

Periodic orbits for periodic eco-epidemiological systems with infected prey

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Abstract. We address the existence of periodic orbits for periodic eco-epidemiological system with disease in the prey for two distinct families of models. For the first one, we use Mawhin's continuation theorem in a wide general system that includes some models discussed in the literature, and for the second family we obtain a sharp result using a recent strategy that relies on the uniqueness of periodic orbits in the disease-free space.

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1 Introduction

Eco-epidemiological models are ecological models that include infected compartments. In many situations, these models describe more accurately the real ecological system than models where the disease is not taken into account.

There is already a large number of works concerning eco-epidemiological models. To mention just a few recent works, we refer [4] where a mathematical study on disease persistence and extinction is carried out; [2] where the authors study the global stability of a delayed eco-epidemiological model with Holling-type III functional response, and [11] where an eco-epidemiological model with harvesting is considered.

One of the main concerns when studying eco-epidemiological models is to determine conditions under which one can predict if the disease persists or dies out. In mathematical epidemiology, these conditions are usually given in terms of the so called basic reproduction number \mathcal{R}_0 , defined in [5] for autonomous systems as the spectral radius of the next generation matrix.

In [3], \mathcal{R}_0 was introduced for the periodic models, and later on, in [16], the definition of \mathcal{R}_0 was adapted to the study of periodic patchy models. In the recent article [6] the theory in [16] was used in the study of persistence of the predator in general periodic predator-prey models.

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When persistence is guaranteed, the obtention of conditions that assure the existence of periodic orbits for periodic eco-epidemiological models is an important issue in the deepening of the description of these models since these orbits correspond to situations where possibly there is some equilibrium in the described ecological system, reflected in the fact that the behaviour of the theoretical model is the same over the years. In [13] it was proved that there is an endemic periodic orbit for the periodic version of the model considered in [18] when the infected prey is permanent and some additional conditions are fulfilled, partially giving a positive answer to a conjecture in this last paper.

The models in [18] and [13] assume that there is no predation on uninfected preys. In spite of that, this assumption is not suitable for the description of many eco-epidemiological models. The main purpose of this paper is to present some results on the existence of an endemic periodic orbit for periodic eco-epidemiological systems with disease in the prey that generalize the systems in [18] and [13] by including in the model a general function corresponding to the predation of uninfected preys. Two slightly distinct families of models will be considered separately, one of them in section 2 and the other is section 4. The proof of the main result in section 2 relies on Mawhin's continuation theorem. Following the approach in [13], we begin by locating the components of possible periodic orbits for the one parameter family of systems that arise in Mawhin's result, allowing us to check that the conditions of that theorem are fulfilled. Although the main steps in our proof correspond to the ones in [13], several additional nontrivial arguments are needed in our case. Additionally, there is also a substantial difference between our approach and the one in [13, 18]. In fact, we take as a departure point some prescribed behaviour of the uninfected subsystem, corresponding to the dynamics of preys and predators in the absence of disease: we will assume in this work that we have global asymptotic stability of solutions of some special perturbations of the bidimensional predator-prey system (the system obtained by letting I = 0 in the first and third equations in (1.1)). Thus, when applying our results to particular situations, one must verify that the underlying uninfected subsystem satisfies our assumptions. On the other hand, our approach allows us to construct an eco-epidemiological model from a previously studied predator-prey model (the uninfected subsystem) that satisfies our assumptions. This approach has the advantage of highlighting the link between the dynamics of the eco-epidemiological model and the dynamics of the predator-prey model used in its construction. For the family of systems in section 4, we were able to obtain a sharp result using a recent strategy available in the literature instead of Mawhin's continuation theorem.

Considering what was said, as a generalization of the model studied in [13], a periodic version of the general non-autonomous model introduced in [18], we consider the following periodic eco-epidemiological model:

$$\begin{cases} S' = \Lambda(t) - \mu(t)S - a(t)f(S, I, P)P - \beta(t)SI, \\ I' = \beta(t)SI - \eta(t)g(S, I, P)I - c(t)I, \\ P' = h(t, P) + \gamma(t)a(t)f(S, I, P)P + \theta(t)\eta(t)g(S, I, P)I, \end{cases}$$
(1.1)

where *S*, *I* and *P* correspond, respectively, to the susceptible prey, infected prey and predator. In our model h(t, P) correspond to the vital dynamics of predators in the absence of this prey.

In this work we consider two different scenarios: in the first one we will take

$$h(t, P) = (r(t) - b(t)P)P.$$
 (1.2)

When r(t) > 0 for all *t*, we obtain a model with linear vital dynamics of susceptible prey in the absence of predators and disease and with logistic vital dynamics of predators in the

absence of the considered prey. This model generalizes [18]. When r(t) < 0 for all t, we obtain a model with a classical vital dynamics of the predators as in the family of Lotka–Volterra models considered in [6]. In the second scenario we consider a linear vital dynamics for predators by taking

$$h(t, P) = Y(t) - \zeta(t)P.$$
(1.3)

This model has no periodic solutions on the axis, allowing us to use a different set of arguments to establish the existence of an endemic periodic orbit. Note that, when h is given by (1.2), there is space in our model for the possibility that predators survive in the absence of this prey. In fact, when r(t) is nonnegative, predator have a logistic behaviour. A possible biological interpretation is that predators in this ecosystem possess different sources of food and, in the absence of the prey in this model, the behaviour of the predator population is logistic. When r(t) is nonpositive we obtain a usual behaviour for predators in the absence of preys. When h is given by (1.3) predators always survive in the absence of the prey considered in the model and we also interpret this fact as in the corresponding situation for the first scenario.

In the first scenario, for technical reasons, we have to make the restriction g(S, I, P) = P, while in the second scenario we let g be a general function that satisfies some natural assumptions.

In the first situation, r(t) and b(t) are parameters related to the vital dynamics of the predator population that include the intra-specific competition between predators. This vital dynamics is assumed to follow a logistic law when r(t) > 0 for all $t \ge 0$ and that is similar to the vital dynamics of predator in a family of Lotka–Volterra models considered in [6] when r(t) < 0 for all $t \ge 0$. In both scenarios $\Lambda(t)$ is the recruitment rate of the prey population, $\mu(t)$ is the natural death rate of the prey population, a(t) is the predation rate of susceptible prey, $\beta(t)$ is the incidence rate, $\eta(t)$ is the predation rate of infected prey, c(t) is the death rate in the infective class ($c(t) \ge \mu(t)$), $\gamma(t)$ is the rate of converting susceptible prey into predator (biomass transfer), $\theta(t)$ is the rate of converting infected prey into predator. It is assumed that only susceptible preys *S* are capable of reproducing, i.e., the infected prey is removed by death (including natural and disease-related death) or by predation before having the possibility of reproducing.

2 Eco-epidemiological models with classical or logistic vital dynamics for predators

In this section we let g(S, I, P) = P and h(t, P) = (r(t) - b(t)P)P, obtaining a model that generalizes the model in [13] by considering a function that corresponds to the predation of uninfected preys:

$$\begin{cases} S' = \Lambda(t) - \mu(t)S - a(t)f(S, I, P)P - \beta(t)SI, \\ I' = \beta(t)SI - \eta(t)PI - c(t)I, \\ P' = (r(t) - b(t)P)P + \gamma(t)a(t)f(S, I, P)P + \theta(t)\eta(t)PI. \end{cases}$$
(2.1)

Given an ω -periodic function f, we will use throughout the paper the notations $f^{\ell} = \inf_{t \in (0,\omega]} f(t)$, $f^u = \sup_{t \in (0,\omega]} f(t)$ and $\bar{f} = \frac{1}{\omega} \int_0^{\omega} f(s) ds$. We will assume the following structural hypothesis concerning the parameter functions and the function f appearing in our model:

- S1) The real valued functions Λ , μ , a, β , η , c, γ , θ and b are periodic with period ω , nonnegative and continuous; the real valued function r is periodic with period ω and continuous and can be nonnegative or nonpositive;
- S2) Function f is nonnegative and C^1 ;
- S3) Function $x \mapsto f(x, y, z)$ is nondecreasing;
- S4) Functions $z \mapsto f(x, y, z)$ and $y \mapsto f(x, y, z)$ are nonincreasing;
- S5) For all (x, y, z) we have

$$f(x,y,z) + z\frac{\partial f}{\partial z}(x,y,z) > 0, \quad \overline{\eta} + \overline{a}\frac{\partial f}{\partial y}(x,y,z) > 0 \quad \text{and} \quad \overline{\theta\eta} + \overline{\gamma a}\frac{\partial f}{\partial y}(x,y,z) > 0;$$

- S6) $\overline{\Lambda} > 0$, $\overline{\mu} > 0$ and $\overline{b} > 0$;
- S7) There is $\alpha \ge 1$ and K > 0 such that $f(x, 0, 0) \le Kx^{\alpha}$.

Note that our functional response must depend on *I* to be able to include functional response functions with saturation, that must depend on the total population of preys (see [1, 14]). Our setting includes several of the most common functional responses for the functional response function *f*, including, among others, f(S, I, P) = kS (Holling-type I), f(S, I, P) = kS/(1 + m(S + I)) (Holling-type II), $f(S, I, P) = kS^{\alpha}/(1 + m(S + I)^{\alpha})$ (Holling-type III), $f(S, I, P) = kS/(a + b(S + I) + c(S + I)^2)$ (Holling-type IV), f(S, I, P) = kS/(a + b(S + I) + cP) (Beddington–De Angelis), f(S, I, P) = kS/(a + b(S + I) + cP + d(S + I)P) (Crowley–Martin). Also note that conditions S3), S4) are natural from a biological perspective and naturally are satisfied by the usual functional responses considered in the literature. Conditions S5) and S7) are satisfied by most of the usual functional response functions.

To formulate our next assumptions we need to consider two auxiliary equations and one auxiliary system. First, for each $\lambda \in (0, 1]$, we need to consider the following equations:

$$x' = \lambda(\Lambda(t) - \mu(t)x) \tag{2.2}$$

and

$$z' = \lambda(r(t) - b(t)z)z.$$
(2.3)

Note that, if we identify x with the susceptible prey population, equation (2.2) gives the behaviour of the susceptible preys in the absence of infected preys and predator and identifying z with the predator population, equation (2.3) gives the behaviour of the predator in the absence of preys.

Equation (2.2) is a linear equation that was considered in countless papers on epidemiological models and equation (2.3) was already studied in [8]. These equations have a well known behaviour, given in the following lemmas:

Lemma 2.1. For each $\lambda \in (0, 1]$ there is a unique ω -periodic solution of equation (2.2), $x_{\lambda}^{*}(t)$, that is globally asymptotically stable in \mathbb{R}^+ .

Lemma 2.2. If the function r is nonnegative, for each $\lambda \in (0,1]$ there is a unique ω -periodic solution of equation (2.3), $z_{\lambda}^{*}(t)$, that is globally asymptotically stable in \mathbb{R}^{+} . If the function r is nonpositive for each $\lambda \in (0,1]$ the zero solution of equation (2.3), that we still denote by $z_{\lambda}^{*}(t)$, is globally asymptotically stable in \mathbb{R}_{0}^{+} .

For each $\lambda \in (0, 1]$, we also need to consider the next family of systems, which corresponds to behaviour of the preys and predators in the absence of infected preys (system (1.1) with I = 0, S = x and P = z):

$$\begin{cases} x' = \lambda(\Lambda(t) - \mu(t)x - a(t)f(x,\varepsilon_3,z)z - \varepsilon_1 x), \\ z' = \lambda(\gamma(t)a(t)f(x,\varepsilon_4,z) + r(t) - b(t)z + \varepsilon_2)z. \end{cases}$$
(2.4)

We now make our last structural assumption on system (1.1):

S9) For each $\lambda \in (0, 1]$ and each $\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4 \ge 0$ sufficiently small, system (2.4) has a unique ω -periodic solution, $(x^*_{\lambda,\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t), z^*_{\lambda,\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t))$, with

$$x^*_{\lambda,\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t) > 0$$
 and $z^*_{\lambda,\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t) > 0$,

that is globally asymptotically stable in the set

$$\{(x,z)\in (\mathbb{R}^+_0)^2: x \ge 0 \ \land \ z > 0\}.$$

We assume that $(\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4) \mapsto (x^*_{\lambda, \varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4}(t), z^*_{\lambda, \varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4}(t))$ is continuous.

Denoting $x_{\lambda}^* = x_{\lambda,0,0,0,0}^*$ and $z_{\lambda}^* = z_{\lambda,0,0,0,0}^*$, we introduce the numbers

$$\overline{\mathcal{R}}_{0} = \frac{\overline{\beta}\overline{\Lambda}/\overline{\mu}}{\overline{c} + \overline{\eta}\overline{r}/\overline{b}}, \quad \mathcal{R}_{0}^{\lambda} = \frac{\overline{\beta}x_{\lambda}^{*}}{\overline{c} + \overline{\eta}z_{\lambda}^{*}} \quad \text{and} \quad \widetilde{\mathcal{R}}_{0} = \inf_{\lambda \in (0,1]} \mathcal{R}_{0}^{\lambda}$$
(2.5)

Before presenting our main result we have to consider the averaged system corresponding to (2.1):

$$\begin{cases} S' = \overline{\Lambda} - \overline{\mu}S - \overline{a}f(S, I, P)P - \overline{\beta}SI, \\ I' = \overline{\beta}SI - \overline{\eta}PI - \overline{c}I, \\ P' = (\overline{r} - \overline{b}P)P + \overline{\gamma}\overline{a}f(S, I, P)P + \overline{\theta}\overline{\eta}PI. \end{cases}$$
(2.6)

The number $\overline{\mathcal{R}}_0$ is the basic reproductive number of (2.6) when $f \equiv 0$ (see [13, 18]). We now present our main result.

Theorem 2.3. If $\tilde{R}_0 > 1$, conditions S1) to S9) hold and there is a unique equilibrium of the averaged system (2.6) in $(\mathbb{R}^+)^3$, the interior of the first octant, then system (1.1) possesses an endemic periodic orbit of period ω .

Our proof relies on an application of Mawhin's continuation theorem. We will proceed in several steps. Firstly, in subsection 2.1, we consider a one parameter family of systems and obtain uniform bounds for the components of any periodic solution of these systems. Next, in subsection 2.2 we make a suitable change of variables in our family of systems to establish the setting where we will apply Mawhin's continuation Theorem. Finally, in subsection 2.3, we use Mawhin's continuation Theorem to obtain our result.

2.1 Uniform persistence for the periodic orbits of a one parameter family of systems.

In this section, to obtain uniform bounds for the components of any periodic solution of the family of systems that we can obtain multiplying the right hand side of (1.1) by $\lambda \in (0, 1]$, we

need to consider the auxiliary system

$$\begin{cases} S'_{\lambda} = \lambda(\Lambda(t) - \mu(t)S_{\lambda} - a(t)f(S_{\lambda}, I_{\lambda}, P_{\lambda})P_{\lambda} - \beta(t)S_{\lambda}I_{\lambda}), \\ I'_{\lambda} = \lambda(\beta(t)S_{\lambda}I_{\lambda} - \eta(t)P_{\lambda}I_{\lambda} - c(t)I_{\lambda}), \\ P'_{\lambda} = \lambda(\gamma(t)a(t)f(S_{\lambda}, I_{\lambda}, P_{\lambda})P_{\lambda} + \theta(t)\eta(t)P_{\lambda}I_{\lambda} + r(t)P_{\lambda} - b(t)P_{\lambda}^{2}). \end{cases}$$

$$(2.7)$$

We will consider separately each of the several components of any periodic orbit.

Lemma 2.4. Let $x_{\lambda}^{*}(t)$ be the unique solution of (2.2). There is $L_{1} > 0$ such that, for any $\lambda \in (0, 1]$ and any periodic solution $(S_{\lambda}(t), I_{\lambda}(t), P_{\lambda}(t))$ of (2.7) with initial conditions $S_{\lambda}(t_{0}) = S_{0} > 0$, $I_{\lambda}(t_{0}) = I_{0} > 0$ and $P_{\lambda}(t_{0}) = P_{0} > 0$, we have $S_{\lambda}(t) + I_{\lambda}(t) \leq x_{\lambda}^{*}(t) \leq \Lambda^{u} / \mu^{\ell}$ and $S_{\lambda} \geq L_{1}$, for all $t \in \mathbb{R}$.

Proof. Let $(S_{\lambda}(t), I_{\lambda}(t), P_{\lambda}(t))$ be some periodic solution of (2.7) with initial conditions $S_{\lambda}(t_0) = S_0 > 0$, $I_{\lambda}(t_0) = I_0 > 0$ and $P_{\lambda}(t_0) = P_0 > 0$. Since $c(t) \ge \mu(t)$, we have, by the first and second equations of (2.7),

$$(S_{\lambda} + I_{\lambda})' \leq \lambda \Lambda(t) - \lambda \mu(t) S_{\lambda} - \lambda c(t) I_{\lambda} \leq \lambda \Lambda(t) - \lambda \mu(t) (S_{\lambda} + I_{\lambda}).$$

Since, by Lemma 2.1, equation (2.2) has a unique periodic orbit, $x_{\lambda}^{*}(t)$, that is globally asymptotically stable, we conclude that $S_{\lambda}(t) + I_{\lambda}(t) \leq x_{\lambda}^{*}(t)$ for all $t \in \mathbb{R}$. Comparing equation (2.2) with equation $x' = \lambda \Lambda^{u} - \lambda \mu^{\ell} x$, we conclude that $x_{\lambda}^{*}(t) \leq \Lambda^{u} / \mu^{\ell}$.

Using conditions S3) and S4), by the third equation of (2.7), we have

$$P'_{\lambda} \leq \lambda(r(t) + \gamma(t)a(t)f(x^*_{\lambda}(t), 0, 0) + \theta(t)\eta(t)x^*_{\lambda}(t) - b(t)P_{\lambda})P_{\lambda} \leq (\Theta^u - b^{\ell}P_{\lambda})P_{\lambda},$$

where function Θ is given by

$$\Theta(t) = \max_{t \in [0,\omega]} \{ r(t), 0 \} + \gamma(t) a(t) f(x_{\lambda}^{*}(t), 0, 0) + \theta(t) \eta(t) x_{\lambda}^{*}(t).$$

Thus, comparing with equation (2.3) and using Lemma 2.2, we get $P_{\lambda}(t) \leq P_{\lambda}^{*}(t) \leq \Theta^{u}/b^{\ell}$. Using the bound obtained above, since $-\beta(t)S_{\lambda}(t) \geq -\beta(t)x_{\lambda}^{*}(t)$, we have, by conditions S3), S4) and S7),

$$S_{\lambda}' = \lambda \Lambda(t) - \lambda \mu(t) S_{\lambda} - \lambda a(t) f(S_{\lambda}, I_{\lambda}, P_{\lambda}) P_{\lambda} - \lambda \beta(t) S_{\lambda} I_{\lambda}$$

$$\geq \lambda \Lambda^{\ell} - \left(\lambda \mu^{u} + \lambda a^{u} \frac{f(S_{\lambda}, 0, 0)}{S_{\lambda}} \frac{\Theta^{u}}{b^{\ell}} + \lambda \beta^{u} (x_{\lambda}^{*})^{u}\right) S_{\lambda}$$

$$\geq \lambda \Lambda^{\ell} - \left(\lambda \mu^{u} + \lambda a^{u} K((x_{\lambda}^{*})^{u})^{\alpha - 1} \Theta^{u} / b^{\ell} + \lambda \beta^{u} (x_{\lambda}^{*})^{u}\right) S_{\lambda}.$$

According to computations above we have $x_{\lambda}^{*}(t) \leq \Lambda^{u}/\mu^{\ell}$ and thus

$$S_{\lambda}(t) \geq \frac{\lambda \Lambda^{\ell}}{\lambda \mu^{u} + \lambda a^{u} K (\Lambda^{u} / \mu^{\ell})^{\alpha - 1} \Theta^{u} / b^{\ell} + \lambda \beta^{u} \Lambda^{u} / \mu^{\ell}} =: L_{1}.$$

Lemma 2.5. Let $z_{\lambda}^{*}(t)$ be the unique solution of (2.3). There is $L_{2} > 0$ such that, for any $\lambda \in (0, 1]$ and any periodic solution $(S_{\lambda}(t), I_{\lambda}(t), P_{\lambda}(t))$ of (2.7) with initial conditions $S_{\lambda}(t_{0}) = S_{0} > 0$, $I_{\lambda}(t_{0}) = I_{0} > 0$ and $P_{\lambda}(t_{0}) = P_{0} > 0$, we have $z_{\lambda}^{*}(t) \leq P_{\lambda}(t) \leq L_{2}$, for all $t \in \mathbb{R}$.

$$P_{\lambda}' = \lambda P_{\lambda}(\gamma(t)a(t)f(S_{\lambda}, I_{\lambda}, P_{\lambda}) + \theta(t)\eta(t)I_{\lambda} + r(t) - b(t)P_{\lambda}) \ge (\lambda r(t) - \lambda b(t)P_{\lambda})P_{\lambda}.$$

Comparing the previous inequality with equation (2.3) and using Lemma 2.2, we get $P_{\lambda}(t) \ge z_{\lambda}^{*}(t)$. Using the computations in proof of the previous lemma, we have $P_{\lambda}(t) \le L_{1}$ and we take $L_{2} = L_{1}$.

Lemma 2.6. Let $\widetilde{\mathcal{R}}_0 > 1$. There are $L_3, L_4 > 0$ such that, for any $\lambda \in (0,1]$ and any periodic solution $(S_{\lambda}(t), I_{\lambda}(t), P_{\lambda}(t))$ of (2.7) with initial conditions $S_{\lambda}(t_0) = S_0 > 0$, $I_{\lambda}(t_0) = I_0 > 0$ and $P_{\lambda}(t_0) = P_0 > 0$, we have $L_3 \leq I_{\lambda}(t) \leq L_4$, for all $t \in \mathbb{R}$.

Proof. We will first prove that there is $\varepsilon_1 > 0$ such that, for any $\lambda \in (0, 1]$, we have

$$\limsup_{t \to +\infty} I_{\lambda}(t) \ge \varepsilon_1.$$
(2.8)

By contradiction, assume that (2.8) does not hold. Then, for any $\varepsilon > 0$, there must be $\lambda > 0$ such that $I_{\lambda}(t) < \varepsilon$ for all $t \in \mathbb{R}$. We have

$$\begin{cases} S'_{\lambda} \leq \lambda \Lambda(t) - \lambda \mu(t) S_{\lambda} - \lambda a(t) f(S_{\lambda}, \varepsilon, P_{\lambda}) P_{\lambda}, \\ P'_{\lambda} \leq \lambda(\gamma(t) a(t) f(S_{\lambda}, 0, P_{\lambda}) + r(t) - b(t) P_{\lambda} + \lambda \varepsilon \theta^{u} \eta^{u}) P_{\lambda} \end{cases}$$

and

$$\begin{cases} S'_{\lambda} \geq \lambda \Lambda(t) - \lambda \mu(t) S_{\lambda} - \lambda a(t) f(S_{\lambda}, 0, P_{\lambda}) P_{\lambda} - \varepsilon \lambda \beta^{u} S_{\lambda}, \\ P'_{\lambda} \geq \lambda(\gamma(t) a(t) f(S_{\lambda}, \varepsilon, P_{\lambda}) + r(t) - b(t) P_{\lambda}) P_{\lambda}. \end{cases}$$

By condition S9), we conclude that

$$x^*_{\lambda,\varepsilon\lambda\beta^u,0,0,\varepsilon}(t) \leqslant S_{\lambda}(t) \leqslant x^*_{\lambda,0,\varepsilon\lambda\theta^u\eta^u,\varepsilon,0}(t)$$

and

$$z^*_{\lambda, arepsilon \lambda eta^u, 0, 0, arepsilon}(t) \leqslant P_\lambda(t) \leqslant z^*_{\lambda, 0, arepsilon \lambda heta^u \eta^u, arepsilon, 0}(t).$$

Thus, using condition S9), we have

$$I_{\lambda}' = \lambda(\beta(t)S_{\lambda} - \eta(t)P_{\lambda} - c(t))I_{\lambda}$$

$$\geq (\lambda\beta(t)x_{\lambda,\epsilon\lambda\beta^{\mu},0,0,\epsilon}^{*}(t) - \lambda\eta(t)z_{\lambda,0,\epsilon\lambda\theta^{\mu}\eta^{\mu},\epsilon,0}^{*}(t) - \lambda c(t))I_{\lambda}$$

$$\geq (\lambda\beta(t)x_{\lambda}^{*}(t) - \lambda\eta(t)z_{\lambda}^{*}(t) - \lambda c(t) - \varphi(\epsilon))I_{\lambda},$$
(2.9)

where φ is a nonnegative function such that $\varphi(\varepsilon) \to 0$ as $\varepsilon \to 0$ (notice that, by continuity, we can assume that φ is independent of λ and, by periodicity of the parameter functions, it is independent of *t*).

Integrating in $[0, \omega]$ and using (S9)), we get

$$0 = \frac{1}{\omega} \left(\ln I_{\lambda}(\omega) - \ln I_{\lambda}(0) \right) = \frac{1}{\omega} \int_{0}^{\omega} I_{\lambda}'(s) / I_{\lambda}(s) \, ds$$

$$\geq \lambda \left(\overline{\beta} x_{\lambda}^{*} - \overline{c} - \overline{\eta} \overline{z_{\lambda}^{*}} \right) + \varphi(\varepsilon) = \lambda (\overline{c} + \overline{\eta} \overline{z_{\lambda}^{*}}) (\mathcal{R}_{0}^{\lambda} - 1) + \varphi(\varepsilon)$$

and since

$$\mathcal{R}_0^\lambda \geqslant \inf_{\ell \in (0,1]} \mathcal{R}_0^\ell = \widetilde{\mathcal{R}}_0 > 1,$$

we have a contradiction. We conclude that (2.8) holds. Next we will prove that there is $\varepsilon_2 > 0$ such that, for any $\lambda \in (0, 1]$, we have

$$\liminf_{t \to +\infty} I_{\lambda}(t) \ge \varepsilon_2. \tag{2.10}$$

Assuming by contradiction that (2.10) does not hold, we conclude that there is a sequence $(\lambda_n, I_{\lambda_n}(s_n), I_{\lambda_n}(t_n)) \subset (0, 1] \times \mathbb{R}^+_0 \times \mathbb{R}^+_0$ such that $s_n < t_n, t_n - s_n \leq \omega$,

$$I_{\lambda_n}(s_n) = 1/n$$
, $I_{\lambda_n}(t_n) = \varepsilon_2/2$ and $I_{\lambda_n}(t) \in (1/n, \varepsilon_2/2)$, for all $t \in (s_n, t_n)$

Since $\lambda_n \leq 1$, by Lemma 2.4 we have

$$I_{\lambda_n}' = (\lambda_n \beta(t) S_{\lambda_n} - \lambda_n \eta(t) P_{\lambda_n} - \lambda_n c(t)) I_{\lambda_n} \leqslant \beta^u \Lambda^u I_{\lambda_n} / \mu^\ell$$

and thus

$$\ln(\varepsilon_2 n/2) = \ln(I_{\lambda_n}(t_n)/I_{\lambda_n}(s_n)) = \int_{s_n}^{t_n} I'_{\lambda_n}(s)/I_{\lambda_n}(s) ds \leq \beta^u \Lambda^u \omega/\mu^\ell,$$

which is a contradiction since the sequence $(\ln(\varepsilon_2 n/2))_{n \in \mathbb{N}}$ goes to $+\infty$ as $n \to +\infty$, and thus is not bounded.

We conclude that there is $\varepsilon_2 > 0$ such that (2.10) holds. Letting $L_3 = \varepsilon_2$, we obtain $I_{\lambda}(t) \ge L_3$ for all $\lambda \in (0, 1]$.

Since $I_{\lambda}(t) \leq S_{\lambda}(t) + I_{\lambda}(t)$, by Lemma 2.4, we can take $L_4 = L_2$ and the result is established.

2.2 Setting where Mawhin's continuation theorem will be applied.

To apply Mawhin's continuation theorem to our model we make the change of variables: $S(t) = e^{u_1(t)}$, $I(t) = e^{u_2(t)}$ and $P(t) = e^{u_3(t)}$. With this change of variables, system (1.1) becomes

$$\begin{cases} u_1' = \Lambda(t)e^{-u_1} - a(t)f(e^{u_1}, e^{u_2}, e^{u_3})e^{u_3 - u_1} - \beta(t)e^{u_2} - \mu(t), \\ u_2' = \beta(t)e^{u_1} - \eta(t)e^{u_3} - c(t), \\ u_3' = \gamma(t)a(t)f(e^{u_1}, e^{u_2}, e^{u_3}) + \theta(t)\eta(t)e^{u_2} - b(t)e^{u_3} + r(t). \end{cases}$$
(2.11)

Note that, if $(u_1^*(t), u_2^*(t), u_3^*(t))$ is an ω -periodic solution of (2.11) then $(e^{u_1(t)}, e^{u_2(t)}, e^{u_3(t)})$ is an ω -periodic solution of system (1.1).

To define the operators in Mawhin's theorem (see appendix A), we need to consider the Banach spaces $(X, \|\cdot\|)$ and $(Z, \|\cdot\|)$ where X and Z are the space of ω -periodic continuous functions $u : \mathbb{R} \to \mathbb{R}^3$:

$$X = Z = \{ u = (u_1, u_2, u_3) \in C(\mathbb{R}, \mathbb{R}^3) : u(t) = u(t + \omega) \}$$

and

$$||u|| = \max_{t \in [0,\omega]} |u_1(t)| + \max_{t \in [0,\omega]} |u_2(t)| + \max_{t \in [0,\omega]} |u_3(t)|.$$

Next, we consider the linear map $\mathcal{L} : X \cap C^1(\mathbb{R}, \mathbb{R}^3) \to Z$ given by

$$\mathcal{L}u(t) = \frac{du(t)}{dt} \tag{2.12}$$

and the map $\mathcal{N} : X \to Z$ defined by

$$\mathcal{N}u(t) = \begin{bmatrix} \Lambda(t)e^{-u_1(t)} - a(t)f(e^{u_1}, e^{u_2}, e^{u_3})e^{u_3(t) - u_1(t)} - \beta(t)e^{u_2(t)} - \mu(t) \\ \beta(t)e^{u_1(t)} - \eta(t)e^{u_3(t)} - c(t) \\ \gamma(t)a(t)f(e^{u_1}, e^{u_2}, e^{u_3}) + \theta(t)\eta(t)e^{u_2(t)} - b(t)e^{u_3(t)} + r(t) \end{bmatrix}.$$
(2.13)

In the following lemma we show that the linear map in (2.12) is a Fredholm mapping of index zero

Lemma 2.7. The linear map \mathcal{L} in (2.12) is a Fredholm mapping of index zero.

Proof. We have

$$\ker \mathcal{L} = \left\{ (u_1, u_2, u_3) \in X \cap C^1(\mathbb{R}, \mathbb{R}^3) : \frac{du_i(t)}{dt} = 0, \ i = 1, 2, 3 \right\}$$
$$= \left\{ (u_1, u_2, u_3) \in X \cap C^1(\mathbb{R}, \mathbb{R}^3) : u_i \text{ is constant}, \ i = 1, 2, 3 \right\}$$

and thus ker \mathcal{L} can be identified with \mathbb{R}^3 . Therefore dim ker $\mathcal{L} = 3$. On the other hand

$$\operatorname{Im} \mathcal{L} = \left\{ (z_1, z_2, z_3) \in Z : \exists u \in X \cap C^1(\mathbb{R}, \mathbb{R}^3) : \frac{du_i(t)}{dt} = z_i(t), \ i = 1, 2, 3 \right\}$$
$$= \left\{ (z_1, z_2, z_3) \in Z : \int_0^\omega z_i(s) \, ds = 0, \ i = 1, 2, 3 \right\}.$$

and any $z \in Z$ can be written as $z = \tilde{z} + \alpha$, where $\alpha = (\alpha_1, \alpha_2, \alpha_3) \in \mathbb{R}^3$ and $\tilde{z} \in \text{Im } \mathcal{L}$. Thus the complementary space of Im \mathcal{L} consists of the constant functions. Thus, the complementary space has dimension 3 and therefore codim Im $\mathcal{L} = 3$.

Given any sequence (z_n) in Im \mathcal{L} such that

$$z_n = ((z_1)_n, (z_2)_n, (z_3)_n) \to z = (z_1, z_2, z_3),$$

we have, for i = 1, 2, 3 (note that $z \in Z$ since Z is a Banach space and thus it is integrable in $[0, \omega]$ since it is continuous in that interval),

$$\int_0^\omega z_i(s)\,ds = \int_0^\omega \lim_{n\to+\infty} (z_i)_n(s)\,ds = \lim_{n\to+\infty} \int_0^\omega (z_i)_n(s)\,ds = 0.$$

Thus, $z \in \text{Im } \mathcal{L}$ and we conclude that $\text{Im } \mathcal{L}$ is closed in *Z*. Thus \mathcal{L} is a Fredholm mapping of index zero.

Consider the projectors $P : X \to X$ and $Q : Z \to Z$ given by

$$Pu(t) = \frac{1}{\omega} \int_0^\omega u(s) ds$$
 and $Qz(t) = \frac{1}{\omega} \int_0^\omega z(s) ds.$

Note that $\operatorname{Im} P = \ker \mathcal{L}$ and that $\ker Q = \operatorname{Im}(I - Q) = \operatorname{Im} \mathcal{L}$.

Consider the generalized inverse of \mathcal{L} , \mathcal{K} : Im $\mathcal{L} \to D \cap \ker P$, given by

$$\mathcal{K}z(t) = \int_0^t z(s)ds - \frac{1}{\omega} \int_0^\omega \int_0^r z(s)\,ds\,dr$$

the operator $Q\mathcal{N} : X \to Z$ given by

$$Q\mathcal{N}u(t) = \begin{bmatrix} \frac{1}{\omega} \int_0^{\omega} \Lambda(s)e^{-u_1(s)} - a(s)f(e^{u_1(s)}, e^{u_2(s)}, e^{u_3(s)})e^{u_3(s)} - \beta(s)e^{u_2(s)} ds - \overline{\mu} \\ \frac{1}{\omega} \int_0^{\omega} \beta(s)e^{u_1(s)} - \eta(s)e^{u_3(s)} ds - \overline{c} \\ \frac{1}{\omega} \int_0^{\omega} \gamma(s)a(s)f(e^{u_1(s)}, e^{u_2(s)}, e^{u_3(s)})e^{u_3(s)} + \theta(s)\eta(s)e^{u_2(s)} - b(s)e^{u_3(s)} ds + \overline{r} \end{bmatrix}$$

and the mapping $\mathcal{K}(I-Q)\mathcal{N}: X \to D \cap \ker P$ given by

$$\mathcal{K}(I-Q)\mathcal{N}u(t)=B_1(t)-B_2(t)-B_3(t),$$

where

$$B_{1}(t) = \begin{bmatrix} \int_{0}^{t} \Lambda(s)e^{-u_{1}(s)} - a(s)f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}(s)} - \beta(s)e^{u_{2}(s)} - \mu(s) ds \\ \int_{0}^{t} \beta(s)e^{u_{1}(s)} - \eta(s)e^{u_{3}(s)} - c(s) ds \\ \int_{0}^{t} \gamma(s)a(s)f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}(s)} + \theta(s)\eta(s)e^{u_{2}(s)} - b(s)e^{u_{3}(s)} dt + r(s) ds \end{bmatrix},$$

$$B_{2}(t) = \begin{bmatrix} \frac{1}{\omega} \int_{0}^{\omega} \int_{0}^{r} \Lambda(s)e^{-u_{1}(s)} - a(s)f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}(s)} - \beta(s)e^{u_{2}(s)} - \mu(s) ds dr \\ \frac{1}{\omega} \int_{0}^{\omega} \int_{0}^{r} \beta(s)e^{u_{1}(s)} - \eta(s)e^{u_{3}(s)} - c(s) ds dr \\ \frac{1}{\omega} \int_{0}^{\omega} \int_{0}^{r} \gamma(s)a(s)f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}(s)} + \theta(s)\eta(s)e^{u_{2}(s)} - b(s)e^{u_{3}(s)} + r(s) ds dr \end{bmatrix},$$

and

$$B_{3}(t) = \left(\frac{t}{\omega} - \frac{1}{2}\right) \begin{bmatrix} \int_{0}^{\omega} \Lambda(s)e^{-u_{1}(s)} - a(s)f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}(s)} - \beta(s)e^{u_{2}(s)} - \mu(s) ds\\ \int_{0}^{\omega} \beta(s)e^{u_{1}(s)} - \eta(s)e^{u_{3}(s)} - c(s) ds\\ \int_{0}^{\omega} \gamma(s)a(s)f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}(s)} + \theta(s)\eta(s)e^{u_{2}(s)} - b(s)e^{u_{3}(s)} + r(s) ds \end{bmatrix}.$$

The next lemma shows that ${\mathcal N}$ is ${\mathcal L}\text{-compact}$ in the closure of any open bounded subset of its domain.

Lemma 2.8. The map \mathcal{N} is \mathcal{L} -compact in the closure of any open bounded set $U \subseteq X$.

Proof. Let $U \subseteq X$ be an open bounded set and \overline{U} its closure in X. Then, there is M > 0 such that, for any $u = (u_1, u_2, u_3) \in \overline{U}$, we have that $|u_i(t)| \leq M$, i = 1, 2, 3. Letting $Q\mathcal{N}u = ((Q\mathcal{N})_1 u, (Q\mathcal{N})_2 u, (Q\mathcal{N})_3 u)$, we have

$$\begin{aligned} |(Q\mathcal{N})_1 u(t)| &\leq \mathbf{e}^M \left(\bar{\Lambda} + \bar{a}f(e^M, 0, 0) + \bar{\beta} \right) + \bar{\mu}, \\ |(Q\mathcal{N})_2 u(t)| &\leq e^M (\bar{\beta} + \bar{\eta}) + \bar{c}, \\ |(Q\mathcal{N})_3 u(t)| &\leq \mathbf{e}^M \left(\overline{\gamma a}f(e^M, 0, 0) + \overline{\theta \eta} + \bar{b} \right) + \bar{r}. \end{aligned}$$

and we conclude that $Q\mathcal{N}(\overline{U})$ is bounded.

Let now

$$\mathcal{K}(I-Q)\mathcal{N}u = \left((\mathcal{K}(I-Q)\mathcal{N})_1 u, (\mathcal{K}(I-Q)\mathcal{N})_2 u, (\mathcal{K}(I-Q)\mathcal{N})_3 u\right).$$

Let $B \subset X$ be a bounded set. Note that the boundedness of B implies that there is M such that $|u_i| < M$, for all i = 1, 2, 3, and all $u = (u_1, u_2, u_3) \in B$. It is immediate that $\{\mathcal{K}(I - Q)\mathcal{N}u : u \in B\}$ is pointwise bounded. Given $u = (u_1, u_2, u_3)_{n \in \mathbb{N}} \in B$ we have

$$\begin{aligned} (K(I-Q)\mathcal{N})_{1}u(t) &- (\mathcal{K}(I-Q)\mathcal{N})_{1}u(v) \\ &= \int_{v}^{t} \Lambda(s)e^{-u_{1}(s)} - a(s)f(e^{u_{1}(s)}, e^{u_{2}(s)}, e^{u_{3}(s)})e^{u_{2}(s)} - \beta(s)e^{u_{2}(s)} - \mu(s)\,ds \\ &- \frac{t-v}{\omega}\int_{0}^{\omega} \Lambda(s)e^{-u_{1}(s)} - a(s)f(e^{u_{1}(s)}, e^{u_{2}(s)}, e^{u_{3}(s)})e^{u_{2}(s)} - \beta(s)e^{u_{2}(s)} - \mu(s)\,ds \\ &\leqslant 2(t-v)\left[e^{M}(\Lambda^{u} + a^{u}f(e^{M}, 0, 0) + \beta^{u}e^{M}) + \mu^{M}\right], \end{aligned}$$

and similarly

$$(\mathcal{K}(I-Q)\mathcal{N})_2 u(t) - (\mathcal{K}(I-Q)\mathcal{N})_2 u(v) \leq 2(t-v) \left[e^M (\beta^u + \eta^u) + c^u \right]$$
(2.15)

and

$$(\mathcal{K}(I-Q)\mathcal{N})_{3}u(t) - (\mathcal{K}(I-Q)\mathcal{N})_{3}u(v)) \\ \leqslant 2(t-v) \left[(\gamma^{u}a^{u}f(e^{M},0,0) + \theta^{u}\eta^{u} + b^{u})e^{M} + r^{u} \right].$$

$$(2.16)$$

By (2.14), (2.15) and (2.16), we conclude that { $\mathcal{K}(I-Q)\mathcal{N}u : u \in B$ } is equicontinuous. Therefore, by the Ascoli–Arzelà theorem, $\mathcal{K}(I-Q)\mathcal{N}(B)$ is relatively compact. Thus the operator $\mathcal{K}(I-Q)\mathcal{N}$ is compact.

We conclude that \mathcal{N} is \mathcal{L} -compact in the closure of any bounded set contained in X.

2.3 Application of Mawhin's continuation theorem.

In this section we will construct the set where, applying Mahwin's continuation theorem, we will find the periodic orbit in the statement of our result.

Consider the system of algebraic equations:

$$\begin{cases} \overline{\Lambda}e^{-u_{1}} - \overline{a}f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}})e^{u_{3}-u_{1}} - \overline{\beta}e^{u_{2}} - \overline{\mu} = 0, \\ \overline{\beta}e^{u_{1}} - \overline{\eta}e^{u_{3}} - \overline{c} = 0, \\ \overline{\gamma}\overline{a}f(e^{u_{1}}, e^{u_{2}}, e^{u_{3}}) + \overline{\theta}\overline{\eta}e^{u_{2}} - \overline{b}e^{u_{3}} + \overline{r} = 0. \end{cases}$$
(2.17)

Note that, by hypothesis, the system above has a unique solution on the interior of the first octant. Denote this solution by $p^*(t) = (p_1^*, p_2^*, p_3^*)$. Note also that, by the second equation, we get

$$\overline{\eta}e^{u_3} = \overline{\beta}e^{u_1} - c. \tag{2.18}$$

By Lemmas 2.4, 2.5 and 2.6, there is a constant $M_0 > 0$ such that $||u_\lambda(t)|| < M_0$, for any $t \in [0, \omega]$ and any periodic solution $u_\lambda(t)$ of (2.7). Let

$$U = \{(u_1, u_2, u_3) \in X : \|(u_1, u_2, u_3)\| < M_0 + \|p^*\|\}.$$
(2.19)

Conditions M1. and M2. in Mawhin's continuation theorem (see Appendix A) are fulfilled in the set U defined in (2.19).

Using the notation $v = (e^{p_1^*}, e^{p_2^*}, e^{p_3^*})$, the Jacobian matrix of the vector field corresponding to (2.17) computed in (p_1^*, p_2^*, p_3^*) is

$$J = \begin{bmatrix} -\overline{a}\frac{\partial f}{\partial S}(v) e^{p_3^*} - \overline{\beta} e^{p_2^*} - \overline{\mu} & -\overline{\beta} e^{p_2^*} - \overline{a}\frac{\partial f}{\partial I}(v) e^{p_3^* + p_2^* - p_1^*} & -\overline{a}\frac{\partial f}{\partial P}(v) e^{2p_3^* - p_1^*} - \overline{a}f(v) e^{p_3^* - p_1^*} \\ \overline{\beta} e^{p_1^*} & 0 & -\overline{\eta} e^{p_3^*} \\ \overline{\gamma a}\frac{\partial f}{\partial S}(v) e^{p_1^*} & \overline{\theta \eta} e^{p_2^*} + \overline{\gamma a}\frac{\partial f}{\partial I}(v) e^{p_2^*} & \overline{\gamma a}\frac{\partial f}{\partial P}(v) e^{p_3^*} - \overline{b} e^{p_3^*} \end{bmatrix}.$$

Thus

$$\begin{split} \det J(p_1^*, p_2^*, p_3^*) \\ &= -\overline{\beta} \, \mathrm{e}^{p_1^*} \left(-\overline{\beta} \, \mathrm{e}^{p_2^*} \left(\overline{\gamma a} \frac{\partial f}{\partial P}(v) \, \mathrm{e}^{p_3^*} - \overline{b} \, \mathrm{e}^{p_3^*} \right) + \left(\overline{a} \frac{\partial f}{\partial P}(v) \, \mathrm{e}^{2p_3^* - p_1^*} + \overline{a} f(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \overline{\theta \eta} \, \mathrm{e}^{p_2^*} \right) \\ &- \overline{\beta} \, \mathrm{e}^{p_1^*} \left(-\overline{a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_2^* + p_3^* - p_1^*} \left(\overline{\gamma a} \frac{\partial f}{\partial P}(v) \, \mathrm{e}^{p_3^*} - \overline{b} \, \mathrm{e}^{p_3^*} \right) + \left(\overline{a} \frac{\partial f}{\partial P}(v) \, \mathrm{e}^{2p_3^* - p_1^*} + \overline{a} f(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \overline{\gamma a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_2^*} \right) \\ &+ \overline{\eta} \, \mathrm{e}^{p_3^*} \left(\left(-\overline{a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_3^*} - \overline{\beta} \, \mathrm{e}^{p_2^*} - \overline{\mu} \right) \overline{\eta a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_2^*} + \overline{a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_1^*} \right) \\ &+ \overline{\eta} \, \mathrm{e}^{p_3^*} \left(\left(-\overline{a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_3^*} - \overline{\beta} \, \mathrm{e}^{p_2^*} - \overline{\mu} \right) \overline{\gamma a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_2^*} + \overline{a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_2^* + p_3^* - p_1^*} \, \overline{\gamma a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_1^*} \right) \\ &= -\overline{\beta} \, \mathrm{e}^{p_1^*} \left(- \left(\overline{\beta} + \overline{a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \, \mathrm{e}^{p_2^*} \left(\overline{\gamma a} \frac{\partial f}{\partial P}(v) \, \mathrm{e}^{p_3^*} - \overline{b} \, \mathrm{e}^{p_3^*} \right) \\ &+ \left(\overline{a} \frac{\partial f}{\partial P}(v) \, \mathrm{e}^{2p_3^* - p_1^*} + \overline{a} f(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \left(\overline{\theta \eta} + \overline{\gamma a} \frac{\partial f}{\partial I}(v) \right) \, \mathrm{e}^{p_2^*} \right) \\ &+ \overline{\eta} \, \mathrm{e}^{p_3^*} \left(\left(-\overline{a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \left(\overline{\theta \eta} + \overline{\gamma a} \frac{\partial f}{\partial I}(v) \right) \, \mathrm{e}^{p_2^*} \right) \\ &+ \overline{\eta} \, \mathrm{e}^{p_3^*} \left(\left(-\overline{a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \left(\overline{\theta \eta} + \overline{\gamma a} \frac{\partial f}{\partial I}(v) \right) \, \mathrm{e}^{p_2^*} \right) \\ &+ \left(\overline{\beta} \, \mathrm{e}^{p_2^*} + \overline{a} \frac{\partial f}{\partial I}(v) \, \mathrm{e}^{p_3^* - p_1^*} \right) \overline{\gamma a} \frac{\partial f}{\partial S}(v) \, \mathrm{e}^{p_1^*} \right). \end{split}$$

Taking into account S5) and (2.18), we have

$$\det J(p_1^*, p_2^*, p_3^*) = -\overline{\beta} e^{p_1^*} \left(-\frac{\overline{\beta}}{\overline{\eta}} \left(\overline{\eta} + \overline{a} \frac{\partial f}{\partial I}(v) - \frac{\overline{ac}}{\overline{\beta}} \frac{\partial f}{\partial I}(v) e^{-p_1^*} \right) e^{p_2^*} \left(\overline{\gamma a} \frac{\partial f}{\partial P}(v) e^{p_3^*} - \overline{b} e^{p_3^*} \right) + \overline{a} e^{p_3^* - p_1^*} \left(\frac{\partial f}{\partial P}(v) e^{p_3^*} + f(v) \right) \left(\overline{\theta \eta} + \overline{\gamma a} \frac{\partial f}{\partial I}(v) \right) e^{p_2^*} \right) + \overline{\eta} e^{p_3^*} \left(\left(-\overline{a} \frac{\partial f}{\partial S}(v) e^{p_3^*} - \overline{\beta} e^{p_2^*} - \overline{\mu} \right) \left(\overline{\theta \eta} + \overline{\gamma a} \frac{\partial f}{\partial I}(v) \right) e^{p_2^*} + \frac{\overline{\beta}}{\overline{\eta}} \left(\overline{\eta} + \overline{a} \frac{\partial f}{\partial I}(v) - \frac{\overline{ac}}{\overline{\beta}} \frac{\partial f}{\partial I}(v) e^{-p_1^*} \right) e^{p_2^*} \overline{\gamma a} \frac{\partial f}{\partial S}(v) e^{p_1^*} \right) < 0.$$

Let $\mathcal{I} : \operatorname{Im} Q \to \ker \mathcal{L}$ be an isomorphism. Thus

$$\deg(\mathcal{IQN}, U \cap \ker \mathcal{L}, 0) = \det J(p_1^*, p_2^*, p_3^*) \neq 0$$
(2.20)

and condition M3) in Mawhin's continuation theorem (see appendix A) holds. Taking into account Lemma 2.6, the proof of Theorem 2.3 is completed.

3 Examples.

In this section we present some examples to illustrate the main result in the previous section.

3.1 A model with Holling-type I functional response.

Letting f(S, I, P) = S (Holling-type I functional response) in system (2.1), we obtain the model:

$$\begin{cases} S' = \Lambda(t) - \mu(t)S - a(t)SP + \beta(t)SI, \\ I' = \beta(t)SI - \eta(t)PI - c(t)I, \\ P' = (r(t) - b(t)P)P + \gamma(t)a(t)SP + \theta\eta(t)PI. \end{cases}$$
(3.1)

Since f(S, I, P) = S, conditions S2) to S5) are trivially satisfied and S7) is satisfied with $K = \alpha = 1$. We obtain the following corollary.

Corollary 3.1. Assume that that conditions S1), S6) and S9) hold. If $\tilde{R}_0 > 1$, $\bar{\beta} \bar{b} - \bar{\gamma} \bar{a\eta} > 0$ and

$$\overline{\mathcal{R}}_{0} > 1 + \overline{a\eta} \, \frac{\overline{\gamma} \,\overline{\Lambda}}{\overline{\mu}(\overline{r} \,\overline{\eta} + \overline{b} \,\overline{c})} + a \frac{\overline{\beta} \,\overline{r} + \overline{\gamma} \overline{a} \,\overline{c}}{\overline{\mu}(\overline{b} \,\overline{\beta} - \overline{\gamma} \,\overline{a\eta})} \tag{3.2}$$

then system (3.1) possesses an endemic periodic orbit of period ω .

Proof. Consider the system of algebraic equations

$$\begin{cases} \overline{\Lambda}e^{-u_1} - \overline{a}e^{u_3} - \overline{\beta}e^{u_2} - \overline{\mu} = 0, \\ \overline{\beta}e^{u_1} - \overline{\eta}e^{u_3} - \overline{c} = 0, \\ \overline{\gamma}\overline{a}e^{u_1} + \overline{\theta}\overline{\eta}e^{u_2} - \overline{b}e^{u_3} + \overline{r} = 0. \end{cases}$$
(3.3)

By the second and third equations we get

$$e^{u_1} = \frac{\overline{\eta} e^{u_3} + \overline{c}}{\overline{\beta}}$$
 and $e^{u_2} = \frac{\overline{\beta} \overline{b} - \overline{\gamma} \overline{a\eta}}{\overline{\beta} \overline{\theta} \overline{\eta}} e^{u_3} - \frac{\overline{\beta} \overline{r} + \overline{\gamma} \overline{a} \overline{c}}{\overline{\beta} \overline{\theta} \overline{\eta}}.$

Notice that by hypothesis $\overline{\beta} \overline{b} - \overline{\gamma} \overline{a\eta} > 0$ and the right hand side of the second equation is positive as long as $e^{u_3} > (\overline{\beta} \overline{r} + \overline{c} \overline{\gamma a}) / (\overline{\beta} \overline{b} - \overline{\gamma} \overline{a\eta})$. Using the first equation we get

$$\frac{\overline{\beta}\,\overline{\Lambda}}{\overline{\eta}\,\mathrm{e}^{u_3}+\overline{c}}-\left(\overline{a}+\frac{\overline{\beta}\,\overline{b}-\overline{\gamma}\,\overline{a\eta}}{\overline{\theta}\,\overline{\eta}}\right)\mathrm{e}^{u_3}+\frac{\overline{\beta}\,\overline{r}+\overline{\gamma}\overline{a}\,\overline{c}}{\overline{\theta}\,\overline{\eta}}-\overline{\mu}=0.$$

Taking into account that we must have $e^{u_3} > (\overline{\beta} \,\overline{r} + \overline{c} \,\overline{\gamma a})/(\overline{\beta} \,\overline{b} - \overline{\gamma} \,\overline{a\eta})$, we consider the function $F : [(\overline{\beta} \,\overline{r} + \overline{c} \,\overline{\gamma a})/(\overline{\beta} \,\overline{b} - \overline{\gamma} \,\overline{a\eta}), +\infty[\rightarrow \mathbb{R}$ given by

$$F(x) = \frac{\overline{\beta}\,\overline{\Lambda}}{\overline{\eta}\,x + \overline{c}} - \left(\overline{a} + \frac{\overline{\beta}\,\overline{b} - \overline{\gamma}\,\overline{a\eta}}{\overline{\theta}\,\overline{\eta}}\right)x + \frac{\overline{\beta}\,\overline{r} + \overline{\gamma}\overline{a}\,\overline{c}}{\overline{\theta}\,\overline{\eta}} - \overline{\mu}.$$

It is immediate that *F* is decreasing and that, by the hypothesis in our corollary, we have

$$F\left(\frac{\overline{\beta}\,\overline{r}+\overline{c}\,\overline{\gamma}\overline{a}}{\overline{\beta}\,\overline{b}-\overline{\gamma}\,\overline{a}\overline{\eta}}\right) = \overline{\mu}\left(\overline{\mathcal{R}}_0 - 1 - \frac{\overline{a}\overline{\eta}\,\overline{\gamma}\,\overline{\Lambda}}{\overline{\mu}(\overline{r}\,\overline{\eta}+\overline{b}\,\overline{c})} - a\frac{\overline{\beta}\,\overline{r}+\overline{\gamma}\overline{a}\,\overline{c}}{\overline{\mu}(\overline{b}\,\overline{\beta}-\overline{\gamma}\,\overline{a}\overline{\eta})}\right) > 0$$

and $\lim_{x\to+\infty} F(x) = -\infty$. We conclude that there is $x_0 \in [(\overline{\beta} \overline{r} + \overline{c} \overline{\gamma a})/(\overline{\beta} \overline{b} - \overline{\gamma} \overline{a\eta}), +\infty[$ such that $F(x_0) = 0$. This implies that there is a unique solution of (3.3). The result follows now from Theorem 2.3.

We now assume that the real valued functions Λ , μ , r, b, γ and a are constant and positive. Model (3.1) becomes

$$\begin{cases} S' = \Lambda - \mu S - aSP + \beta(t)SI, \\ I' = \beta(t)SI - \eta(t)PI - c(t)I, \\ P' = (r - bP)P + \gamma aSP + \theta\eta(t)PI. \end{cases}$$
(3.4)

We have the following corollary.

Corollary 3.2. Assume that that conditions S1) and S6) hold. If $\tilde{R}_0 > 1$, $b\overline{\beta} - \gamma a\overline{\eta} > 0$, $\Lambda < \mu^2/a$ and

$$\overline{\mathcal{R}}_0 > 1 + \frac{a}{\mu} \left(\frac{\overline{\eta} \gamma \Lambda}{r \, \overline{\eta} + b \, \overline{c}} + \frac{\overline{\beta} \, r + \gamma a \, \overline{c}}{b \, \overline{\beta} - \gamma \, a \overline{\eta}} \right)$$

then system (3.4) possesses an endemic periodic orbit of period ω .

Proof. We begin by noticing that system (2.4) becomes in our context

$$\begin{cases} x' = \lambda(\Lambda - \mu x - axz - \varepsilon_1 x), \\ z' = \lambda(r - bz + \gamma ax + \varepsilon_2)z. \end{cases}$$
(3.5)

System (3.5) has two equilibriums: $E_1 = (\Lambda/(\mu + \varepsilon_1), 0)$ and

$$E_2 = \left(\frac{\sqrt{V^2 + 4\Lambda\gamma a^2/b} - V}{2\gamma a^2/b}, \frac{\sqrt{V^2 + 4\Lambda\gamma a^2/b} - V}{2\gamma a^2/b} + r + \varepsilon_2\right),$$

where $V = \mu + \varepsilon_1 + a(r + \varepsilon_2)/b$. It is easy to check that E_2 is locally attractive and that E_1 is a saddle point whose stable manifold coincides with the x-axis. If $0 < \alpha < (r + \varepsilon_2)/b$ then, in the line $z = \alpha$ the flow points upward. Additionally, if $\Lambda < \mu(\mu + \varepsilon_1)/a$, in the line $x = \mu/a$ the flow points to the left and the *x*-coordinate of E_1 is less than μ/a . Thus the region $R = \{(x, z) \in \mathbb{R}^2 : 0 \le x \le \mu/a \land z \ge \alpha\}$ is positively invariant. Since the divergence of the vector field is given by $-\mu - \varepsilon_1 + \varepsilon_2 - (a + 2b)z + \gamma ax$, we conclude that it is null on the line $z = \frac{-\mu - \varepsilon_1 + \varepsilon_2}{a + 2b} + \frac{\gamma a}{a + 2b}x$. Thus the divergence of the vector field doesn't change sign on the region *R* and this forbids the existence of a periodic orbit on *R*. There is also no periodic orbit on $(\mathbb{R}_0^+)^2 \setminus R$ since there is no additional equilibrium in $(\mathbb{R}_0^+)^2$. Since E_2 is locally asymptotically stable, there is no homoclinic orbit connecting E_2 to itself. Therefore, the ω -limit of any orbit in $(\mathbb{R}^2)^+$ must be the equilibrium point E_2 and the global asymptotic stability of (3.5) for sufficiently small $\varepsilon_1, \varepsilon_2 > 0$ follows. We conclude that condition S9) holds.

To do some simulation, we consider the following particular set of parameters: $\Lambda = 0.1$; $\mu = 0.6$; $\beta(t) = 20(1 + 0.9\cos(2\pi t))$; $\eta(t) = 0.7(1 + 0.7\cos(\pi + 2\pi t))$; c(t) = 0.1; r = 0.2; b = 0.3; $\theta = 10$, $\gamma(t) = 0.1$ and a = 3. We obtain the model

$$\begin{cases} S' = 0.1 - 0.6S - 20(1 + 0.9\cos(2\pi t))SI - 3SP, \\ I' = 20(1 + 0.9\cos(2\pi t))SI - 0.7(1 + 0.7\cos(\pi + 2\pi t))PI - 0.1I, \\ P' = (0.2 - 0.3P)P + 7(1 + 0.7\cos(\pi + 2\pi t))PI + 0.3SP. \end{cases}$$
(3.6)

Notice that, for our model, $\Lambda = 0.1 > 0.012 = \mu^2/a$, $b\overline{\beta} - \gamma a\overline{\eta} = 3.99 > 0$, $\overline{R}_0 \approx 5.88 > 1 + 1.86$ and $\widetilde{R}_0 \approx 24.8 > 1$, and thus the conditions in Corollary 3.1 are fulfilled. Considering the initial condition (S_0 , I_0 , P_0) = (0.03567, 0.02047, 0.88021) we obtain the periodic orbit in Figure 3.1. Although

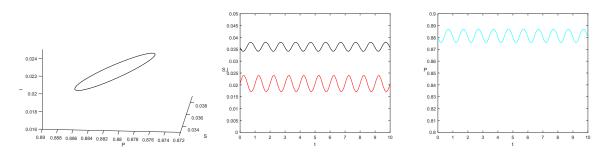


Figure 3.1: Periodic orbit for model (3.6)

our theoretical result doesn't imply the attractivity of the periodic solution, the simulations carried out suggest that this is the case.

3.2 A model with no predation on susceptible preys.

Letting $f \equiv 0$ in system (1.1), and still assuming that the real valued functions Λ , μ , β , η , c, γ , r, θ and b are periodic with period ω , nonnegative, continuous and also that $\bar{\Lambda} > 0$, $\bar{\mu} > 0$, $\bar{r} > 0$ and $\bar{b} > 0$, we

obtain the periodic model considered in [13, 18]:

$$\begin{cases} S' = \Lambda(t) - \mu(t)S - \beta(t)SI, \\ I' = \beta(t)SI - \eta(t)PI - c(t)I, \\ P' = (r(t) - b(t)P)P + \theta(t)\eta(t)PI. \end{cases}$$
(3.7)

In [18], the authors refer that the assumption that predator mainly eats the infected prey (that is modelled by assuming that no predation on uninfected preys occur) is in accordance with the fact that the infected individuals are less active and can be caught more easily, or that infection modifies the behavior of the preys in such a way that they start living in parts of the habitat which are accessible to the predator. Some examples available in the literature are also provided in [18]: as an example of a situation where infected individuals can be caught more easily, the authors cite [10], where it is showed that wolf attacks on moose on Isle Royale in Lake Superior are more successful if the moose are heavily infected with a lungworm; as an example of a situation where the behavior of the prey individuals is modified, favoring predation, the authors cite [7].

Note that conditions S2) to S5) and S7) are trivially satisfied since $f \equiv 0$. Also note that system (2.4) becomes in this context

$$\begin{cases} x' = \lambda(\Lambda(t) - \mu(t)x - \varepsilon_1 x), \\ z' = \lambda(r(t) - b(t)z + \varepsilon_2)z. \end{cases}$$
(3.8)

and, by Lemmas 1 to 4 in [18] we conclude that condition S9) holds in this setting. Note also that condition (3.2) becomes $\overline{\mathcal{R}}_0 > 1$ and condition $\overline{b}\overline{\beta} - \overline{\gamma}\overline{a\eta} \leq 0$ is trivially satisfied since we can take $\gamma = 0$ or a = 0. We obtain the following corollary that recovers the result in [13]:

Corollary 3.3. If $\tilde{\mathcal{R}}_0 > 1$ and $\overline{\mathcal{R}}_0 > 1$ hold, then system (3.7) possesses an endemic periodic orbit of period ω .

4 Eco-epidemiological models with linear vital dynamics for predators

In this section we let $h(t, P) = Y(t) - \zeta(t)P$, obtaining the following model:

$$\begin{cases} S' = \Lambda(t) - \mu(t)S - a(t)f(S, I, P)P - \beta(t)SI, \\ I' = \beta(t)SI - \eta(t)g(S, I, P)I - c(t)I, \\ P' = Y(t) - \zeta(t)P + \gamma(t)a(t)f(S, I, P)P + \theta(t)\eta(t)g(S, I, P)I. \end{cases}$$
(4.1)

To establish the existence of an endemic periodic orbit for system (4.1) we assume the following natural conditions:

- R1) The real valued functions Λ , μ , a, β , η , c, Y, ζ , γ and θ are periodic with period ω , nonnegative and continuous;
- R2) Functions $y \mapsto f(x, y, z)$ and $z \mapsto f(x, y, z)$ is nonincreasing; function $x \mapsto f(x, y, z)$ is nondecreasing;
- R3) Functions $x \mapsto g(x, y, z)$, $y \mapsto g(x, y, z)$ are nonincreasing; function $z \mapsto g(x, y, z)$ is nondecreasing;
- R4) Function f is C^1 ;
- R5) $\bar{\Lambda} > 0$, $\bar{\mu} > 0$, $\bar{Y} > 0$ and $\bar{\zeta} > 0$.

Note that our setting includes several of the most common functional responses for both functions f and g: f(S, I, P) = kS and g(S, I, P) = kP (Holling-type I), f(S, I, P) = kS/(1 + m(S + I)) and g(S, I, P) = kP/(1 + m(S + I)) (Holling-type II), $f(S, I, P) = kS^{\alpha}/(1 + m(S + I)^{\alpha})$ and $g(S, I, P) = kP^{\alpha}/(1 + m(S + I)^{\alpha})$ (Holling-type III), $f(S, I, P) = kS/(a + b(S + I) + c(S + I)^2)$ and $g(S, I, P) = kP/(a + b(S + I) + c(S + I)^2)$ (Holling-type IV), f(S, I, P) = kS/(a + b(S + I) + cP) and $g(S, I, P) = kP/(a + b(S + I) + c(S + I)^2)$ (Holling-type IV), f(S, I, P) = kS/(a + b(S + I) + cP) and g(S, I, P) = kP/(a + b(S + I)

kP/(a + b(S + I) + cP) (Beddington–De Angelis), f(S, I, P) = kS/(a + b(S + I) + cP + d(S + I)P) and g(S, I, P) = kP/(a + b(S + I) + cP + d(S + I)P) (Crowley–Martin). Also note that conditions S3), S4) are natural from a biological perspective and naturally are satisfied by the usual functional responses considered in the literature. Conditions S5) and S7) are satisfied by most of the usual functional response functions.

We also need to consider the following auxiliary system that corresponds to perturbations of the disease-free system for (4.1):

$$\begin{cases} x' = \Lambda(t) - \mu(t)x - a(t)f(x,\varepsilon_3,z)z - \varepsilon_1 x, \\ z' = \Upsilon(t) - \zeta(t)z + \gamma(t)a(t)f(x,\varepsilon_4,z)z + \varepsilon_2 z. \end{cases}$$
(4.2)

We now make our last structural assumption on system (4.1):

R5) For each ε_1 , ε_2 , ε_3 , $\varepsilon_4 \ge 0$ sufficiently small, system (4.2) has a unique ω -periodic solution

$$(x^*_{\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t), z^*_{\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t))$$

with

$$x^*_{\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t) > 0$$
 and $z^*_{\varepsilon_1,\varepsilon_2,\varepsilon_3,\varepsilon_4}(t) > 0$

that is globally asymptotically stable in the set

$$\{(x,z)\in (\mathbb{R}^+_0)^2: x \ge 0 \land z \ge 0\}.$$

We assume that $(\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4) \mapsto (x^*_{\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4}(t), z^*_{\varepsilon_1, \varepsilon_2, \varepsilon_3, \varepsilon_4}(t))$ is continuous.

To obtain the basic reproductive number for our model we consider the ordering (I, S, P) instead of (S, I, P), so that the infected compartment becomes the first one and the uninfected compartments became the last ones. Our new notation corresponds to the one in [12]. With this ordering, the functions \mathcal{F} , \mathcal{V}^+ and \mathcal{V}^- in [12] become respectively

$$\mathcal{F}(t, (I, S, P)) = (\beta(t)SI, 0, 0),$$

$$\mathcal{V}^{+}(t, (I, S, P)) = (0, 0, Y(t) + \gamma(t)a(t)f(S, I, P)P + \theta(t)\eta(t)g(S, I, P)I)$$

and

$$\mathcal{V}^{-}(t, (I, S, P)) = (\eta(t)g(S, I, P)I + c(t)I, \mu(t)S + a(t)f(S, I, P)P + \beta(t)SI, \zeta(t)P)$$

Having identified \mathcal{F} and \mathcal{V} we can compute the matrices F(t) and V(t) in [12] that in our context reduce to one dimensional matrices (that we identify with real numbers). In fact, we have

$$F(t) = \frac{\partial}{\partial I} (\beta(t)SI)|_{(x^*(t),0,z^*(t))} = \beta(t)x^*(t)$$

and

$$V(t) = \frac{\partial}{\partial I}(\eta(t)g(S, P, I)I + c(t)I)|_{(x^*(t), 0, z^*(t))} = \eta(t)g(x^*(t), 0, z^*(t)) + c(t).$$

The evolution operator $W(s,t,\lambda)$ associated with the linear ω -periodic parametric system $w' = (-V(t) + F(t)/\lambda)w$ is easily seen to be given by

$$W(s,t,\lambda) = \mathrm{e}^{-\int_s^t \beta(r) x^*(r)/\lambda - c(r) - \eta(r)g(x^*(r),0,z^*(r))\,dr}$$

and thus

$$W(\omega,0,\lambda) = 1 \quad \Leftrightarrow \quad \overline{\beta x^*} / \lambda - \overline{c} - \overline{\eta g(x^*,0,z^*)} = 0 \quad \Leftrightarrow \quad \lambda = \frac{\beta x^*}{\overline{c} + \overline{\eta g(x^*,0,z^*)}}.$$

Define

$$\mathcal{R}_0 = \frac{\overline{\beta}x^*}{\overline{c} + \overline{\eta g(x^*, 0, z^*)}}.$$
(4.3)

Note that our system satisfies conditions (A_1) to (A_7) in [6].

Theorem 4.1. Assume conditions R1) to R5). If $\mathcal{R}_0 > 1$, then model (4.1) has an endemic periodic orbit in $(\mathbb{R}^+_0)^3$.

The proof of our theorem adapts to our situation the strategy in [6,12]. It will be developed in two steps: using a result derived in [12], we obtain persistence of the infective prey in subsection 4.1 and then, using a Poincaré map, we establish the existence of a periodic orbit in subsection 4.2.

4.1 Uniform persistence

The first step in the proof of Theorem 4.1 is to establish the persistence of all the compartments in our model. To do so we will use Theorem 2 in [12]. Note first that, as long as $\alpha_3 \max\{\theta, \gamma\} < \alpha_2 < \alpha_1$, we have

$$\langle (S', I', P'), (\alpha_1, \alpha_2, \alpha_3) \rangle = \alpha_1 (\Lambda(t) - \mu(t)S - a(t)f(S, I, P)P - \beta(t)SI) + \alpha_2 (\beta(t)SI - \eta(t)g(S, I, P)I - c(t)I) + \alpha_3 (Y(t) - \zeta(t)P + \gamma(t)a(t)f(S, I, P)P + \theta(t)\eta(t)g(S, I, P)I) < \alpha_1\Lambda^u + \alpha_3Y^u - \min\{\mu^\ell + c^\ell + \zeta^\ell\}(\alpha_1S + \alpha_2I + \alpha_3P).$$

$$(4.4)$$

Thus, defining

$$K = \frac{\alpha_1 \Lambda^u + \alpha_3 \Upsilon^u}{\min\{\mu^\ell + c^\ell + \zeta^\ell\}}$$

we conclude $\langle (S', I', P'), (\alpha_1, \alpha_2, \alpha_3) \rangle < 0$ when $\alpha_1 S + \alpha_2 I + \alpha_3 P < K$ and that the set

$$\mathcal{K} = \{ (S, I, P) \in (\mathbb{R}_0^+)^3 : \alpha_1 S + \alpha_2 I + \alpha_3 P \le K \}$$
(4.5)

is forward invariant for the flow of system (4.1). Additionally, letting $W = \alpha_1 S + \alpha_2 I + \alpha_3 P$, $t_0 \ge 0$ and $W_0 = \alpha_1 S(t_0) + \alpha_2 I(t_0) + \alpha_3 P(t_0)$, by (4.4) we have for $t \ge t_0$

$$W(t) < K - (K - W_0) e^{-\min\{\mu^{\ell} + c^{\ell} + \zeta^{\ell}\}(t - t_0)}$$

and thus $\limsup_{t\to+\infty} W(t) < K$. We conclude that \mathcal{K} is an absorbing set for the flow. Thus the set \mathcal{K} satisfies assumption (A_8) in [6].

Let now (S(t), I(t), P(t)) be a solution of (4.1) such that $I(t) \leq \varepsilon$, for $t \geq 0$. Since, by the first and third equations in (4.1), we have

$$\begin{cases} S' \ge \Lambda(t) - \mu(t)S - a(t)f(S, 0, P)P - \beta^{u}S\varepsilon, \\ P' \ge Y(t) - \zeta(t)P + \gamma(t)a(t)f(S, \varepsilon, P)P \end{cases}$$

and

$$\begin{cases} S' \leq \Lambda(t) - \mu(t)S - a(t)f(S,\varepsilon,P)P, \\ P' \leq \Upsilon(t) - \zeta(t)P + \gamma(t)a(t)f(S,0,P)P + \theta^{u}\eta^{u}P\varepsilon, \end{cases}$$

condition R5), allows us to conclude that for sufficiently large t > 0 we have $S(t) \ge x_{\beta^{\mu}\varepsilon,0,0,\varepsilon}^{*}(t) \ge x^{*}(t) - \sigma_{1}(\varepsilon)$ and $P(t) \le z_{0,\theta^{\mu}\eta^{\mu}\varepsilon,\varepsilon,0}^{*}(t) \le z^{*}(t) + \sigma_{2}(\varepsilon)$ with $\sigma_{1}(\varepsilon), \sigma_{2}(\varepsilon) \to 0$ as $\varepsilon \to 0$. Thus, taking into account R2) and R3), if $I(t) \le \varepsilon$ we have

$$I' = \beta(t)SI - \eta(t)g(S, I, P)I - c(t)I$$

$$\geq \left(\beta(t)x^*(t) - \beta^{\ell}\sigma_1(\varepsilon) - \eta(t)g(x^*(t) - \sigma_1(\varepsilon), 0, z^*(t) + \sigma_2(\varepsilon)) - c(t)\right)I$$

$$\geq (F(t)/\lambda(\varepsilon) - V(t))I$$

where $\lambda : [0, \varepsilon^*] \to \mathbb{R}$, well-defined when we take $\varepsilon^* > 0$ sufficiently small, is given by

$$\lambda(\varepsilon) = \max_{t \in]0,\varepsilon[} \frac{\beta(t)x^*(t)}{\beta(t)x^*(t) - \beta^{\ell}\sigma_1(\varepsilon) + \eta(t)g(x^*(t), 0, z^*(t)) - \eta(t)g(x^*(t) - \sigma_1(\varepsilon), 0, z^*(t) + \sigma_2(\varepsilon)))}$$

and we can immediately see that $\lambda(\varepsilon) \to 1$ as $\varepsilon \to 0$.

By Theorem 2 in [12], we conclude that the infective prey is uniformly strong persistent in system (4.1). The uniform strong persistence of the susceptible prey and the predator, in our situation, is a consequence of the uniform strong persistence of the infectives. In fact, given $\delta > 0$, if $\limsup_{t\to+\infty} S(t) < \delta$ for some solution (S(t), I(t), P(t)) then $I' \leq (\beta^u \delta - c^\ell)I$. Thus, if we had a solution such that $\delta < c^\ell / \beta^u$ it would follow that $I(t) \to 0$, contradicting the uniform persistence of *I*. Therefore *S* is uniformly weak persistent. By Theorem 1.3.3 in [17], we conclude that *S* must be uniformly strong persistent. Finally, the uniform strong persistence of *P* is a consequence of the bound $P' \geq Y^\ell - \zeta^u P$.

4.2 Existence of a periodic orbit

Next, to establish the existence of a positive periodic orbit for (4.1) we use the following result.

Theorem 4.2 ([17, Theorem 1.3.6]). Let $\tau : X \to X$ be a continuous map with $\tau(X_0) \subset X_0$ that is point dissipative, compact and uniform persistent with respect to $(X_0, \partial X_0)$. Then there exists a global attractor A_0 for S in X_0 that attracts strongly bounded sets in X_0 and S has a coexistence state $x_0 \in A_0$.

To apply this result to our model we let $X = (\mathbb{R}_0^+)^3$, $X_0 = \mathcal{K}$ and $S = \tau$, where $\tau : (\mathbb{R}_0^+)^3 \to (\mathbb{R}_0^+)^3$ ia a time- ω map associated to our system and given by $\tau(S_0, I_0, P_0) = (S(\omega), I(\omega), P(\omega))$, where (S(t), I(t), P(t)) is the solution of (4.1) such that $(S(0), I(0), P(0)) = (S_0, I_0, P_0)$.

Since the bounded set \mathcal{K} is an absorbing set for the flow of (4.1), we conclude that τ is point dissipative. It is immediate that τ is compact and, by the discussion in subsection 4.1, we conclude that τ is uniformly persistent with respect to ($\mathcal{K}, \partial \mathcal{K}$). Therefore, Theorem 4.2 allows us to conclude that τ has a coexistence state in \mathcal{K} . This coexistence state is a periodic orbit of our system contained in \mathcal{K} . This established our result.

A Mawhin's continuation theorem

In this appendix we state Mawhin's continuation theorem [9, Part IV]. Let X and Z be Banach spaces.

Definition A.1. A linear map $\mathcal{L} : D \subseteq X \to Z$ is called a Fredholm mapping of index zero if

- 1. dim ker $\mathcal{L} = \operatorname{codim} \operatorname{Im} \mathcal{L} \leqslant \infty$;
- 2. Im \mathcal{L} is closed in Z.

Given a Fredholm mapping of index zero $\mathcal{L} : D \subseteq X \to Z$ it is well known that there are continuous projectors $P : X \to X$ and $Q : Z \to Z$ such that:

- 1. Im $P = \ker \mathcal{L}$;
- 2. ker $Q = \operatorname{Im} \mathcal{L} = \operatorname{Im}(I Q);$
- 3. $X = \ker \mathcal{L} \oplus \ker P$;
- 4. $Z = \operatorname{Im} \mathcal{L} \oplus \operatorname{Im} Q$.

It follows that $\mathcal{L}|_{D \cap \ker P} : (I - P)X \to \operatorname{Im} \mathcal{L}$ is invertible. We denote the inverse of that map by \mathcal{K} .

Definition A.2. A continuous mapping $\mathcal{N} : X \to Z$ is called \mathcal{L} -compact on $\overline{U} \subset X$, where U is an open bounded set, if

- 1. $QN(\overline{U})$ is bounded;
- 2. $\mathcal{K}(I-Q)\mathcal{N}:\overline{U}\to X$ is compact.

Note that, since Im Q is isomorphic to ker \mathcal{L} , there is an isomophism $\mathcal{I} : \text{Im}Q \to \text{ker}\mathcal{L}$. We are now prepared to state the Mawhin's continuation theorem.

Theorem A.3 (Mawhin's continuation theorem). Let X and Z be Banach spaces and let $U \subset X$ be an open set. Assume that $\mathcal{L} : D \subseteq X \to Z$ is a Fredholm mapping of index zero and let $\mathcal{N} : X \to Z$ be \mathcal{L} -compact on \overline{U} . Additionally, assume that

- *M1)* for each $\lambda \in (0, 1)$ and $x \in \partial U \cap D$ we have $\mathcal{L}x \neq \lambda \mathcal{N}x$;
- M2) for each $x \in \partial U \cap \ker \mathcal{L}$ we have $Q\mathcal{N}x \neq 0$;
- *M3*) deg($\mathcal{I}Q\mathcal{N}, U \cap \ker \mathcal{L}, 0$) $\neq 0$.

Then the operator equation $\mathcal{L}x = \mathcal{N}x$ has at least one solution in $D \cap \overline{U}$.

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