, then $\forall a \in [0, a_1]$, $\lim_{t\to\infty} x(t, a) = \infty$. Consequently we have $\lim_{t\to\infty} \|x(t, \cdot)\|_{L^1(\mathbb{R}_+)} = \infty$.

   Now, let us suppose that $\exists M > 0$ such that $\forall t \geq 0, y(t) \leq M$.

   Then a lower bound of Problem (1) gives, for every $t \geq 0$:

$$x(t,a) \geq \begin{cases} x_0(a-t)e^{-(\|\mu\|_{L^\infty}+M\|\gamma\|_{L^\infty})t} & \text{if } a \geq t, \\ \psi(t-a)e^{-(\|\mu\|_{L^\infty}+M\|\gamma\|_{L^\infty})a} & \text{if } a < t. \end{cases}$$

   Since $\lim_{t\to\infty} \psi(t) = \infty$, then $\forall \overline{M} > 0$, $\exists t^\star > 0$ such that $\forall t \geq t^\star : \psi(t) \geq \overline{M}$.

   Consequently, we have for every $t \geq t^\star + a_2$ and every $a \in (a_1, a_2)$:

$$x(t, a) \geq \overline{M}e^{-(\|\mu\|_{L^\infty}+M\|\gamma\|_{L^\infty}} a_2) =: \overline{M}C.$$

   From Problem (1) and Remark 1 we deduce that for every $t \geq t^\star + a_2$:

$$\frac{dy}{dt}(t) \geq \left[\alpha \int_{a_1}^{a_2} \gamma(a)x(t,a)\mathrm{d}a - \delta\right] y(t) \geq \left[\alpha\gamma_-\overline{M}C - \delta\right] y(t) =: \overline{C}y(t).$$

   Taking $\overline{M}$ big enough, we get $\overline{C} > 0$.

   Finally, an integration of the latter equation gives, for every $t \geq t^\star + a_2$:

$$y(t) \geq y(t^\star + a_2)e^{-\overline{C}(t^*+a_2)}e^{\overline{C}t} \underset{t\to\infty}{\rightarrow} \infty$$

   which is a contradiction with the fact that y is bounded.

5. Consequently there exists an increasing sequence $(t_n)_{n\in\mathbb{N}}$ such that $\lim_{n\to\infty} t_n = \infty$ and such that $\lim_{n\to\infty} y(t_n) = \infty$. So $\forall M > 0, \exists n^\star \in \mathbb{N} : \forall n \geq n^\star, y(t_n) \geq M$.

   Suppose that $y(t)$ does not go to ∞ when t goes to ∞.

   Then $\exists\ \varepsilon > 0 : \forall n \in \mathbb{N}, \exists\ \bar{t} > t_n$ such that $y(\bar{t}) < \varepsilon$. Obviously $\exists n^\star \in \mathbb{N}$ such that $\bar{t} \in [t_{n^\star}, t_{n^\star+1}]$, meaning that $y(t_{n^\star}) \geq M, y(\bar{t}) < \varepsilon$ and $y(t_{n^\star+1}) \geq M$.

   So, by taking $M \geq K := \varepsilon e^{\delta(a_2-a_1)}$, we can find by the fact that $y'(t) \geq -\delta y(t)$ and by continuity of y, an interval $[t^\star, t^\star+(a_2-a_1)] \subset [t_{n^\star}, t_{n^\star+1}]$ such that $y(t) \leq K$ and such that $y'(t^\star+(a_2-a_1)) < 0$.

   By definition of a_1, we can find a_2 such that $a_2 - a_1 < a_1$ even if we reduce γ_-.

   Since $\lim_{t\to\infty} x(t,a) = \infty,\ \forall a \in [0, a_1]$ then $\exists \underline{t} > 0$ such that $\forall t > \underline{t}$ and $\forall a \in [a_1 - (a_2 - a_1), a_1]$:

$$x(t,a) \geq \frac{\delta}{\alpha\gamma_-} e^{-(a_2-a_1)(\|\mu\|_{L^\infty}+K\|\gamma\|_{L^\infty})},$$

   so $\forall a \in [a_1, a_2] : x(t + (a_2 - a_1), a) \geq \delta/(\alpha\gamma_-)$ and then $y'(t + (a_2 - a_1)) \geq 0$.

   Finally, taking a time big enough to have both conclusions, we get a contradiction.

   We have then $\lim_{t\to\infty} y(t) = \infty$ and the proof is completed.

$\square$

Corollary 1. *Prey population and predator population are uniformly strongly persistent.*

The following result states that persistence may hold in the case where $R_- < 1$ but under the assumption $R_0 > 1$.

Theorem 3.9. *Suppose that $R_0 > 1$ and $R_- < 1$. Then the total population of prey and the total population of predator are uniformly weakly persistent.*

Proof.

1. First, suppose that given a fixed $\varepsilon > 0$, there exists $(x_0, y_0) \in X_{\mathrm{P}}$ (that may depend on ε) such that $\sigma^+(x_0, y_0) < \varepsilon$. Since we have $R_0 > 1$, then $\exists\ a^\star > 0$ such that $C := \int_0^{a^\star} \beta(z)e^{-\int_0^z \mu(s)\mathrm{d}s}\mathrm{d}z > 1$. Let us take $\overline{C} \in]1, C[$ and define:

$$\overline{M} = \frac{1}{a^\star\|\gamma\|_{L^\infty}} \ln\left(\frac{C}{\overline{C}}\right) > 0.$$

   Taking ε small enough and since $\sigma^+(x_0, y_0) < \varepsilon$, we get $y(t) \leq \overline{M}, \forall t \geq \bar{t}$ big enough.

   Moreover y is bounded by a positive constant M and, using the last proof, we get $\psi(t) > 0, \forall t \geq t^\star$.

Consequently, defining $\tilde{t} = \max\{t^\star, \bar{t}\}$, we get $\psi(\tilde{t} + a^\star) \geq \psi(\underline{t})\overline{C}$ where $\psi(\underline{t}) = \overline{C} \min_{u \in [\tilde{t}, \tilde{t}+a^\star]} \psi(u)$. Using the last proof with respectively $\tilde{t}, a^\star, \overline{C}$ instead of $t^\star, a_1, R_-$: we get $\lim_{t\to\infty} \psi(t) = \infty$ then $\lim_{t\to\infty} \|x(t,\cdot)\|_{L^1(\mathbb{R}_+)} = \infty$ and $\lim_{t\to\infty} y(t) = \infty$ since y is bounded, which is a contradiction. Thus we get the persistence result for the predator.

2. Now suppose that for $\varepsilon > 0$ fixed, there exists $(x_0, y_0) \in X_{\mathrm{P}}$ such that $\sigma^+_{\rho_1}(x_0, y_0) < \varepsilon$.

   Taking ε small enough we get:
$$\|x(t,.)\|_{L^1(\mathbb{R}_+)} < \frac{\delta}{\alpha\|\gamma\|_{L^\infty}}$$
   for all $t \geq \bar{t}$ big enough, so $\lim_{t\to\infty} y(t) = 0$ with the second equation of (1). We then get a contradiction by using the first point. Consequently the proof is completed.

□

4 Numerical Simulations

The following numerical simulations, that are performed using the finite volume method, aim at investigating other behavior of the dynamical system (1) under some biologically reasonable parameters.

4.1 Numerical Scheme

We define the intervals $a \in [0, a_{\max}]$ and $t \in [0, T]$ then we note Δa and Δt respectively the age and the time steps. We define $a_{j+1/2} = j\Delta a$ and $t^n = n\Delta t$, for $j, n \in \mathbb{N}$ then we note $K_j = (a_{j-1/2}, a_{j+1/2})$. We denote x_j^n the approximation of the average of $x(t^n, a)$ over K_j and we compute the initial states:

$$x_j^n \approx \frac{1}{\Delta a}\int_{K_j} x(t^n, a)\mathrm{d}a, \quad x_j^0 = \frac{1}{\Delta a}\int_{K_j} x_0(a)\mathrm{d}a, \quad y^0 = y_0, \quad \forall j \geq 1.$$

Then we set $\alpha, \delta > 0$ and once β, μ, γ are chosen, we compute the data:

$$\beta_j = \frac{1}{\Delta a}\int_{K_j} \beta(a)\mathrm{d}a, \quad \mu_j = \frac{1}{\Delta a}\int_{K_j} \mu(a)\mathrm{d}a, \quad \gamma_j = \frac{1}{\Delta a}\int_{K_j} \gamma(a)\mathrm{d}a, \quad \forall j \geq 1.$$

We define $\mathcal{T}(\gamma x^n) = \Delta a \sum_{j\geq 1} \gamma_j x_j^n$. An implicit Euler's Scheme for the second equation of (1) gives:

$$y_{n+1} = \frac{y_n(1 + \alpha\Delta t\mathcal{T}(\gamma x^n))}{1 + \delta\Delta t}, \forall n \geq 0.$$

Integrating the first equation of (1) regarding a over K_j and supposing x regular enough, we get:

$$\frac{\partial}{\partial t}\int_{K_j} x(t,a)\mathrm{d}a + x(t,a_{j+1/2}) - x(t,a_{j-1/2}) = -\int_{K_j} [\mu(a) + y(t)\gamma(a)]\, x(t,a)\mathrm{d}a.$$

Then, a implicit Euler's scheme and the integrals estimates gives us:

$$x_{j+1}^{n+1} = \frac{x_{j+1}^{n} + \dfrac{\Delta t}{\Delta a} x_j^{n+1}}{1 + \dfrac{\Delta t}{\Delta a} + \Delta t \mu_{j+1} + \Delta t y^{n+1}\gamma_{j+1}}, \ \forall j \geq 0, \forall n \geq 1.$$

Moreover, the boundary conditions gives us $x_0^{n+1} = \Delta a \sum_{j\geq 1} \beta_j x_j^n,\ \forall n \geq 1$.

Then we have the following theorem which guarantees positivity of the numerical solution.

Theorem 4.1. *If $(x_0, y_0) \in X_+$ then $\forall j \geq 1, n \geq 1$, we have $x_j^n \geq 0$ and $y_j \geq 0$.*

4.2 Simulations

According to biological considerations, let us use the following functions:

1. $\mu(a) = \mu_0 + \mu_0 a/(1 + ah)$ with $\mu_0 > 0$ and $h \in \mathbb{R}_+^*$: the older is the prey, the easier she dies naturally,

2. $\beta(a) = \beta_0 a e^{-ca}$ with $\beta_0, c > 0$: the middle-aged preys are the one that reproduce themselves the most,

3. $\gamma(a) = \gamma_0(1 - age^{1-ga})$, with $\gamma_0 > 0, g > 0$: the young and the old preys are more easily killed by the predators.

For our simulations we take the parameters: $a_{\max} = 20, \Delta a = 0.1, \alpha = 0.7, \delta = 0.1, \mu_0 = 0.05, h = 1$, $c = 1, g = 0.25, \gamma_0 = 0.5$ and we represent the trajectory of the solution with on the x-axis the quantity of predator and on the y-axis the total quantity $\|x\|_{L^1}$ of prey.

If we take $\beta_0 = 1$, we have $R_0 < 1$, so for all $(x_0, y_0) \in X_+$ the solution will converge to E_0: Theorem 3.5 (see figure 1).

If we take $\beta_0 = 4$ or $\beta_0 = 7$, then the simulations make us suppose that the solution is bounded for any positive initial conditions $(x_0, y_0) \in X_{\mathrm{P}}$. Moreover we have $R_0 > 1$, $R_- < 1$ and (H2) is verified since $\beta_0(a) > 0$ f.a.e. $a \geq 0$. Consequently of Theorem 3.9, the total populations are uniformly weakly persistent and the solution will either converge to a periodic function if $\beta_0 = 4$ (see figure 2) or converge to E_2 if $\beta_0 = 7$ (see figure 3).

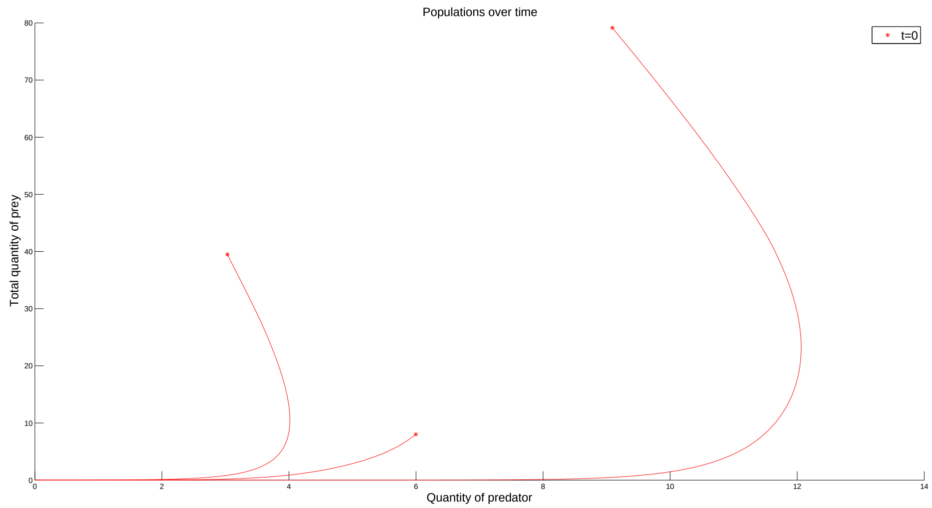

Figure 1: Convergence to E_0

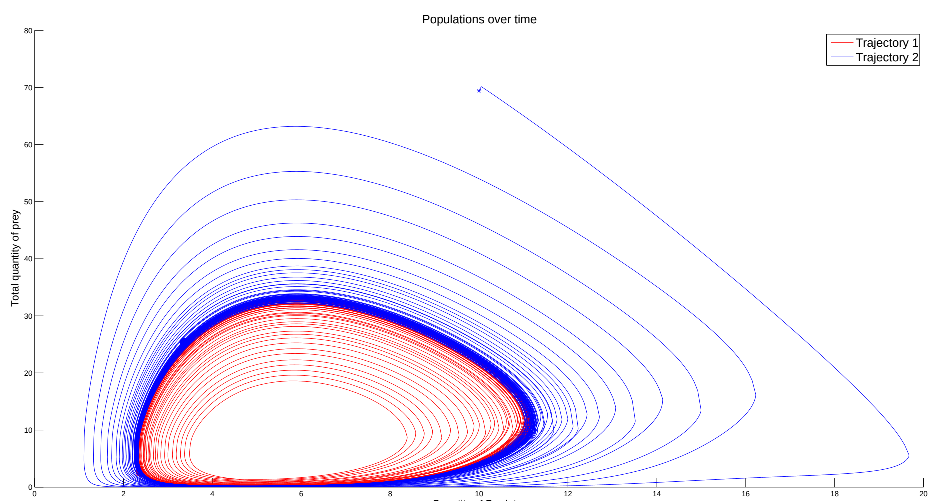

Figure 2: Convergence to a periodic function

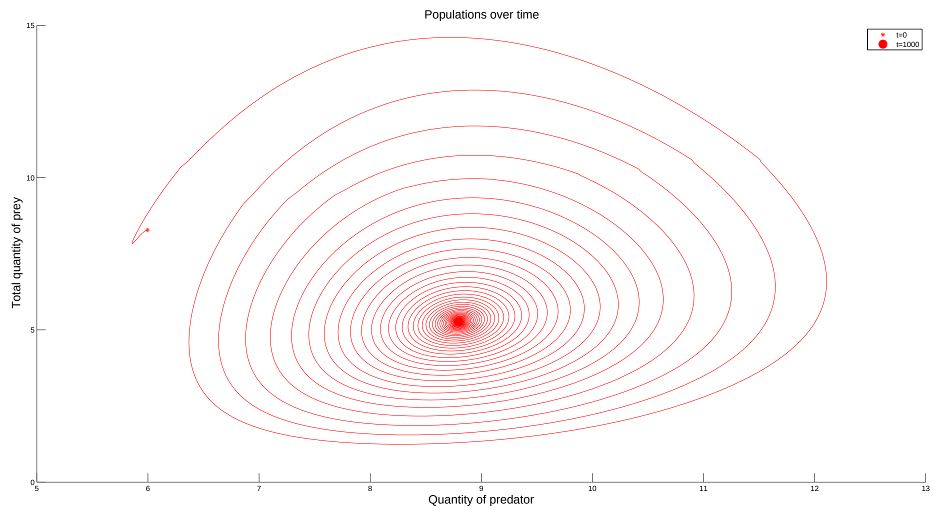

Figure 3: Convergence to E_2

If we take $\beta_0 = 7$ and if we modify the function γ to: $\gamma(a) = \gamma_0(1 - age^{1-ga})\mathbb{1}_{[2,\infty[}(a)$ then (P), (H2) are verified and $R_- > 1$ so consequently to Theorem 3.8: the solutions are unbounded (see figure 4).

4.3 Final remarks

All the cases that we have studied theoretically and numerically are gathered in Table 1. One can note that, even when considering a linear functional response, a structure according to the age of the preys provides more complex dynamics of the predator-prey interactions than the Lotka Volterra ODE model. In particular, the realistic case of extinction of the population may occur. Indeed, we proved that, depending on the age distribution of the fertility rate and of the mortality rate of the preys, the total population tends to disappear. This phenomenon happens when a prey will produce, in average, less than one direct offspring during its lifespan, translated by $R_0 < 1$. In the opposite case, when $R_0 > 1$, we proved that under the assumption that the initial prey population is young enough (i.e. assumption (P)) then the total population is uniformly weakly persistent.

The model shows another unexpected behavior: if the young preys "uncatchable" by predators have a high enough ability to reproduce, which is translated by ($R_- > 1$), then both populations explode. This

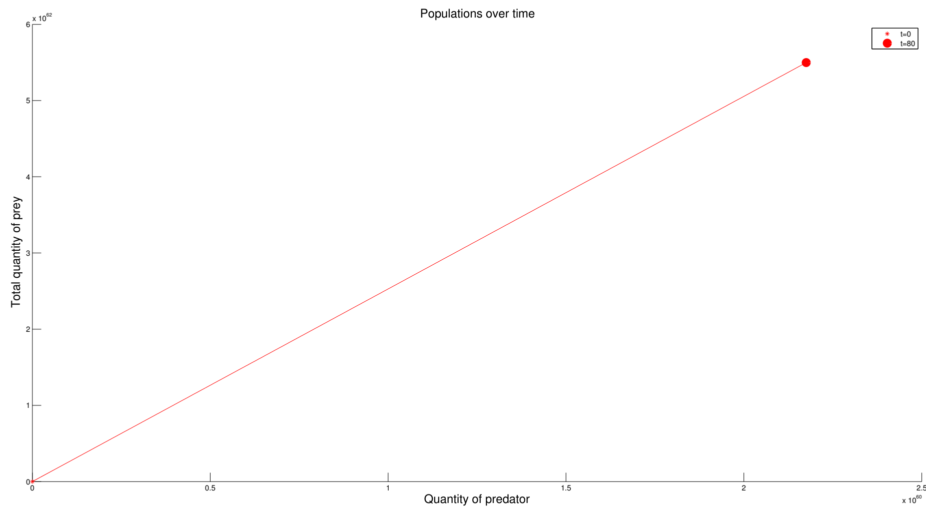

Figure 4: Unbounded solution

phenomenon, even if rare and perhaps biologically impossible, was not possible in the ODE case as well as in the PDE model incorporating a constant predation parameter. Finally in the other cases that were numerically investigated (i.e. when $R_0 > 1, R_- < 1$ and (P) is verified) the solution converges either to a periodic function or to a positive equilibrium.

A further work will be dedicated to a deeper analysis of the equilibrium E_2 in order to determine under which conditions it is asymptotically stable, and to theoretically look for the existence of periodic trajectories.

<table>
<tr><td>$R_0 < 1$</td><td colspan="2">$R_0 > 1$ and (P)</td></tr>
<tr><td rowspan="2">Convergence to E_0</td><td>$R_- < 1$</td><td>$R_- > 1$</td></tr>
<tr><td>Limit cycle or Convergence to E_2</td><td>Unbounded solutions</td></tr>
</table>

Table 1: Different behaviors

Appendix: A Brief Reminder of Lotka Volterra

The Lotka Volterra equations are used to describe the dynamics of biological systems in which two species interact. The classical Lotka Volterra ODE system is the following:

$$\begin{cases} X'(t) &= a_1 X(t) &- &a_2 X(t)Y(t), \\ Y'(t) &= a_3 X(t)Y(t) &- &a_4 Y(t), \\ X(0) &= X_0 &\text{and} &Y(0) = Y_0, \end{cases} \tag{15}$$

with a_1, a_2, a_3, a_4 some positive real parameters. For such a system, we have the following well-known result (see [9] or [28]):

Theorem 4.2. *For any positive initial condition (X_0, Y_0), Problem (15) has a unique positive solution that is time periodic.*

A consequence of the latter theorem is that for a given positive initial condition, the total population never extincts even when considering an infinite time horizon.

A formal integration with respect to the age variable a explains how the age-structured PDE problem (1) can be seen as a generalization of the Lotka Volterra equations, as stated in the following proposition:

Proposition 4.1. *Suppose that parameters γ, β and μ are independent of the age, given by the following constants: $\gamma(a) = \gamma_0$, $\beta(a) = \beta_0$ and $\mu(a) = \mu_0$ f.a.e. $a \geq 0$. Then $(X(t), Y(t)) := (\int_0^\infty x(t,a)\, da, y(t))$ is the solution of system (15) with $a_1 = \beta_0 - \mu_0$, $a_2 = \gamma_0$, $a_3 = \alpha\gamma_0$, $a_4 = \delta$, $X_0 = \int_0^\infty x_0(a) da$ and $Y_0 = y_0$.*

Remark 5. *As it was explained in Section 2, $D(A) \subset W^{1,1}(\mathbb{R}_+) \times \mathbb{R}$, where $D(A)$ is the domain of the differential operator in Problem (1). Then for any initial condition $(x_0, y_0) \in D(A)$, $a \mapsto x(t,a)$ remains in $W^{1,1}(\mathbb{R}_+)$ for every $t \geq 0$. A consequence is that for every $t \geq 0$, $\lim_{a\to\infty} x(t,a) = 0$ and consequently $\int_0^\infty \partial_a x(t,a) da = -\beta_0 X(t)$, and the formal integration w.r.t. a is possible.*

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Short title: Predator-prey model with age structure

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