A predator-prey model with disease in the prey

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1. Introduction

After the seminal models of Vito Volterra and Alfred James Lotka in the mid 1920s for predator-prey interactions, mutualist and competitive mechanisms have been studied extensively in the recent years by researchers. There are so many references in this context, we have just cited here some books (e.g. see, [14, 16–18, ?] and the references therein). Similarly, after the pioneering work of Kermack–McKendrick on SIRS (susceptible-infective-removal-susceptible) epidemiological models have also received much attention from scientists. Relevant references in this context are also vast and we shall again mention here some books (see [1, 2, 4], to mention a few). But little attention has been paid so far to merge these two important areas of research (see [7, 21]). In this paper, we shall put emphasis in such an eco-epidemiological system.

We consider a three species eco-epidemiological system, namely, sound prey (susceptible), infected prey (infective) and predator. We consider the case when the predator mainly eats the infected prey. This is in accordance with a previous model by Hadeler and Freedman [7] which describes a predator-prey model where the prey is infected by a parasite, and the prey in turn infects the predator with that parasite. The infection weakens the prey and increases its susceptibility to predation, while no predator impairing effect is accounted for. While the paper is mainly theoretical and does not address any specific situation, the reader may find several examples in [7]. We derive persistence and extinction conditions of the populations and we also determine conditions for which the system enters a Hopf-type bifurcation. Moreover, we observe that the bifurcated branches are supercritical in some parametric region space in a special case when the predator response function is a Holling-type II function.

The organization of the paper is as follows: Section 2 deals with some basic results, e.g. positivity, uniqueness, boundedness of the solutions. Using these properties and also making an assumption on the intrinsic growth rate of susceptible population, we convert our three-dimensional system to a two-dimensional one. A seemingly awkward fact about our model is that positivity is not preserved in the whole positive octant. In fact, it holds only if the total prey population is not too much above its carrying capacity (see Section 2.3). This reflects a resolute choice for this study: the demographic dynamics of the prey is supposed to be fast, compared to the other two processes, the epidemics and the demographic dynamics of the predator. Our main result for the prey-predator dynamics (Theorem 19) assumes that the parameter r, which is the growth rate of the prey, is large enough. So, oscillations around the carrying capacity of the prey are not significant in this work. And, the main practical conclusion of our study is that the asymptotic behaviour of the system is very close to the one of the two-dimensional system we just mentioned, to which it reduces when $r = +\infty$. The study when the prey population is near to a constant is a distinctive feature of our model, compared to previous models by Hadeler and Freedman [7], and Venturino [21]. Section 3 is devoted to studying the dynamical behaviour of the linearized two-dimensional system around each of the equilibria. In Section 4, we present conditions for supercritical Hopf bifurcation. We remark without a proof that the Hopf bifurcation is subcritical in some parameter range. Finally, in Section 5, we show, by using a Poincaré map, that our analysis for the two-dimensional system is also valid for the three-dimensional system, for r large. Mathematically, this result belongs to the category of singular perturbations results.The paper ends with a discussion on the model and the assumptions.

Part of the mathematical analysis will sound familiar to readers experienced in the study of two-dimensional systems. This is particularly true for Sections 3 and 4 devoted to the study of the asymptotic behaviour of the solutions and the onset of Hopf bifurcation. By now, there are many references of extensive treatments of Hopf bifurcation in o.d.e, a small selection of which are the following books: [13, 10, 8, ?]. So, we are not claiming here the least novelty in the methods we used. Novelty lies in the ecological framework upon which the model is built. With regards reference sources for the computations entailed by Hopf bifurcation, to our knowledge or possibly to our taste, none of the presentations of the Hopf bifurcation theory can be considered the easiest book of recipes in the world, which by its simplicity would outclass all the others. As Hassard et al. [10] put it "the question, what is the "best" technique (when analysing a Hopf bifurcation), has no single answer" (p.92). In fact, system (5) with a Holling-type-II nonlinearity (given in Eq. (3)) was studied some years ago by Freedman and Waltman [5] and Kazarinoff and Van Den Driessche [10]. The method used in [10] was developed by Hassard and Wan [8]. The estimates given in Theorem 15 are based on computations made by Talibi in [20]. Our choice of the method developed in [20] is justified first of all by the fact that our familiarity to it is greater. We want also to stress that the bifurcation analysis established in [10] corresponds to the near-linear Holling-type function, while the sensititve paraemter in our work is the conversion rate ε of the diseased prey into new predators. Investigating the formula stated in [10] in that situation would have cost probably as much work as the direct computation performed here.

2. The mathematical model

2.1. The basic ecological assumptions

We shall consider an eco-epidemiological system consisting of three species, namely, the sound prey (which is susceptible), the infected prey (which becomes infective by some viruses) and the predator population.

For simplicity, we assume that the sound prey population grows according to a logistic law involving the whole prey population (sound and infected), which is best regarded as a purely descriptive equation. The transmission rate among the sound prey populations and the infected prey populations follows the simple law of mass action. The disease is spread among the prey population only and that disease is not genetically inherited. The infected populations do not recover or become immune. The predator population predates mostly the infective prey and the functional response (trophic function) is of Holling-type II (Michaelis–Menten kinetics).

2.2. The basic differential equations

From the above assumptions we can now write the following differential equations:

$$\frac{\mathrm{d}s}{\mathrm{d}t} = r(s+i)\left(1 - \frac{s+i}{k}\right) - bsi - \eta\gamma_1(s)y,$$

$$\frac{\mathrm{d}i}{\mathrm{d}t} = bsi - \gamma(i)y - ci, \tag{1}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = (\varepsilon\gamma(i) + \eta\varepsilon\gamma_1(s) - d)y.$$

System (1) has to be analysed with the following initial conditions:

$$s(0)>0, i(0)>0, y(0)>0, \tag{2}$$

where, s is the number of sound prey, i the number of infected prey population, y the number of predator population, r the intrinsic growth rate of sound population, k the ecosystem support or environmental carrying capacity, b the rate of transmission from sound prey populations to infected prey populations, c the natural death rate of infected prey(not due to predation), d the death rate of predator population, ε the conversion rate, and $\gamma(i)$ and $\eta\gamma_1(s)$ the predator response functions.

Remark 1. *It is to be noted here that we assume that $\gamma(i)$ and $\gamma_1(s)$ are increasing and bounded functions of i and s. As an example, we shall consider these response*

functions as of Holling type II, given by

$$\gamma(i) = \frac{mi}{a+i} \tag{3}$$

and

$$\gamma_1(s) = \frac{m_1 s}{a_1 + s}. \tag{4}$$

Remark 2. m and m_1 are the search rates and a and a_1 are the search rates multiplied by handling times (see, [15]).

Remark 3. In the subsequent part of this paper we shall consider the case $\eta = 0$, that is to say, we assume that the predator eats only the infected prey. The case when the predator eats also a small fraction ($\eta > 0$, small) of the sound prey will be briefly discussed in Remark 20.

2.3. Some basic results

We first observe that the right-hand side of Eq. (1) is a smooth function of the variables (s, i, y) and the parameters, as long as these quantities are non-negative, so local existence and uniqueness properties hold in the positive octant.

From the third equation of Eq. (1), it follows that $y = 0$ is an invariant subset, that is, $y \equiv 0$ if and only if $y(t) = 0$ for some t. Thus, $y(t) > 0$ for all t if $y(0) > 0$. The same argument follows for the second equation (1) if we assume $\gamma(0) = 0$.

So, either $i = 0$ in which case the first equation of Eq. (1) reduces to a pure logistic law verified by s, and y is going to zero asymptotically; or, $i(t) > 0$ for all t. Summing up the first two equations of system (1), one obtains

$$\frac{\mathrm{d}}{\mathrm{d}t}(s+i) = r(s+i)\left(1 - \frac{s+i}{k}\right) - \gamma(i)y - ci,$$

from which one can see that

$$(s+i)(t_0) \le k \implies (s+i)(t) \le k, \quad \text{for } t \ge t_0,$$

and $(s+i)(t)$ is asymptotically $\le k$.

We should notice that positivity of s is not guaranteed and, in fact, if we assume that $s(0) = 0$ and $i(0) > k$ then we have $s(t) < 0$ for $t > 0$ small. This inadequacy is of course entailed by the assumed dependence of the logistic part of the equation upon $s + i$. There is no problem, however, if $s + i \le k$. One can also correct the problem by putting $(1 - (s+i)/k)^+$ instead of $(1 - (s+i)/k)$. This means that the logistic part of the equation is just counting births and there is no birth if the total population exceeds the carrying capacity.

Throughout the paper, we will assume that

$$s(0) + i(0) \le k.$$

We can also relax the above condition and allow $s(0) + i(0)$ to exceed k, that is,

$$s(0) + i(0) \le k + \frac{c}{b}, \quad i(0) \le k.$$

With these latter conditions on the initial values, we have

$$s(t) + i(t) \le k + \frac{c}{b}, \quad i(t) \le k, \ \forall t \ge 0.$$

In this case, we first show that $i(t) \le k \ \forall t \ge 0$. In fact, if this were not true, and for some $t_0 \ge 0$, we have $i(t_0) = k$, we will have at the same time $s(t_0) \le c/b$, therefore, $di/dt(t_0) \le 0$. By standard argument on invariant subsets, we conclude that $i(t)$ cannot exceed k. Now, this in turn implies that $s(t) \ge 0$ for all $t \ge 0$, because, at each point where $s(t) = 0$, we have

$$\frac{ds}{dt} = ri(t)\left(1 - \frac{i(t)}{k}\right) \ge 0, \quad \text{since } 0 \le i(t) \le k.$$

So, we can allow $s + i$ to exceed k provided that it does not exceed

$$k + \frac{c}{b} \quad \text{and} \quad i \le k.$$

We have $0 \le s, i \le k$. It remains to show that y is ultimately bounded too.

Adding together the second equation and $1/\varepsilon$ times the third equation of system (1), we obtain

$$\frac{d}{dt}\left(i + \frac{1}{\varepsilon}y\right) = (bs - c)i - \frac{d}{\varepsilon}y \le bk^2 - \min(c,d)\left(i + \frac{1}{\varepsilon}y\right),$$

which implies that

$$i(t) + \frac{1}{\varepsilon}y(t) \le \max\left(\frac{bk^2}{\min(c,d)}, i(0) + \frac{1}{\varepsilon}y(0)\right).$$

This also implies that

$$i(t) + \frac{1}{\varepsilon}y(t) \le \frac{bk^2}{\min(c,d)} \quad \text{for all } t \ge 0,$$

if it is true for $t = 0$, and

$$\lim_{t \to +\infty} \sup\left(i(t) + \frac{1}{\varepsilon}y(t)\right) \le \frac{bk^2}{\min(c,d)}$$

for solutions defined up to $+\infty$, as long as the solution is defined on positive axis.

We summarize the above results in the next proposition.

Proposition 4. *Every solution initiating in the positive octant and such that $s(0) + i(0) \le k$ satisfies the same properties for all $t \ge 0$ as long as it exists. Moreover, the following inequality holds:*

$$i(t) + \frac{1}{\varepsilon}y(t) \le \max\left(\frac{bk^2}{\min(c,d)}, i(0) + \frac{1}{\varepsilon}y(0)\right).$$

As a consequence, every solution with initial value in $\mathbb{R}^3$ verifying, in addition the condition $(s+i)(0) \leq k$ can be extended up to $+\infty$.

Remark 5. *In system (1), the number r represents the growth rate of the population. The greater r, the faster the population reaches its carrying capacity. For $r = \infty$, one can consider that $s+i=k$ and system (1) reduces to the following two dimensional system: Using $s+i=k$, in (1), we obtain:*

$$\frac{di}{dt} = bi(k-i) - \gamma(i)y - ci,$$

$$\frac{dy}{dt} = (\varepsilon\gamma(i) - d)y. \tag{5}$$

The relationship between systems (1) and (5) will be examined in detail in Section 5.

The next section is devoted to the study of sytem (5). We shall determine the biologically feasible equilibria and shall carry out the local stability (instability) properties of the linearized system (5) around each of the equilibria.

3. Equilibria and local stability

In this section we are dealing with a two-dimensional system obtained by taking $r = +\infty$. We first consider the equilibria of system (5), and discuss their local stability properties in terms of the linearization of system (5) near each equilibrium. Next, we consider global asymptotic properties for the solutions of system (5), namely, we will show that apart from the solutions lying on the boundary of the positive quadrant – each solution initiating from the interior of the positive quadrant approaches the orbit of a periodic solution. Finally, we will show that for some values of the parameters some of the periodic solutions are asymptotically stable. The latter result which is obtained as an application of the Hopf bifurcation theorem is preparatory to a result established in Section 5 of existence of a periodic solution for the complete system, for r large enough.

The model equation (5) has the following nonnegative equilibria, namely,

$$E_0 : (0,0),$$

$$E_1 : \left(k - \frac{c}{b}, 0\right)$$

and

$$E_* : (i^*, y^*),$$

where

$$\varepsilon\gamma(i^*) = d$$

and

$$y^* = \frac{\varepsilon i^*((bk-c) - bi^*)}{d}.$$

The boundary equilibrium E_1 exists if

$$k > \frac{c}{b} \tag{6}$$

and the existence condition for the positive equilibrium E_* is

$$\gamma\left(\frac{bk - c}{b}\right) > \frac{d}{\varepsilon}. \tag{7}$$

Remark 6. *From Eq. (5), it is clear that $k > c/b$ is necessary for the existence of component of i^* of the positive equilibrium. It is to be also noted here that this condition implies the existence of E_1. Hence, we can conclude that the existence of E_* implies the existence of E_1, but the reverse is not true. It is also interesting to observe that the equilibrium E_1 arises from E_0 for the value of the parameter k equal to c/b and persists for all $k > c/b$, while E_* arises from E_1 when k reaches the value $c/b + \gamma^{-1}(d/\varepsilon)$ and persists beyond this value.*

Now, we shall present the existence condition of the equilibria taking into consideration the predator response function as defined in Eq. (3). It is to be noted here that the existence conditions for zero and boundary equilibria are the same as in the general case. The only variation is in the computation of i^* and y^*. In this particular case, i^* and y^* should be read as

$$i^* = \frac{ad}{\varepsilon m - d}$$

and

$$y^* = \frac{a\varepsilon\{b(k(\varepsilon m - d) - ad) - c(\varepsilon m - d)\}}{(\varepsilon m - d)^2}. \tag{8}$$

It is clear that the existence condition for this is

$$\varepsilon m > d + \frac{bad}{bk - c}.$$

The local stability analysis can be performed by computing the variational matrices corresponding to each of the equilibria.

Let V_0 be the variational matrix corresponding to E_0. V_0 is given by

$$V_0 = \begin{pmatrix} bk - c & 0 \\ 0 & -d \end{pmatrix} \tag{9}$$

and, consequently, the eigenvalues are

$$\lambda_1 = -d(d > 0) \quad \text{and} \quad \lambda_2 = bk - c.$$

Now, we can state the following lemma:

Lemma 7. *E_0 is locally asymptotically stable (LAS) if $k < c/b$ and is unstable if $k > c/b$. Moreover, when E_0 is LAS it is in fact globally asymptotically stable (GAS).*

Remark 8. *$bk < c$ means that the maximal renewal rate of infected is less than their natural mortality rate. Therefore, $i \to 0$ and $y \to 0$.*

Remark 9. *It is to be noted here that when E_0 is LAS, then the other two equilibria E_1 and E_* do not exist.*

Now, we shall discuss the dynamical behaviour of system (5) around E_1.

Let V_1 be the variational matrix corresponding to the equilibrium E_1. V_1 is given by

$$V_1 = \begin{pmatrix} c - bk & -\gamma(i^*) \\ 0 & \varepsilon\gamma(i^*) - d \end{pmatrix} \tag{10}$$

and, consequently, the eigenvalues are

$$\lambda_1 = c - bk \quad \text{and} \quad \lambda_2 = \varepsilon\gamma(i^*) - d.$$

Now, we can state the following lemma.

Lemma 10. *E_1 is LAS if both*
  (i) *$k > \frac{c}{b}$*
      and
 (ii) *$\varepsilon\gamma(i^*) - d < 0$*
      hold true. And E_1 is unstable if one of the above-mentioned conditions is violated.

Remark 11. *The point is that condition* (i) *of the above lemma is necessary for the existence of E_1 as a feasible equilibrium, that is, a point in the positive quadrant and hence only violation of condition* (ii) *gives rise to instability of the system around E_1. It is also to be noted here that condition* (ii) *contradicts the existence criteria for the strictly positive equilibrium. Hence, we finally conclude that if E_1 is LAS then E_* does not exist. These facts are in accordance with the observations made in Remark 6 about the appearance of E_1 and E_*: the curve constituted by the pairs (k, E_1) in $(\mathbb{R} \times \mathbb{R}^2)$ branches off the curve $\mathbb{R} \times \{E_0\}$ as k crosses the value c/b, where a simple bifurcation occurs. At this point, E_0 loses its stability which passes to the new equilibrium. This is the phenomenon known as an "exchange of stability" through bifurcation (see* [19]*). The same phenomenon takes place at the cross point of the branches determined by E_1 and E_* respectively.*

3.1. Biological interpretation

If E_1 is LAS then the predator population will not persist, but on the other hand, the infected population will survive. Necessary and sufficient conditions for this sort of phenomenon are the following:

The environmental carrying capacity should have an upper threshold value determined by the ratio of the death rate of infected populations and the transmission coefficient of susceptible and infected individuals.

Now, if we consider the predator response function (3), then E_1 is LAS if both
(i) $k > c/b$
    and

(ii) $\varepsilon m < d + bad/bk - c$

hold true. And it is unstable if one of the above-mentioned conditions is violated. That is, in this case, εm, the product of the conversion rate and the search rate must have to attain a lower threshold value.

Now, we shall investigate the local stability properties of system (5) around the strictly positive equilibrium E_*.

Let V_2 be the variational matrix corresponding to the equilibrium E_*. V_2 is given by

$$V_2 = \begin{pmatrix} -bi^* + \frac{\gamma(i^*)y^*}{i^*} - \gamma'(i^*)y^* & -\gamma(i^*) \\ \varepsilon\gamma'(i^*)y^* & 0 \end{pmatrix}. \tag{11}$$

The characteristic equation of Eq. (11) is

$$\lambda^2 - \lambda\left(\frac{\gamma(i^*)y^*}{i^*} - bi^* - \gamma'(i^*)y^*\right) + \varepsilon\gamma(i^*)\gamma'(i^*)y^* = 0. \tag{12}$$

From above, it is clear that if $(\gamma(i^*)y^*/i^* - bi^* - \gamma'(i^*)y^*) > 0$, then the positive equilibrium is unstable and if it is less than zero then the system around the positive equilibrium is stable. Hopf bifurcation occurs when it is equal to zero.

Now, if we consider the predator response function (3), then the characteristic equation of system (5) around the positive equilibrium can be written as

$$\lambda^2 + \lambda i^*\left(b - \frac{my^*}{(a+i^*)^2}\right) + \frac{\varepsilon am^2 y^* i^*}{(a+i^*)^3} = 0. \tag{13}$$

Substituting the value of y^* from Eq. (8) in to (13), we obtain

$$\lambda^2 + \lambda\frac{bi^*}{a+i^*}\left(a + \frac{c}{b} + 2i^* - k\right) + \frac{\varepsilon mai^*(bk - bi^* - c)}{(a+i^*)^2} = 0. \tag{14}$$

A Hopf bifurcation takes place at

$$k = a + \frac{c}{b} + 2i^* \tag{15}$$

and we shall denote this value by k_0.

Thus, we find a value k_0, below which the system is stable and above which it is unstable.

In the next section, we shall show that the bifurcation branches are supercritical in some parametric region space for this particular situation and from which one can draw the bifurcation diagram with respect to k.

Proposition 12. *If $kb > c$ and $\varepsilon\gamma(k - c/b) > d$ then for any (i_0, y_0) in the positive quadrant with $y_0 > 0$, $\omega(i_0, y_0) \cap \{E_0, E_1\} = \emptyset$.*

Proof. First, we shall prove that $E_1 \notin \omega(i_0, y_0)$. Assuming the contrary, for some (i_0, y_0) one can determine a double sequence $t_n, q_n : t_n \to \infty, q_n \to \infty$ and $\delta > 0$ such that $i(t_n) \to k - c/b, y(t_n) \to 0$ and $i(t_n + q_n) = -\delta + k - c/b$. Now, $(k - c/b) > i(t_n + q) > -\delta + k - c/b, 0 \le q < q_n$. Therefore, we can build a solution $(\bar{i}, \bar{y})$ such that $\bar{i}(0) = k - c/b - \delta$

and $k - c/b \geq \bar{i}(t) \geq k - c/b - \delta$, $\forall t \leq 0$ and $\delta > 0$ as small as we wish. Choose $\delta > 0$ so small as to make $\varepsilon\gamma(k - c/b - \delta) > d$. This implies $\bar{y}(t) = 0, \forall t \leq 0$ (otherwise $\bar{y}$ will be unbounded).

Now,

$$\frac{d\bar{i}}{dt} = (bk - c)\bar{i} - b\bar{i}^2 \geq 0$$

$$\Rightarrow \bar{i}(t) \leq \bar{i}(0), \quad \forall t \leq 0$$

$$\Rightarrow \bar{i}(t) \leq k - \frac{c}{b} - \delta, \quad \forall t \leq 0.$$

Combined with the fact that $\bar{i}(t) \geq k - c/b - \delta$, $\forall t \leq 0$, we conclude that $\bar{i}(t) = k - c/b - \delta$, $\forall t \leq 0$. Substituting this value for $\bar{i}$ in the above differential equation, we obtain $d\bar{i}/dt \geq \delta b\bar{i} > 0$, $t \leq 0$, which yields a contradiction and, therefore $E_1 \notin \omega(i_0, y_0)$. This proves our first case.

Now, we shall prove $E_0 \notin \omega(i_0, y_0)$. As in the previous case, assuming it is not true, one can determine a double sequence $t_n, q_n : t_n \to \infty, q_n \to \infty, i(t_n), y(t_n) \to 0, i(t_n + q_n) = \delta$ or $y(t_n + q_n) = \delta$ and $(i, y)(t + q) \in \bar{\Omega}$, $0 \leq q \leq q_n$ and $\bar{\Omega} = [0, \delta] \times [0, \delta]$. From this, we deduce $(\bar{i}, \bar{y})$ such that $(\bar{i}(0), \bar{y}(0)) \in \partial\Omega$ and $(\bar{i}(t), \bar{y}(t)) \in \bar{\Omega}$, $\forall t \leq 0$. For $\delta > 0$ small enough, we can conclude that $\bar{y} = 0$, and $\bar{i}(t) \to k - c/b$ as $t \to -\infty$ and this implies that $E_1 \in \omega(i_0, y_0)$. We have already established that it is impossible. Hence $E_0 \notin \omega(i_0, y_0)$ and this completes our proof. $\quad\square$

Now, we shall present the following remark:

Remark 13. *As both eigenvalues of E_* have a real part greater than zero, each solution stays away from a neighbourhood of E_*.*

Now, we are in a position to describe the asymptotic behaviour of solutions in the case when E_* is unstable.

Theorem 14. *If the strictly positive steady state is unstable, then every strictly positive solution of system (5) tends to a non-constant periodic solution.*

Proof. We have already established the fact that the system is bounded and also E_* is unstable. We have also proved in the above proposition and the Remark 13 that none of the equilibria E_0, E_1 nor E_* is in the omega limit set of such solutions. Thus, as a result of the Poincaré Bendixson theorem, the omega limit set of any initial value (i_0, y_0) in the interior of the positive quadrant is made of a single closed orbit of a periodic solution, that is, any such solution approaches asymptotically the orbit of a single periodic solution-this ascertains our claim. $\quad\square$

In the next section, we shall find out the direction of the Hopf bifurcation branch.

4. Direction of Hopf bifurcation

We consider the Holling-type-II predator response function.

Theorem 15. *If εm, the product of the conversion and the search rate, satisfies the following inequalities*:

$$d + \frac{bad}{bk - c} < \varepsilon m < \min\left(\frac{d}{1-b}, ab\sqrt{\alpha_0} + d - 3ad\right),$$

where $\alpha_0 = \sqrt{abd}$, then the bifurcation branches are supercritical.

Proof. To prove this result we shall follow the approach of Talibi [20, Ch. 7]. We shall normalize system (5) by the following change of variables (time scale). We keep the same notation i, y and t for the new variable.

$$\begin{pmatrix} i'(t) \\ y'(t) \end{pmatrix} = \begin{pmatrix} i(\frac{1}{\sqrt{\alpha_0}}t) \\ y(\frac{1}{\sqrt{\alpha_0}}t) \end{pmatrix} \tag{16}$$

with

$$\alpha_0 = \sqrt{\frac{\varepsilon m a i^*(bk - bi^* - c)}{(a + i^*)^2}} = \sqrt{abd},$$

we obtain

$$\frac{d}{dt}\begin{pmatrix} i \\ y \end{pmatrix} = \begin{pmatrix} \frac{1}{\sqrt{\alpha_0}}\{bi(k - i) - \gamma(i)y - ci\} \\ \frac{1}{\sqrt{\alpha_0}}\{(\varepsilon\gamma(i) - d)y\} \end{pmatrix} = \begin{pmatrix} f_1(i, y) \\ f_2(i, y) \end{pmatrix}. \tag{17}$$

Linearizing the above sytem around the positive equilibrium E_* we obtain the eigenvalues which are purely imaginary with the imaginary part equal to 1.

Let $k(\eta)$ be the value of the bifurcating parameter. If we write,

$$k(\eta) = k_0 + \eta k_1 + \eta^2 k_2 + o(\eta^2)$$

and using the main theorem of Talibi [20], we obtain that $k_1 = 0$ and k_2 is given by

$$k_2 2\pi r_1 + I + J = 0, \tag{18}$$

where

$$r_1 = \mathrm{Re}\frac{d}{dk}(\lambda(k_0)),$$

$$I = \frac{\pi}{6}\{3\varepsilon_1 qu^3 + 3\varepsilon_1 quv^2 + 3\varepsilon_2 qvu^2 + 3\varepsilon_2 qv^3\},$$

$$J = \frac{\pi}{2}\left\{\begin{array}{l} \varepsilon_1 pu^2\varepsilon_2 pu^2 - \varepsilon_1 pu^2\varepsilon_1 puv - \varepsilon_1 puv\varepsilon_1 pv^2 + \varepsilon_2 pu^2\varepsilon_2 puv \\ + \varepsilon_2 puv\varepsilon_2 pv^2 - \varepsilon_2 pv^2\varepsilon_1 pv^2 \end{array}\right\},$$

$$\varepsilon_1 = 2u^*, \quad \varepsilon_2 = 2v^*, \tag{19}$$

and the derivatives

$$p = D^2 f(k_0, E_*), \qquad q = D^3 f(k_0, E_*).$$

Here, $u + iv$ is the vector associated with the eigenvalue i of the characteristic equation obtained from the linearized equation and $u^* + iv^*$ is the row vector in $\mathbb{C}^2$ such that

$$u^* u = \tfrac{1}{2} = -(v^* v)$$

and

$$u^* v = v^* u = 0.$$

A few computations yield the following expression (see the appendix):

$$k_2 = \frac{\varepsilon m}{d} \left(\frac{\varepsilon m - d}{a \varepsilon m}\right)^2 \left[-3ad + d - \varepsilon m + \sqrt{\alpha_0} ab + 2bd \left(\frac{\varepsilon m - d}{\varepsilon \alpha_0}\right) \right.$$
$$\left. - \frac{2ma^2 d}{\alpha_0} \left(\frac{\varepsilon m - d}{a \varepsilon m}\right)^2 \right]. \tag{20}$$

The direction of the bifurcation branch is given by the signature of the value of k_2 and after a little algebraic calculation we can conclude that the bifurcation branches are supercritical if the sufficient condition as stated in the theorem holds. □

Remark 16. *If the product of the conversion and the search rate has a lower threshold value determined by $\varepsilon m > \max(d + bad/(bk - c), d/(1 - b), ab\sqrt{\alpha_0} + d - 3ad)$, then the bifurcation branches are subcritical. In this case the strictly positive equilibrium is not GAS.*

5. Relation between the two-dimensional and the three-dimensional system

It is important for the three-dimensional case to show that $s + i$ is ultimately bounded below by $k - Ck/r$, for some $C > 0$, and that C can be chosen so that if $s(0) + i(0) \in [k - Ck/r, k], i(0) + (1/\varepsilon) y(0) \le bk^2/\min(c, d)$, then this holds true for all $t \ge 0$.

In view of Proposition 4, we just have to show that $s(t) + i(t) \ge k - Ck/r$ holds for all $t \ge 0$. This will be concluded by finding C so that $(d/dt)(s + i) \ge 0$ when $s + i = k - Ck/r$.

$$\frac{d}{dt}(s + i) = r(s + i)\left(1 - \frac{s + i}{k}\right) - \gamma(i)y - ci$$

and

$$s + i = k - \frac{Ck}{r}$$

gives

$$\frac{d}{dt}(s + i) = \left(k - \frac{Ck}{r}\right) C - \gamma(i)y - ci,$$

so, we have,

$$\frac{d}{dt}(s+i) \geq k\left(1 - \frac{C}{r}\right)C - \frac{\gamma(+\infty)\varepsilon bk^2}{\min(c,d)} - ck.$$

Now, it is sufficient to show that the right-hand side of the above expression is greater than zero, which can be achieved by choosing C in the following way:

$$C_1 \leq C \leq C_2,$$

where

$$C_1 = \frac{(1 - \sqrt{\Delta})}{2}r, \qquad C_2 = \frac{(1 + \sqrt{\Delta})}{2}r$$

with

$$\Delta = 1 - 4\frac{1}{r}\left(\frac{\gamma(+\infty)\varepsilon bk}{\min(c,d)} + c\right).$$

Note that with $\varepsilon, b, k, c, 1/c, 1/d$ bounded above, we have

$$C_1 \rightarrow \frac{\gamma(+\infty)\varepsilon bk}{\min(c,d)} + c \quad \text{as } r \rightarrow \infty$$

while

$$C_2 \rightarrow +\infty,$$

so that there exist $r_0 > 0$ and $C_0 > 0$, such that $(d/dt)(s+i) \geq 0$, if $s+i = k - kC_0/r, r \geq r_0$.

We summarize the above results in the following proposition.

Proposition 17. *It is assumed here that E_* exists and is unstable. Then there exist $r_0 > 0$, $C_0 > 0$ such that for each $r \geq r_0$ every solution of Eq. (1) verifying $i(0) \geq 0$, $y(0) \geq 0$ and $i(0) + (1/\varepsilon)y(0) \leq bk^2/\min(c,d)$ and $k - kC_0/r \leq s(0) + i(0) \leq k$, is such that $k - kC_0/r \leq s(t) + i(t) \leq k$, for all $t \geq 0$. We will denote J_r the subset of $\mathbb{R}^3$, defined as,*

$$J_r = \left\{(s,i,y): s,i,y \geq 0; \; k - \frac{kC_0}{r} \leq s+i \leq k, \; i + \frac{1}{\varepsilon}y \leq \frac{bk^2}{\min(c,d)}\right\}.$$

Remark 18. *The above proposition can be rephrased as J_r being positively invariant for $r \geq r_0$.*

Now, consider an orbit Y of a periodic solution of Eq. (5), in the positive quadrant, assumed to be orbitally asymptotically stable. We will show the following result:

Theorem 19. *There exists $r_1 \geq r_0$ so that for every $r \geq r_1$, system (1) has a periodic solution in the neighbourhood of the set $[k - kC_0/r, k] \times Y$. Moreover, one can determine a neighbourhood U of Y in the plane such that the set $[k - kC_0/r, k] \times U$ is positively invariant with respect to the system.*

Before proving the theorem, let us draw its consequence for the systems we are considering. In Section 4, we have established the fact that the bifurcation branches of system (5) are supercritical in a certain parameter region space. When this is true, we can take for Y the orbit of any of the periodic solutions which are on the branch of bifurcation. The main condition of Theorem 19 is satisfied, so the theorem applies to this situation.

Proof. Choose a point A on $Y.l$ is a straight line normal to Y at A. We will represent l as the set

$$\{(i, y) \in \mathbb{R}^2 : \lambda(i, y) = \langle \lambda_0, (i, y) \rangle + C_1 = 0\},$$

where λ_0 is $\neq 0$ and tangent to Y at A.

The assumption on orbital asymptotic stability implies that the Poincaré map P defined on l, in the usual way, satisfies the condition $|P'(A)| < 1$.

The periodic orbit associated with Eq. (5) verifies the condition $\bar{i}(t) + (1/\varepsilon)\bar{y}(t) < bk^2/4(\min(c, d))$ for all t. This in particular is true for A. Choosing an interval small enough about A, we have $i + (1/\varepsilon)/y \leq bk^2/4(\min(c, d))$.

Now, restricting our attention to solutions in J_r, for such a solution the last two equations of system (1) can be written as

$$\frac{di}{dt} = b(k - i)i - \gamma(i)y - ci + b(s + i - k)i,$$

$$\frac{dy}{dt} = (\varepsilon\gamma(i) - d)y.$$

$$(21)$$

We shall treat Eq. (21) as a perturbation of system (5).

We shall build a Poincaré map on a two-dimensional convex subset of $\mathbb{R}^3$, that is

$$(s + i, i, y) \in \left[k - \frac{C_0}{r}, k\right] \times l.$$

More precisely, we will restrict the map to a product

$$\Gamma_r = \left[k - \frac{kC_0}{r}, k\right] \times [-V, V]$$

$$(22)$$

for some $V > 0$, small enough. The interval $[-V, V]$ corresponds to a subinterval of the line l, denoted the same way. 0 corresponds to the point A. First of all, V has to be taken so small as to have $(s + i, i, y) \in \Gamma_r \Rightarrow (s, i, y) \in J_r$. The possibility of such a choice is ascertained by the above observation that $A \in J_r$.

In view of Proposition 17, we already know that solutions of system (1) with initial value in J_r satisfy

$$s(t) + i(t) \in \left[k - \frac{kC_0}{r}, k\right] \qquad \text{for all } t \geq 0.$$

It remains to show that the (i, y) component takes its values in a certain subinterval $[-V, V]$ of the line l. Restricting V further if necessary, the vector field associated

with Eq. (5) at each point of $[-V,V]$ is close to its value at A. Therefore, it can be made transverse to l uniformly in $[-V,V]$. This can be made more precise:

$$\left| \left\langle \begin{pmatrix} b(k-i)i - \gamma(i)y - ci \\ (\varepsilon\gamma(i) - d)y \end{pmatrix}, \lambda_0 \right\rangle \right| \geq \delta \geq 0$$

for some $\delta > 0$ and all $(i,y) \in [-V,V]$.

Now, take two time values t_1, t_2 ($t_1 < 0 < t_2$), where θ is the minimal period of the periodic solution of Eq. (5), and, $t_2 - t_1$ will be chosen suitably small. Now, we have

$$\lambda(i(t_1), y(t_1)).\lambda(i(t_2), y(t_2)) < 0$$

for every $(i_0, y_0) \in [-V,V]$.

This implies that $(i(t), y(t))$ hits the line l at a time $t \in]t_1, t_2[$ and this time is unique, since the vector field is transverse to l.

By continuous dependence, the same property holds for the perturbed system (21). So we can determine a Poincaré map for system (1).

Finally, we shall show that the Poincaré map takes its values in Γ_r.

From now on, we consider an initial value $(s_0, i_0, y_0) \in \Gamma_r$; $(s(t), (i(t), y(t)))$ is the solution of system (1) associated with (s_0, i_0, y_0). The Poincaré map for system (1) is the map Q_r defined by

$$Q_r(s_0, i_0, y_0) = (s(t), (i(t), y(t))), \quad t = t(s_0, i_0, y_0),$$

from Γ_r into $[k - kC_0/r, k] \times l$, where t is the first positive time when the solution hits the plane Γ_r close to $[k - kC_0/r, k] \times \{A\}$: t is determined by the equation

$$\langle (i(t), y(t)), \lambda \rangle = 0.$$

We shall have to show that for that value of t, we have

$$(i(t), y(t)) \in [-V,V].$$

This will be done by evaluating the distance from $(i(t), y(t))$ to A. For this evaluation, we introduce an auxiliary point denoted $(\bar{i}(t), \bar{y}(t))$, the value at time t of the solution of Eq. (5) starting from (i_0, y_0). We denote $\bar{t}$ the first positive time when $(\bar{i}, \bar{y}))$ hits the line l close to (i_0, y_0).

Now, recall the assumption $|P'(0)| < 1$, then there exists $\kappa \in [0,1[$, so that for $V > 0$ small enough and $z \in [-V,V]$, we have

$$|Pz| \leq \kappa|z|. \tag{23}$$

If instead of Eq. (5), we consider a perturbation of system (5), of magnitude not larger than C_0/r, then provided we possibly restrict the $[-V,V]$ further, for some $M > 0$ and for each $(i_0, y_0) \in [-V,V]$, $t \in [t_1, t_2]$, we have

$$|(i(t), y(t)) - (\bar{i}(t), \bar{y}(t))| \leq \frac{MC_0}{r}.$$

Provided we choose $t_2 - t_1 \leq 1/r$, and in view of the fact that solutions of system (5) starting from $[-V, V]$ have a uniformly bounded derivative on any bounded time interval, one obtains the following estimate:

$$|(\bar{i}(t), \bar{y}(t)) - (\bar{i}(\bar{t}), \bar{y}(\bar{t}))| \leq \frac{M'}{r},$$

where $M' = M'(b, c, d, \varepsilon, \gamma)$. Finally, using inequality (23), we have

$$|(\bar{i}(\bar{t}), \bar{y}(\bar{t})) - A| \leq \kappa V.$$

We are now in a position to conclude the proof of the theorem. Summing up the right-hand sides of the three above inequalities yields

$$|(i(t), y(t)) - A| \leq \frac{MC_0}{r} + \frac{M'}{r} + \kappa V.$$

If we choose r large enough, then $Q_r : \Gamma_r \to \Gamma_r$. For this , it is enough that

$$\frac{MC_0 + M'}{r} + \kappa V \leq V,$$

which gives

$$r \geq r_1 = \max\left(\frac{MC_0 + M'}{(1 - \kappa)V}, r_0\right).$$

Therefore, for each $r \geq r_1$, Q_r has a fixed point in Γ_r which corresponds to a periodic solution of Eq. (1). Moreover, Γ_r is positively invariant: this result corresponds to a weak form of stability. This completes the proof of the theorem. $\square$

Remark 20. *One can now extend our analysis to the case when $\eta \neq 0$, that is, one may assume that the predator predates also the sound population. Assuming $\eta > 0$ small enough, for example, so that $\eta \varepsilon \gamma_1(k) < d$, one obtains an ultimate bound for $i + y/\varepsilon$, similar to the one derived in Proposition 4. Then, one can determine a positively invariant subset like the set J_r given in Proposition 17. Finally, one can determine $V > 0$ and a value r_2 such that for $r > r_2$, $\Gamma_r \subset J_r$ and $Q_r : \Gamma_r \to \Gamma_r$. Thus, the conclusion of the theorem can be extended to the case when $\eta > 0$ small enough.*

6. Conclusion

Here, we proposed and analysed a model of a three species eco-epidemiological system, namely, sound prey, infected prey and predator. We considered the predator response function as an increasing and bounded one. In particular, we assumed that this function is of Holling-type II, as an example.

Using the boundedness property and making an assumption on the intrinsic growth rate of the susceptible population, we reduced our three dimensional system to a two dimensional system. And then we observed the following main results:

(1) equilibrium E_1 arises from E_0 for the value of the parameter k equal to c/b and persists for all $k > c/b$, while the strictly positive equilibrium E_* arises from E_1

when k reaches the value $c/b + \gamma^{-1}(d/\varepsilon)$ and persists beyond this value. That is to say, we are able to relate the persistence (or the extinction) conditions in terms of environmental carrying capacity which is an essential observation from the biological point of view.
(2) We observed that when the maximal renewal rate of the infected population is less than its natural mortality rate then both populations (the infected and the predator ones) go to extinction.
(3) We also pointed out the well-known phenomenon of "exchange of stability" through simple bifurcation at the crossing point of E_0 to E_1 as well as at the crossing point of E_1 to E_*.
(4) We observed that under certain parametric conditions the strictly positive equilibrium enters a Hopf-type bifurcation. Moreover, considering a Holling-type-II predator response function we found that the bifurcated branches are supercritical in some parametric region space which confirmed us the local asymptotic stability of the bifurcated orbit.
(5) Finally, by using a Poincaré map we observed the connection between the reduced and the original system. It was also pointed out that our analysis for the reduced system is valid for the original system.

All these and more results were interpreted in terms of biological parameters in the text either in the subheading of remark or in the subheading of biological interpretation.

Now, we discuss the contact process. We considered in our system that the contact rate between infectives and susceptibles follows the "law of mass action". The contact process is admittedly debatable. Some authors argue that the proportional mixing rate is more appropriate than that of simple mass action law. The data of the Greenwood experiment suggest that there is no change in qualitative properties upon the contact process whether it follows the law of mass action or it follows the proportional mixing rate (see [3]). Heesterbeek and Metz [11] suggest that a Holling-type function is more appropriate to describe the contact process. For a detailed review on contact processes, see [6]. To conclude on this point, let us point out that, for r large, the prey population is near to constant, and hence the two contact processes are roughly equivalent to each other.

Finally, we mention some future directions of work extending the present paper:
(1) One can consider the case in which the disease also affects the predator population in contact with the infected population.
(2) One can consider the case of a portion of infected population recovering and coming back to the susceptible population.
(3) The spatial spread of the disease is also an important phenomenon to study.
(4) The delay effect incurred in contacts between susceptible and infected populations is an important characteristic to be considered.

Acknowledgements

Appendix

Recall that in Talibi [20], to compute the Hopf bifurcation elements $E(\eta)$, $\omega(\eta)$ and $k(\eta)$, one considers Taylor expansions

$$E(\eta) = E_* + \eta E_1 + \eta^2 E_2 + \cdots,$$

$$\omega(\eta) = 2\pi + \eta \omega_1 + \eta^2 \omega_2 + \cdots$$

and

$$k(\eta) = k_0 + \eta k_1 + \eta^2 k_2 + \cdots,$$

where $\omega(\eta)$ is the period of the solution $E(\eta)$ of system (17) for the value of the parameter $k(\eta)$ and by using equalization according to powers of η, one deduces formulae for E_i, ω_i and k_i, for $i = 1, 2$.

Let us now give the details of application of formula (18) to system (17).

If $E = \binom{i}{y}$ and $f = \binom{f_1}{f_2}$, we obtain

$$Df(E)\binom{u_1}{v_1} = \begin{pmatrix} u_1 \dfrac{\partial}{\partial i} f_1 + v_1 \dfrac{\partial}{\partial y} f_1 \\ u_1 \dfrac{\partial}{\partial i} f_2 + v_1 \dfrac{\partial}{\partial y} f_2, \end{pmatrix},$$

$$D^2 f(E)\binom{u_1}{v_1}\binom{u_2}{v_2} = \begin{pmatrix} u_1 u_2 \dfrac{\partial^2}{\partial i^2} f_1 + (u_2 v_1 + u_1 v_2) \dfrac{\partial^2}{\partial i \partial y} f_1 + v_1 v_2 \dfrac{\partial^2}{\partial y^2} f_1 \\ u_1 u_2 \dfrac{\partial^2}{\partial i^2} f_2 + (u_2 v_1 + u_1 v_2) \dfrac{\partial^2}{\partial i \partial y} f_2 + v_1 v_2 \dfrac{\partial^2}{\partial y^2} f_2 \end{pmatrix},$$

$$D^3 f(E)\binom{u_1}{v_1}\binom{u_2}{v_2}\binom{u_3}{v_3} = A + B$$

with

$$A = \begin{pmatrix} u_1 u_2 u_3 \dfrac{\partial^3}{\partial i^3} f_1 + ((u_2 v_1 + u_1 v_2)u_3 + u_1 u_2 v_3) \dfrac{\partial^3}{\partial i^2 \partial y} f_1 \\ u_1 u_2 u_3 \dfrac{\partial^3}{\partial i^3} f_2 + ((u_2 v_1 + u_1 v_2)u_3 + u_1 u_2 v_3) \dfrac{\partial^3}{\partial i^2 \partial y} f_2 \end{pmatrix}$$

and

$$B = \begin{pmatrix} (v_1 v_2 u_3 + (u_2 v_1 + u_1 v_2) v_3) \dfrac{\partial^3}{\partial i \partial y^2} f_1 + v_1 v_2 v_3 \dfrac{\partial^3}{\partial y^3} f_1 \\[2mm] (v_1 v_2 u_3 + (u_2 v_1 + u_1 v_2) v_3) \dfrac{\partial^3}{\partial i \partial y^2} f_2 + v_1 v_2 v_3 \dfrac{\partial^3}{\partial y^3} f_2 \end{pmatrix}.$$

As $u = \binom{1}{0}$, $v = \binom{0}{\alpha}$, $u^* = (\frac{1}{2}, 0)$, $v^* = (0, \frac{1}{2\alpha})$, with $\alpha = -\frac{\varepsilon}{d} \sqrt{\alpha_0}$, we get

$$\frac{\partial^3}{\partial i^3} f_1 = \varepsilon_1 q u^3, \qquad \alpha^2 \frac{\partial^3}{\partial i \partial y^2} f_1 = \varepsilon_1 q u v^2,$$

$$\frac{\partial^3}{\partial i^2 \partial y} f_2 = \varepsilon_2 q v u^2, \qquad \alpha^2 \frac{\partial^3}{\partial y^3} f_2 = \varepsilon_2 q v^3,$$

where ε_1 and ε_2 are defined in Eq. (19).

Thus,

$$I = \frac{\pi}{2} \left\{ \frac{\partial^3}{\partial i^3} f_1 + \alpha^2 \frac{\partial^3}{\partial i \partial y^2} f_1 + \frac{\partial^3}{\partial i^2 \partial y} f_2 + \alpha^2 \frac{\partial^3}{\partial y^3} f_2 \right\}.$$

Similarly, we get

$$\varepsilon_1 p u^2 = \frac{\partial^2}{\partial i^2} f_1, \quad \varepsilon_1 p u v = \alpha \frac{\partial^2}{\partial i \partial y} f_1, \quad \varepsilon_1 p v^2 = \alpha^2 \frac{\partial^2}{\partial y^2} f_1,$$

$$\varepsilon_2 p u^2 = \frac{\partial^2}{\partial i^2} f_2, \quad \varepsilon_2 p u v = \alpha \frac{\partial^2}{\partial i \partial y} f_2, \quad \varepsilon_2 p v^2 = \alpha^2 \frac{\partial^2}{\partial y^2} f_2$$

and

$$J = \frac{\pi}{2} \left\{ \frac{1}{\alpha} \frac{\partial^2}{\partial i^2} f_1 \frac{\partial^2}{\partial i^2} f_2 - \alpha \frac{\partial^2}{\partial i^2} f_1 \frac{\partial^2}{\partial i \partial y} f_1 - \alpha^3 \frac{\partial^2}{\partial i \partial y} f_1 \frac{\partial^2}{\partial y^2} f_1 + \frac{1}{\alpha} \frac{\partial^2}{\partial i^2} f_2 \frac{\partial^2}{\partial i \partial y} f_2 \right.$$

$$\left. + \frac{\partial^2}{\partial i^2} f_2 \frac{\partial^2}{\partial y^2} f_2 - \alpha^3 \frac{\partial^2}{\partial y^2} f_2 \frac{\partial^2}{\partial y^2} f_1 \right\}.$$

For $E = E(k_0) = E_*$, we obtain

$$I(k_0) = \frac{\pi}{\sqrt{\alpha_0}} \left(\frac{\varepsilon m - d}{\varepsilon a m} \right)^2 \{ 3ab - d + \varepsilon m \}$$

and

$$J(k_0) = -\frac{\pi \, mad}{\alpha_0 \sqrt{\alpha_0}} \left(\frac{\varepsilon m - d}{\varepsilon a m} \right)^2 \left\{ 2b \left(\frac{\varepsilon m - d}{\varepsilon a m} \right) - 2a \left(\frac{\varepsilon m - d}{\varepsilon a m} \right)^2 + \alpha_0 \sqrt{\alpha_0} \frac{b}{dm} \right\}.$$

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