



A Lyapunov functional for a stage-structured predator–prey model with nonlinear predation rate

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ABSTRACT

We consider the dynamics of a general stage-structured predator–prey model which generalizes several known predator–prey, SEIR, and virus dynamics models, assuming that the intrinsic growth rate of the prey, the predation rate, and the removal functions are given in an unspecified form. Using the Lyapunov method, we derive sufficient conditions for the local stability of the equilibria together with estimations of their respective domains of attraction, while observing that in several particular but important situations these conditions yield global stability results. The biological significance of these conditions is discussed and the existence of the positive steady state is also investigated.

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1. Introduction

Due to the complexity of real-life biological phenomena, it is sometimes the case that certain key parameters characterizing the underlying interactions are difficult to estimate, and their nature and dependences are not well understood. One example is the length of delay between the infection with HIV and the onset of AIDS, mainly due to difficulty in pinpointing the precise time when the infection occurs. Moreover, the choice or identification of a particular type of model or function to fit the gathered experimental data may not always be apparent, some examples being the precise choice of the functional response which describes a predator–prey interaction or the choice of the removal rate of the virus for a virus transmission model. Hence it is desirable to concentrate as much as possible on establishing the qualitative properties of the mathematical model based on a set of general and biologically motivated hypotheses which captures the distinctive features of the biological interactions under consideration.

The Lyapunov method is a robust approach towards proving the local or global stability of a sufficiently large class of mathematical models which may involve, among others, predator–prey interactions and disease transmission, without the need of knowing the exact form of the functional coefficients involved. A Lyapunov functional of type $V(x, y) = d_x \left(x - x^* - \ln \frac{x}{x^*} \right) + d_y \left(y - y^* - \ln \frac{y}{y^*} \right)$ has been used by Volterra in [1] in order to establish the stability of a system modeling the interaction between sharks and predated fish in the Mediterranean Sea. See also [2], where authors used a related functional, consisting also in a weighted sum of Lyapunov functionals for each member species, to study the stability of a n -dimensional Lotka–Volterra model. In [3], Harrison constructed a Lyapunov functional for a two-dimensional predator–prey model written in an abstract form which vastly generalizes the Lotka–Volterra model and also encompasses the Leslie–Gower model, allowing for very general functional and numerical responses of the predator. Stability results for

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generalized Gause and Holling–Tanner models have been obtained by Ardito and Ricciardi [4] and also by Hsu and Huang [5], respectively, by means of employing suitable Lyapunov functionals, with those used in [4] being constructed in a somewhat different fashion. An extension of a Lyapunov functional proposed by Ardito and Ricciardi [4] was then used by Lindström in [6] to study the dynamics of a system with one prey and two competing predators. See also [7] for a survey on using the Lyapunov method to establish the stability of mathematical models in population biology.

A systematic study on the applicability of the Lyapunov method to various disease propagation models and predator–prey interactions has been made by Korobeinikov and his co-workers. In this regard, see [8] for global stability results for a Leslie–Gower predator–prey model, results which are then extended in [9] to cover a general two-dimensional predator–prey model with abstract predation rate. See also [10] for local stability results for SIR and SEIRS models featuring a very general incidence rate of type $f(S, I, N)$, [11] for global stability results for SIR and SIRS models, and [12] for global stability results for SEIR and SEIS models. The global dynamics of a SEIV model with nonlinear incidence of infection and removal has been studied by Georgescu and Hsieh in [13] by using the same approach, under certain monotonicity assumptions upon the functional quotient between the nonlinear force of infection and the removal rate of the virus, while the stability of a stage-structured predator–prey model with prey-dependent predation has been analyzed in [14]. Some recent developments in this area include the use of the Lyapunov method to establish the stability of certain classes of multigroup models (see [15,16]).

Further related advances include the use of Gaines and Mawhin's coincidence degree theory to discuss the existence and stability of positive periodic solutions for impulsively perturbed ratio-dependent and prey-dependent predator–prey models (see [17–19]) or for models of plankton allelopathy (see [20]). Permanence and global attractivity results for stage-structured predator–prey models which are subject to harvesting and stocking have been obtained by Jiao, Chen, Nieto and Torres in [21] by using Floquet theory together with comparison estimates. The asymptotic properties of competitive Lotka–Volterra models in random environments have been discussed by Zhu and Yin in [22], a stochastic principle of competitive exclusion being derived therein.

These remarks led us to consider the following general stage-structured model:

$$\begin{aligned}x' &= n(x) - \omega(x, y_2); \\y_1' &= k\omega(x, y_2) - c_1m(y_1); \\y_2' &= c_2m(y_1) - d(y_2).\end{aligned}\tag{1}$$

This model assumes the existence of two species, namely the prey, whose density at time t is denoted by $x(t)$, and the predator, whose life cycle consists in two stages, immature and mature, with the density of the immature and mature predator population at time t being denoted by $y_1(t)$ and $y_2(t)$, respectively. The growth of the prey population in the absence of predation is given by the intrinsic growth rate $n(x)$, while the interaction between the prey and mature predator population is described by the predation rate $\omega(x, y_2)$ which characterizes the feeding behavior of the mature predators at different prey densities. It is also assumed that the reproductive rate of the mature predators is proportional to their predation rate, with proportionality constant (consumption efficiency) k , as an increased food intake means that more energy is available for reproduction. The immature predators are not assumed to hunt for prey or reproduce while being raised by their mature parents. The movement of the immature predators outside the immature class due to removal or due to their maturation is given by $c_1m(y_1)$, while the influx of new mature predators coming from the immature class is given by $c_2m(y_1)$. The intrinsic decrease rate of the predator population in the absence of prey is given by $d(y_2)$. Throughout the rest of our paper, we allow n, ω, m, d to be abstract, unspecified functions of their respective variable(s), which permits us to generalize several known models indicated below. Our paper is especially motivated by Korobeinikov [9] and Georgescu and Hsieh [14,13].

Example 1: Stage-structured predator–prey model

If we assume that

$$\begin{aligned}n(x) &= x(r - ax), & \omega(x, y_2) &= \frac{bx}{1 + mx}y_2, & c_1m(y_1) &= (D + d_1)y_1, \\c_2m(y_1) &= Dy_1, & d(y_2) &= d_2y_2,\end{aligned}$$

then (1) reduces to a stage-structured model with stage structure for the predator which has been studied in [23,24,14,25], in the form

$$\begin{aligned}x' &= x(r - ax) - \frac{bx}{1 + mx}y_2, \\y_1' &= k\frac{bx}{1 + mx}y_2 - (D + d_1)y_1, \\y_2' &= Dy_1 - d_2y_2.\end{aligned}\tag{2}$$

In this model, the intrinsic growth rate of the prey population is given by the logistic function $n(x) = x(r - ax)$, with per capita birth rate in the absence of intraspecies competition r and carrying capacity $\frac{r}{a}$. The term $f(x) = \frac{bx}{1 + mx}$ represents the Holling type II functional (behavioral) response of the mature predator, b being the search rate and m being the search rate

multiplied by the handling time. The constants d_1 and d_2 represent the death rates of the immature and mature predators, respectively, and D denotes the rate at which immature predators become mature predators.

Let us define the basic reproduction number of the predator

$$R_0 = k \frac{br}{a + mr} \frac{1}{d_2} \frac{D}{D + d_1} = kf \left(\frac{r}{a} \right) \frac{1}{d_2} \frac{D}{D + d_1}$$

as being the average number of offsprings produced by a mature predator in its lifetime when introduced in a prey-only environment with prey at carrying capacity. It has been proved in [14,25] that if $R_0 > 1$ and the prey is abundant enough in the long term, that is, $\liminf_{t \rightarrow \infty} x(t) > \frac{r}{2a}$, then the unique positive steady state of the system is globally asymptotically stable on $(0, \infty)^3$. This result may again be interpreted in terms of monotonicity properties, namely that if the dynamics of the system is a-priori restricted to the monotonicity domain of n , then the stability of the positive equilibrium is assured by condition $R_0 > 1$.

Consequently, a feature of this model is that if predators are sufficiently aggressive, then the availability of prey in large quantities precludes all oscillatory behavior. Otherwise, if $R_0 \leq 1$ then the prey-only equilibrium $(\frac{r}{a}, 0, 0)$ is globally asymptotically stable. Moreover, if $R_0 > 1$ but condition $\liminf_{t \rightarrow \infty} x(t) > \frac{r}{2a}$ does not necessarily hold, then the prey-only equilibrium $(\frac{r}{a}, 0, 0)$ is unstable, there exists a unique positive equilibrium, and the system becomes uniformly persistent. That is, the predators are able to escape extinction.

Example 2: Virus propagation model

If we assume that

$$\begin{aligned} n(x) &= \lambda - dx, & \omega(x, y_2) &= \beta xy_2, & k &= 1, & c_1 m(y_1) &= ay_1, \\ c_2 m(y_1) &= k_1 y_1, & d(y_2) &= -\mu y_2, \end{aligned}$$

the system reduces to a virus propagation model studied in [26,27], in the form:

$$\begin{aligned} x' &= \lambda - dx - \beta xy_2, \\ y_1' &= \beta xy_2 - ay_1, \\ y_2' &= k_1 y_1 - \mu y_2. \end{aligned} \tag{3}$$

This model has three variables: uninfected cells x , infected cells y_1 and free virus particles y_2 . The constants $\frac{1}{d}, \frac{1}{a}, \frac{1}{\mu}$ represent the average lifetime of uninfected cells, infected cells and free virus, respectively. Uninfected cells are produced at a constant rate λ and die at rate dx . Free virus particles are assumed to infect uninfected cells at rate βxy_2 , the average number of virus particles produced in the lifetime of a single infected cell (the burst size) being given by $\frac{k_1}{a}$. It has been observed (see [28] or [29]) that the virus propagation model (3) is equivalent to an SEIR model with a constant population size assumption, namely, if the equation for the recovered population R is omitted due to the constant population size assumption, then x corresponds to the susceptible class S , y_1 corresponds to the exposed (infected but not infectious) class E and y_2 corresponds to the infective population I .

Let us define the basic reproduction number of the virus $R_0 = \beta \frac{\lambda}{d} \frac{1}{a} \frac{k_1}{\mu}$ as being the average number of newly infected cells that arise from a single infected virus particle introduced in a totally susceptible environment. It has also been shown in [29] that if $R_0 > 1$ then there is a unique endemic equilibrium which is globally asymptotically stable, while if $R_0 \leq 1$ then there is no endemic equilibrium and the infection-free equilibrium is globally asymptotically stable.

Example 3: SEI model with media impact

If we assume that

$$\begin{aligned} n(x) &= rx \left(1 - \frac{x}{K} \right), & \omega(x, y_2) &= \mu e^{-my_2} xy_2, & k &= 1, & c_1 m(y_1) &= (c + d)y_1, \\ c_2 m(y_1) &= cy_1, & d(y_2) &= \gamma y_2, \end{aligned}$$

then (1) reduces to a disease propagation model with media impact studied in [30], in the form:

$$\begin{aligned} x' &= rx \left(1 - \frac{x}{K} \right) - \mu e^{-my_2} xy_2, \\ y_1' &= \mu e^{-my_2} xy_2 - (c + d_1)y_1, \\ y_2' &= cy_1 - \gamma y_2. \end{aligned} \tag{4}$$

In this model, x represents the class of susceptible individuals, y_1 represents the class of exposed individuals and y_2 represents the class of infective individuals. Here, r represents the per capita birth rate of the human population at small population densities and K represents the carrying capacity for the human population of a given area. The term $\beta(y_2) = \mu e^{-my_2} y_2$ represents the contact and transmission term, which measures the spread of the infection. Here the parameter $m > 0$ measures the impact of media coverage to reduce the contact and transmission, assuming that m increases as the

public becomes more alert and aware of the virus. Note that Hsu and Hsieh [31,32] also used a first-order approximation of the term e^{-my_2} in the form of $\frac{1}{1+my_2}$ to model public response to reduce contact and avoid infection during disease outbreaks. The constant c represents the rate per unit time at which the exposed become infective, d is the natural death rate of the susceptible population and γ is the removal rate from the infective compartment, which includes the recovery rate of hospitalized individuals and natural death.

It is shown in [30] that if $R_0 < 1$ (here R_0 is again the basic reproduction number, given by $R_0 = \mu K \frac{c}{c+d_1}$), then the disease-free equilibrium is globally asymptotically stable, while if $R_0 > 1$, then the number of positive equilibria depends on the parameter $m_0 = \frac{8\mu}{rR_0}$, in the sense that if the media coverage is small ($0 < m < m_0$), then the model has a unique endemic equilibrium and if the media coverage is larger ($m > m_0$) then the model has three endemic equilibria. Further, if $R_0 > 1$ and is close enough to 1 and m is also small, then the endemic equilibrium is locally asymptotically stable and if $m = 0$ then the endemic equilibrium is also locally asymptotically stable if $R_0 > 1$ and is small enough.

A few remarks, motivated by the above examples, are now in order. First of all, the basic reproduction number can be used to successfully predict the survival or extinction of the predator population (or of the viral cells), in the sense that if $R_0 < 1$, it is expected that the predators (or viral cells) will become extinct, while $R_0 > 1$ is a necessary condition for predator persistence and for the existence of the positive equilibria. That is, R_0 is understood to be a threshold parameter which gives information about the existence and stability of both the predator-free (virus-free) equilibrium and of the positive equilibria.

The number of positive equilibria and their stability or lack thereof is, in our opinion, tied to the monotonicity of the intrinsic growth rate n and of the predation rate $\omega(x, y_2)$. The existence of multiple positive equilibria in Example 3 can be attributed to the lack of quasi-monotonicity of the predation rate, or to the lack of monotonicity of the functional quotient between the predation rate and of the death rate as a function of the x -variable. In Example 1, where the predation rate ω is monotonic in each variable but the intrinsic growth rate n is non-monotonic, there is a single positive equilibrium whose global stability is assured if the size of the prey class ultimately reaches a monotonicity interval for n , namely, the interval $(\frac{r}{2a}, \infty)$. Finally, in Example 2 both n and ω are monotonic, hence the uniqueness and global stability of the positive equilibrium being assured.

2. The well-posedness of the model

In this section, we shall discuss the global existence of solutions of (1) and their positivity properties, showing that (1) is well-posed in a biological sense. To this purpose, we assume that n, ω, m, d are continuously differentiable and that the following hypotheses hold:

(H1) $\omega(x, y_2) \geq 0$ for $x, y_2 \geq 0$; $\omega(x, y_2) > 0$ for $x, y_2 > 0$ and $w(x, 0) = w(0, y_2) = 0$ for $x, y_2 > 0$.

(H2) $d(0) = 0$; $d(y_2) \geq d'(0)y_2$ for $y_2 \geq 0$, with $d'(0) > 0$.

(H3) $m(0) = 0$; $m(y_1) \geq m'(0)y_1$ for $y_1 \geq 0$, with $m'(0) > 0$.

(H4) $\omega(x, y_2) \leq \frac{\partial \omega}{\partial y_2}(x, 0)y_2$ for $x, y_2 \geq 0$.

(H5) $n(0) \geq 0$ and there is $x_0 > 0$ such that $n(x) > 0$ for $x \in (0, x_0)$ and $n(x) < 0$ for $x \in (x_0, +\infty)$.

Hypothesis (H1) embodies the fact that if there are no prey or no predator individuals, then there is no predation and that predators will successfully hunt for prey if there is any. Hypotheses (H2) and (H3) are satisfied if d and m are linear or convex functions and are needed to show that (1) is biologically well-posed, in the sense that $[0, \infty)^3$ and $(0, \infty)^3$ are invariant sets for (1). Hypothesis (H4) is satisfied if $y_2 \rightarrow \omega(x, y_2)$ is a concave function and states that predators compete for prey when hunting rather than cooperate. However, (H4) may also be satisfied in other situations in which $y_2 \rightarrow \omega(x, y_2)$ is not concave (see, for instance, Example 3). It is easy to see that (H4) is satisfied for classical prey-dependent predation, as defined in [33] or [34], in which the functional response f of the mature predator depends only on the availability of prey and the predation rate ω is given by $\omega(x, y_2) = f(x)y_2$. Hypothesis (H5) implies that there exists a predator-free equilibrium state $(x_0, 0, 0)$ and that the growth of the prey is self-limiting. As this model wishes to accommodate both predator-prey interactions and disease transmission, we note that (H1) may also be justified on the grounds that if there are no susceptibles or infectives (no susceptible cells or no viral cells), there is no disease transmission and that (H4) reflects the occurrence of saturation or crowding phenomena. Also, $n(0)$ may be either 0 (for predator-prey models, where if there is no prey then there is no growth of the prey class, a typical example being $n(x) = x(r - ax)$), or strictly positive (for disease transmission models, when it is often assumed that there is a constant supply of susceptible cells or individuals, a typical example being $n(x) = \lambda - dx$).

Under these circumstances, one may show that $Q_1 = [0, \infty)^3$ is an invariant set for (1). That is, all solutions starting in Q_1 remain there for their whole interval of existence. To this purpose, let us define $A : \mathbb{R}^3 \rightarrow \mathbb{R}^3$ by

$$A((x_1, x_2, x_3)^T) = (n(x_1) - \omega(x_1, x_3), k\omega(x_1, x_3) - c_1m(x_2), c_2m(x_2) - d(x_3))^T$$

and, for a set $M \subset \mathbb{R}^3$ and $x \in \mathbb{R}^3$, let us denote

$$d(x, M) = \inf\{|x - y|, y \in M\}.$$

It is seen that $\lim_{h \rightarrow 0} \frac{d(x+hAx, Q_1)}{h} = 0$ for all $x \in \partial Q_1$, so Nagumo's invariance conditions are satisfied and Q_1 is an invariant set for (1). See [35] for further invariance results and for other tangency concepts. See also [36,37] for an application of flow invariance theory to the study of a parabolic PDE system describing the propagation of HIV in the human body.

We now show the a-priori boundedness of the solutions of (1). To this purpose, let us note first that since $x' \leq n(x)$, it follows that $x(t) \leq \max(x(0), x_0)$ for $t \geq 0$, which ensures the boundedness of x . Let us also define

$$F : \mathbb{R}^3 \rightarrow \mathbb{R}, \quad F(x, y_1, y_2) = x + \frac{1}{k}y_1 + \frac{1}{k} \frac{c_1}{2c_2}y_2.$$

Computing the time derivative of F along the solutions of (1), we observe that

$$\dot{F} = n(x) - \frac{c_1}{2k}m(y_1) - \frac{1}{k} \frac{c_1}{2c_2}d(y_2) \leq n_M - \frac{c_1}{2k}m'(0)y_1 - \frac{1}{k} \frac{c_1}{2c_2}d'(0)y_2,$$

where n_M is an upper boundedness constant for n . Consequently, it is seen that

$$\dot{F} + dF \leq n_M + dx,$$

where $d = \min\left(\frac{c_1 m'(0)}{2}, \frac{d'(0)}{2}\right)$, and so

$$F(x(t), y_1(t), y_2(t)) \leq F(x(0), y_1(0), y_2(0))e^{-dt} + (n_M + d \max(x(0), x_0)) \frac{1 - e^{-dt}}{d}.$$

It follows that all solutions of (1) are bounded, and consequently defined on $[0, \infty)$.

It is now possible to prove that $Q_2 = (0, \infty)^3$ is also an invariant set for (1). To this purpose, suppose that $x(0), y_1(0), y_2(0)$ are all positive and note that

$$y_2'(t) + d'(0)y_2(t) \geq c_2m(y_1(t)) \geq 0,$$

so $t \rightarrow y_2(t)e^{d'(0)t}$ is increasing and consequently y_2 remains strictly positive. Similarly,

$$y_1'(t) + m'(0)y_1(t) \geq k\omega(x(t), y_2(t)) \geq 0,$$

so $t \rightarrow y_1(t)e^{m'(0)t}$ is increasing and consequently y_1 remains strictly positive. To prove that x remains also strictly positive, let us note first that if $n(0) > 0$, then $x'(t)$ becomes positive when $x(t)$ becomes small, so $x(t)$ cannot reach 0. If $n(0) = 0$, we shall argue by contradiction. Suppose that $x(t_0) = 0$ for some $t_0 > 0$. Then one may find $\tilde{y}_1(0)$ and $\tilde{y}_2(0) > 0$ both positive such that the solution which starts at $t = 0$ from $(0, \tilde{y}_1(0), \tilde{y}_2(0))$ also reaches $(0, y_1(t_0), y_2(t_0))$ at $t = t_0$, again by (H2) and (H3). By the uniqueness property, this solution should coincide with the solution which starts at $t = 0$ from $(x(0), y_1(0), y_2(0))$, which is a contradiction. Regarding the behavior of the solutions which start on the boundary of Q_1 , it is easy to see that the solutions which start in the plane y_1Oy_2 tend to the origin while remaining in the plane y_1Oy_2 , the solutions which start on Ox tend to $(x_0, 0, 0)$, the origin may be an (unstable) equilibrium point if $n(0) = 0$, while all other solutions starting on the boundary of Q_1 enter Q_2 and stay there. By $[Ox$ and $\{Ox$ we mean the set $\{(x, 0, 0); x > 0\}$ (the positive x -semi-axis) and the set $\{(x, 0, 0); x \geq 0\}$ (the strictly positive x -semi-axis), respectively.

3. The stability of the x -only equilibrium

Since the equation $n(x) = 0$ admits a single positive solution x_0 , it follows that (1) admits a single x -only equilibrium point (that is, a predator-free or infection-free equilibrium) $(x_0, 0, 0)$. We now turn our attention to the issue of its stability.

Let us first define the basic reproduction number of the mature predator population by

$$R_0 = k \frac{c_2 \frac{\partial \omega}{\partial y_2}(x_0, 0)}{c_1 d'(0)}. \tag{5}$$

In this regard, a quick derivation of R_0 can be performed along the lines of van den Driessche and Watmough [38], noting again that, as seen in Example 2, our model can be thought as a generalized SEIR model with a constant population assumption, so x corresponds to the susceptible class S , y_1 corresponds to the exposed class E and y_2 corresponds to the infective class I . Then (1) can be restated as

$$\begin{pmatrix} y_1' \\ y_2' \\ x' \end{pmatrix} = \begin{pmatrix} k\omega(x, y_2) \\ 0 \\ 0 \end{pmatrix} - \begin{pmatrix} c_1 m(y_1) \\ -c_2 m(y_1) + d(y_2) \\ -n(x) + \omega(x, y_2) \end{pmatrix} = \mathcal{F} - \mathcal{V}.$$

At the x -only equilibrium $\mathbf{x}_0 = (x_0, 0, 0)$, corresponding to the disease-free equilibrium in [38], one has

$$D\mathcal{F}(\mathbf{x}_0) = \begin{pmatrix} F & 0 \\ 0 & 0 \end{pmatrix}, \quad D\mathcal{V}(\mathbf{x}_0) = \begin{pmatrix} V & 0 \\ J_1 & J_2 \end{pmatrix},$$

where the infection matrix F and the transition matrix V are given by

$$F = \begin{pmatrix} 0 & k \frac{\partial \omega}{\partial y_2}(x_0, 0) \\ 0 & 0 \end{pmatrix}, \quad V = \begin{pmatrix} c_1 m'(0) & 0 \\ -c_2 m'(0) & d'(0) \end{pmatrix}.$$

Then R_0 is the largest eigenvalue of the next generation matrix FV^{-1} , so $R_0 = \rho(FV^{-1})$, from which (5) follows. Note that for $\omega(x, y_2) = f(x)y_2$ and $d(y_2) = d_2y_2$, $R_0 = k \frac{c_2 f(x_0)}{c_1 d}$, from which the expressions of R_0 found for Examples 1 and 2 easily follow. One then similarly derives the expression of R_0 found in Example 3.

Let us now consider the Lyapunov functional

$$U_1(x, y_1, y_2) = \int_{x_0}^x \left(1 - \frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{\frac{\partial \omega}{\partial y_2}(\tau, 0)} \right) d\tau + \frac{1}{k}y_1 + \frac{1}{k} \frac{c_1}{c_2}y_2 \tag{6}$$

under the hypothesis

(H6) $x \rightarrow \frac{\partial \omega}{\partial y_2}(x, 0)$ is increasing and $\frac{\partial \omega}{\partial y_2}(x, 0) > 0$ for $x > 0$.

The first part of (H6) is satisfied if $x \rightarrow \omega(x, y_2)$ is increasing for all fixed $y_2 > 0$. As a particular case, (H6) is satisfied for classical prey-dependent predation, that is, $\omega(x, y_2) = f(x)y_2$, if the functional response f of the mature predator is an increasing function of the size of the prey class x and $f(x) > 0$ for $x > 0$, as in this case $\frac{\partial \omega}{\partial y_2}(x, 0) = f(x)$.

We compute the derivative of U_1 along the solutions of (1). Using (H2) and (H4), one then has

$$\begin{aligned} \dot{U}_1 &= \left(1 - \frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{\frac{\partial \omega}{\partial y_2}(x, 0)} \right) (n(x) - \omega(x, y_2)) + \frac{1}{k}(k\omega(x, y_2) - c_1m(y_1)) + \frac{1}{k} \frac{c_1}{c_2}(c_2m(y_1) - d(y_2)) \\ &= n(x) \left(1 - \frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{\frac{\partial \omega}{\partial y_2}(x, 0)} \right) + \frac{1}{k} \frac{c_1}{c_2}d(y_2) \left[\frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{\frac{\partial \omega}{\partial y_2}(x, 0)} \frac{\omega(x, y_2)}{d(y_2)} k \frac{c_2}{c_1} - 1 \right] \\ &\leq n(x) \left(1 - \frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{\frac{\partial \omega}{\partial y_2}(x, 0)} \right) + \frac{1}{k} \frac{c_1}{c_2}d(y_2)(R_0 - 1). \end{aligned}$$

We note that

$$n(x) \left(1 - \frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{\frac{\partial \omega}{\partial y_2}(x, 0)} \right) \leq 0 \quad \text{for } x \in (0, \infty),$$

due to (H5) and (H6), so

$$\dot{U}_1 \leq \frac{1}{k} \frac{c_1}{c_2}d(y_2)(R_0 - 1).$$

Further, since $x \rightarrow \frac{\partial \omega}{\partial y_2}(x, 0)$ is increasing, it follows that $\text{sgn}(x - x_0) = \text{sgn} \left(\frac{\partial \omega}{\partial y_2}(x, 0) - \frac{\partial \omega}{\partial y_2}(x_0, 0) \right)$; therefore, $(x_0, 0, 0)$ is a minimum point for U_1 and $U_1(x, y_1, y_2) \geq 0$ for $(x, y_1, y_2) \in Q_2$. We are now ready to establish our first stability result.

Theorem 3.1. *Suppose that $R_0 \leq 1$ and (H1)–(H5) hold, together with (H6) and the following hypothesis*

(H7) $\int_{0+}^1 \frac{1}{\frac{\partial \omega}{\partial y_2}(\tau, 0)} d\tau = \infty$.

Then the x -only equilibrium $(x_0, 0, 0)$ is globally asymptotically stable in Q_2 .

Proof. Let $m > 0$ and let

$$S_m = \{(x, y_1, y_2) \in Q_2; U_1(x, y_1, y_2) < m\}.$$

Let $k < m$ arbitrary and let $\Omega_k = \{(x, y_1, y_2) \in Q_2; U_1(x, y_1, y_2) \leq k\}$.

Obviously, $\dot{U}_1 \leq 0$ in Ω_k and the equality holds if $x = x_0$ and $y_2 = 0$, or $R_0 = 1$ (note that $\lim_{x \rightarrow 0} U_1(x, y_1, y_2) = +\infty$). In both cases, the only invariant set within the set $E = \{(x, y_1, y_2) \in \Omega_k; \dot{U}_1(x, y_1, y_2) = 0\}$ is the point $P(x_0, 0, 0)$, so all solutions $(x(t), y_1(t), y_2(t))$ starting in Ω_k tend to P as $t \rightarrow \infty$ from LaSalle’s invariance principle (see [39] or [40]). Since $k < m$ was arbitrary, the conclusion follows. \square

Note that (H7) is again satisfied if $\omega(x, y_2) = f(x)y_2$ and $\int_{0+}^1 \frac{1}{f(x)} dx = +\infty$, which is the case, for instance, if f is a Holling type II functional response, $f(x) = \frac{bx}{1+mx}$. Also, Theorem 3.1 leads to the following global stability results.

Corollary 3.2. *If $R_0 \leq 1$, then the predator-free equilibrium $(\frac{r}{a}, 0, 0)$ of (2) is globally asymptotically stable in $(0, \infty)^3$.*

Corollary 3.3. *If $R_0 \leq 1$, then the virus-free equilibrium $(\frac{\lambda}{d}, 0, 0)$ of (3) is globally asymptotically stable in $(0, \infty)^3$.*

4. The uniform persistence of the system

To complement Theorem 3.1, we now investigate the persistence of (1). In this regard, it is said that (1) is uniformly persistent on D if there is $\varepsilon_0 > 0$ (not depending on the initial data) such that any solution of (1) which starts in

$(x(0), y_1(0), y_2(0)) \in \text{Int}(D)$ satisfies

$$\liminf_{t \rightarrow \infty} x(t) \geq \varepsilon_0, \quad \liminf_{t \rightarrow \infty} y_1(t) \geq \varepsilon_0, \quad \liminf_{t \rightarrow \infty} y_2(t) \geq \varepsilon_0.$$

Obviously, the uniform persistence of the system excludes the stability of $(x_0, 0, 0)$ in any sense. From a biological viewpoint, the uniform persistence of the system ensures the long-term coexistence of all populations, none of them facing extinction.

Let us define

$$V(x, y_1, y_2) = y_1 + \frac{c_1}{c_2} y_2.$$

It follows that the derivative of V along the solutions of (1) is given by

$$\dot{V} = \frac{c_1}{c_2} d(y_2) \left[k \frac{c_2}{c_1} \frac{\omega(x, y_2)}{d(y_2)} - 1 \right].$$

We are now ready to formulate our persistence result.

Theorem 4.1. *In addition to (H1)–(H5), suppose that*

(H8) $k \frac{c_2}{c_1} \frac{\omega(x, y_2)}{d(y_2)} - 1 > 0$ for $(x, y) \in (x_L, x_R) \times (0, \varepsilon)$, where $x_0 \in (x_L, x_R)$.

Then (1) is uniformly persistent and $(x_0, 0, 0)$ is unstable, with Ox as its stable manifold.

Proof. From (H8), we know that $\dot{V} > 0$ on a vicinity of $(x_0, 0, 0) \cap Q_1$, except for points with $y_2 = 0$. It follows that any solution which starts in this vicinity goes away from $(x_0, 0, 0)$ except for those starting with $y_1 = y_2 = 0$, which tend to $(x_0, 0, 0)$ (those which start with $y_2 = 0$ but $y_1 > 0$ enter Q_2). Subsequently, the unique compact invariant sets on ∂Q_1 are $(x_0, 0, 0)$ and (possibly, if $n(0) = 0$) $(0, 0, 0)$, their stable manifolds being Ox and $\{(0, 0, 0)\}$, respectively. The use of Theorem 4.1 in [41] finishes the proof. For an alternate approach, based on a result of Fonda [42], see [43] or [25]. \square

In particular, (H8) implies that $R_0 > 1$ and if $\frac{\omega(x, y_2)}{d(y_2)}$ is a function only of the variable x , as is the case when $\omega(x, y_2) = f(x)y_2$ and $d(y_2) = d_2 y_2$, (H8) is actually equivalent to $R_0 > 1$. The following results then hold.

Corollary 4.2. *If $R_0 > 1$, then (2) is uniformly persistent and the predator-free equilibrium $(\frac{r}{a}, 0, 0)$ is unstable, with Ox as its stable manifold.*

Corollary 4.3. *If $R_0 > 1$, then (3) is uniformly persistent and the virus-free equilibrium $(\frac{\lambda}{d}, 0, 0)$ is unstable, with Ox as its stable manifold.*

5. The existence of positive equilibria

We now try to establish some sufficient conditions for the existence of a positive equilibrium (x^*, y_1^*, y_2^*) . To this purpose, we note that x^*, y_1^* , and y_2^* must satisfy

$$n(x^*) = \omega(x^*, y_2^*), \quad k\omega(x^*, y_2^*) = c_1 m(y_1^*), \quad c_2 m(y_1^*) = d(y_2^*). \tag{7}$$

To solve (7), let us define

$$F : [0, \infty)^2 \rightarrow \mathbb{R}, \quad F(x, y_2) = n(x) - \frac{1}{k} \frac{c_1}{c_2} d(y_2);$$

$$G : [0, \infty)^2 \rightarrow \mathbb{R}, \quad G(x, y_2) = \omega(x, y_2) - \frac{1}{k} \frac{c_1}{c_2} d(y_2)$$

$$= \frac{1}{k} \frac{c_1}{c_2} d(y_2) \left[k \frac{c_2}{c_1} \frac{\omega(x, y_2)}{d(y_2)} - 1 \right].$$

With these notations, it is easy to see that the equalities $F(x^*, y_2^*) = 0, G(x^*, y_2^*) = 0$ should be satisfied. Let us assume that the following hypotheses hold.

(E1) $x \rightarrow \omega(x, y_2)$ is increasing for all fixed $y > 0$.

(E2) The equation $k \frac{c_2}{c_1} \omega(x, y_2) = d(y_2)$ has a unique solution $x = \varphi(y_2)$ for all fixed $y_2 \in (0, n_M k \frac{c_2}{c_1} \frac{1}{d'(0)} + \varepsilon]$, where $\varepsilon > 0$.

Moreover, the function φ is increasing.

Let us note again that if (E1) holds, then $x \rightarrow \frac{\partial \omega}{\partial y_2}(x, 0)$ is increasing and that (E1) holds if $\omega(x, y_2) = f(x)y_2$, with f increasing. Also, if $\omega(x, y_2) = f(x)y_2$ and $d(y_2) = d_2 y_2$, as is the case in Example 1, then the equation $k \frac{c_2}{c_1} \omega(x, y_2) = d(y_2)$ reduces to $k \frac{c_2}{c_1} f(x) = d_2$, which always has a unique solution $x^*, 0 < x^* < x_0$, if $R_0 > 1$, irrespective of y_2 . In this particular case, φ is constant. If $\omega(x, y_2) = \mu e^{-my_2} x y_2$ and $d(y_2) = \gamma y_2$, as it is the case in Example 3, then the equation $k \frac{c_2}{c_1} \omega(x, y_2) = d(y_2)$ reduces to $k \frac{c}{c+d_1} \mu e^{-my_2} x = \gamma$, which always has a unique solution $x = \frac{\gamma}{k} \frac{c+d_1}{c} \frac{1}{\mu} e^{my_2}$. In this case, φ is nonconstant.

Note, however, that (E1) precludes the use of our stability results to the situations in which the feeding behavior of the mature predator is described by a Monod–Haldane (Holling type IV) functional response $(f(x) = \frac{cx}{m^2+bx+x^2})$, which is not monotonic as a function of x .

Theorem 5.1. *Suppose that (H1)–(H5) hold, together with (E1):*

1. *if (E2) holds and $R_0 > 1$, then (1) has positive equilibria;*
2. *if $R_0 \leq 1$, then there is no positive equilibrium for (1).*

Proof. First, we note that the equation $F(x, y_2) = 0$ defines a continuous curve γ in the first quadrant of the plane xOy_2 . Note also that for a fixed y_2 there might be several solutions (x, y_2) of this equation. Further, all points of this curve have their x -coordinate in $[0, x_0]$, since $n(x) < 0$ for $x > x_0$ and, due to (H2), the y -coordinate belongs to the bounded interval $[0, n_M k \frac{c_2}{c_1} \frac{1}{d'(0)}]$. This curve crosses $(Ox$ uniquely at $(x_0, 0)$, while if $n(0) = 0$ the curve crosses $[Oy_2$ uniquely at $(0, 0)$. If $n(0) > 0$, then the curve crosses $[Oy_2$ uniquely at $(0, y_*)$, where $y_* > 0$. Here, $(Ox$ and $[Oy_2$ refer to the strictly positive x -semiaxis and the positive y_2 -semiaxis of the plane xOy_2 (the sets $\{(x, 0); x > 0\}$ and $\{(0, y_2); y_2 \geq 0\}$, respectively).

Now, due to (E2), the equation $G(x, y_2) = 0$ has a unique solution $x = \varphi(y_2)$ for all fixed y_2 . Furthermore, φ increases. Since φ is well-defined outside $[0, n_M k \frac{c_2}{c_1} \frac{1}{d'(0)}]$, a necessary and sufficient condition for the existence of the positive equilibrium is that $x_0 > L = \lim_{y_2 \rightarrow 0} \varphi(y_2)$.

If $R_0 > 1$, since

$$\lim_{y_2 \rightarrow 0} k \frac{c_2}{c_1} \frac{\omega(x_0, y_2)}{d(y_2)} = k \frac{c_2}{c_1} \frac{\frac{\partial \omega}{\partial y_2}(x_0, 0)}{d'(0)} = R_0 > 1$$

and $x \rightarrow \omega(x, y_2)$ increases for all y_2 , it follows that $x = \varphi(y_2) < u < x_0$ for y_2 small enough and u close to x_0 . Consequently, $\lim_{y_2 \rightarrow 0} \varphi(y_2) < x_0$ and there are positive equilibria.

If $R_0 \leq 1$, one then has due to (H2) and (H4) that

$$\begin{aligned} G(x, y) &= \frac{1}{k} \frac{c_1}{c_2} d(y_2) \left[k \frac{c_2}{c_1} \frac{\omega(x, y_2)}{d(y_2)} - 1 \right] \\ &\leq \frac{1}{k} \frac{c_1}{c_2} d(y_2) \left[k \frac{c_2}{c_1} \frac{\frac{\partial \omega}{\partial y_2}(x, 0)}{d'(0)} - 1 \right] \\ &\leq \frac{1}{k} \frac{c_1}{c_2} d(y_2) \left[k \frac{c_2}{c_1} \frac{\frac{\partial \omega}{\partial y_2}(x, 0)}{d'(0)} - R_0 \right] \\ &= \frac{d(y_2)}{d'(0)} \left[\frac{\partial \omega}{\partial y_2}(x, 0) - \frac{\partial \omega}{\partial y_2}(x_0, 0) \right] \end{aligned}$$

so $\frac{\partial \omega}{\partial y_2}(x, 0) \geq \frac{\partial \omega}{\partial y_2}(x_0, 0)$ for all $x = \varphi(y_2)$, which implies that $x \geq x_0$. Consequently, the curves $F(x, y_2) = 0$ and $G(x, y_2) = 0$ have no positive contact (x^*, y_2^*) .

Furthermore, since $m(0) = 0$ and $\lim_{y_1 \rightarrow \infty} m(y_1) = +\infty$ from (H3), it follows that the equation $m(y_1) = \frac{1}{c_2} d(y_2^*)$ has at least a positive solution y_1^* . □

Note, however, that the above hypotheses do not ensure the uniqueness of the positive equilibrium, since the curves defined by $F(x, y_2) = 0$ and $G(x, y_2) = 0$ can cross several times, one particular reason being the fact that the curve defined by $F(x, y_2) = 0$ may not even be the graph of a function. Further, the equation $m(y_1) = \frac{1}{c_2} d(y_2^*)$ can have more than one solution. However, if $R_0 > 1$, $\omega(x, y_2) = f(x)y_2$, $d(y_2) = d_2 y_2$ and m is strictly monotonic, then the positive equilibrium (x^*, y_1^*, y_2^*) is unique. One then obtains the following results.

Corollary 5.2. *If $R_0 > 1$, then (2) has a unique positive equilibrium. If $R_0 \leq 1$, then there is no positive equilibrium of (2).*

Corollary 5.3. *If $R_0 > 1$, then (3) has a unique positive equilibrium. If $R_0 \leq 1$, then there is no positive equilibrium of (3).*

6. The stability of the positive equilibria

In this section, we assume that the system (1) admits (at least) a positive equilibrium (x^*, y_1^*, y_2^*) and study its stability. We also assume that the following sign and divergence conditions hold

$$\begin{aligned} (m(y) - m(y_1^*))(y - y_1^*) &> 0 && \text{for } y \neq y_1^*, \quad y \geq 0 \\ (\omega(x, y_2) - \omega(x^*, y_2))(x - x^*) &> 0 && \text{for } x \neq x^*, \quad y_2 > 0 \\ (\omega(x^*, y_2) - \omega(x^*, y_2^*))(y_2 - y_2^*) &> 0 && \text{for } y \neq y_2^* \end{aligned} \tag{S}$$

and

$$\int_{0+}^1 \frac{1}{\omega(\tau, y_2)} d\tau = +\infty, \quad \int_{0+}^1 \frac{1}{m(\tau)} d\tau = +\infty, \quad \int_{0+}^1 \frac{1}{\omega(x, \tau)} d\tau = +\infty \quad \text{for all fixed } x, y_2 > 0. \tag{D}$$

Note that the sign conditions (S) are satisfied if m strictly increases, $x \rightarrow \omega(x, y_2)$ strictly increases for all fixed $y_2 > 0$, and $y_2 \rightarrow \omega(x^*, y_2)$ also strictly increases. We consider the Lyapunov functional

$$U_2(x, y_1, y_2) = \int_{x^*}^x \frac{\omega(\tau, y_2^*) - \omega(x^*, y_2^*)}{\omega(\tau, y_2^*)} d\tau + \frac{1}{k} \int_{y_1^*}^{y_1} \frac{m(\tau) - m(y_1^*)}{m(\tau)} d\tau + \frac{1}{k c_2} \int_{y_2^*}^{y_2} \frac{\omega(x^*, \tau) - \omega(x^*, y_2^*)}{\omega(x^*, \tau)} d\tau. \tag{8}$$

Here (x^*, y_1^*, y_2^*) is a minimum point for U_2 , $U_2(x, y_1, y_2)$ increases whenever any one of $|x - x^*|, |y_1 - y_1^*|, |y_2 - y_2^*|$ increases and $U_2(x, y_1, y_2) \geq 0$ for all $(x, y_1, y_2) > 0$. Also, if any one of the variables x, y_1 , and y_2 tends to 0, then $U_2(x, y_1, y_2)$ tends to ∞ , due to the divergence conditions (D). It then follows that the level sets of U_2 have no limit points on the boundary of Q_1 .

We now compute the derivative of U_2 along the solutions of (1).

Lemma 6.1. *The time derivative of U_2 along the solutions of (1) is given by*

$$\begin{aligned} \dot{U}_2(x, y_1, y_2) = & \left[n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) - n(x^*) \left(1 - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right) \right] \\ & + \omega(x^*, y_2^*) \left[3 - \frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right] \\ & + \omega(x^*, y_2^*) \left[\frac{\omega(x, y_2)}{\omega(x, y_2^*)} - \frac{d(y_2)}{d(y_2^*)} + \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{d(y_2)}{d(y_2^*)} - 1 \right]. \end{aligned} \tag{9}$$

Proof. We have

$$\begin{aligned} \dot{U}_2(x, y_1, y_2) = & \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) (n(x) - \omega(x, y_2)) + \frac{1}{k} \left(1 - \frac{m(y_1^*)}{m(y_1)} \right) (k\omega(x, y_2) - c_1 m(y_1)) \\ & + \frac{1}{k c_2} \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \right) (c_2 m(y_1) - d(y_2)) \\ = & n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) + \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \omega(x, y_2) - \frac{m(y_1^*)}{m(y_1)} \omega(x, y_2) \\ & + \frac{c_1}{k} m(y_1^*) - \frac{1}{k c_2} d(y_2) - \frac{1}{k c_1} \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} m(y_1) + \frac{1}{k c_2} \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} d(y_2). \end{aligned}$$

Using the equilibrium relations (7), it follows that

$$\begin{aligned} \dot{U}_2(x, y_1, y_2) = & n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) + \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \omega(x, y_2) - \frac{m(y_1^*)}{m(y_1)} \omega(x, y_2) + \omega(x^*, y_2^*) \\ & - \frac{1}{k c_2} d(y_2) - \frac{1}{k c_1} \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} m(y_1) + \frac{1}{k c_2} \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} d(y_2) \\ = & n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) + \omega(x^*, y_2^*) \left(1 - \frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right) \\ & + \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \omega(x, y_2) + \omega(x^*, y_2^*) \frac{\omega(x^*, y_2)}{\omega(x, y_2)} + \frac{1}{k c_2} \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} d(y_2) - \frac{1}{k c_2} d(y_2). \end{aligned}$$

Consequently,

$$\begin{aligned} \dot{U}_2(x, y_1, y_2) = & n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) + \omega(x^*, y_2^*) \left(3 - \frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right) \\ & + \left(\omega(x^*, y_2^*) \frac{\omega(x^*, y_2)}{\omega(x, y_2)} - \omega(x^*, y_2^*) \right) + \left(\frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \omega(x, y_2) - \frac{1}{k c_2} d(y_2) \right) \\ & + \left(\frac{1}{k c_2} \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} d(y_2) - \omega(x^*, y_2^*) \right). \end{aligned}$$

This implies that

$$\begin{aligned} \dot{U}_2(x, y_1, y_2) &= \left[n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) - \omega(x^*, y_2^*) \left(1 - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right) \right] \\ &\quad + \omega(x^*, y_2^*) \left[3 - \frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right] \\ &\quad + \left(\omega(x^*, y_2^*) \frac{\omega(x, y_2)}{\omega(x, y_2^*)} - \frac{\omega(x^*, y_2^*)}{d(y_2^*)} d(y_2) + \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \omega(x^*, y_2^*) \frac{d(y_2)}{d(y_2^*)} - \omega(x^*, y_2^*) \right) \\ &= \left[n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) - n(x^*) \left(1 - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right) \right] \\ &\quad + \omega(x^*, y_2^*) \left[3 - \frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right] \\ &\quad + \omega(x^*, y_2^*) \left[\frac{\omega(x, y_2)}{\omega(x, y_2^*)} - \frac{d(y_2)}{d(y_2^*)} + \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{d(y_2)}{d(y_2^*)} - 1 \right] \end{aligned}$$

which finishes the proof. \square

Note that the AM–GM inequality, which says that the algebraic mean is not smaller than the arithmetic mean, implies that

$$3 - \frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} - \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \leq 0 \quad (10)$$

with equality if and only if

$$\frac{m(y_1^*)}{m(y_1)} \frac{\omega(x, y_2)}{\omega(x^*, y_2^*)} = \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{m(y_1)}{m(y_1^*)} = \frac{\omega(x^*, y_2)}{\omega(x, y_2)} = 1. \quad (11)$$

It is then seen that the stability of the positive equilibrium (x^*, y_1^*, y_2^*) is determined by the signs of the first and third terms in the right-hand side of (9). If both terms are negative, then the time derivative of U_2 is the negative in the phase space of (1) and one may derive the local stability of (x^*, y_1^*, y_2^*) from LaSalle's invariance principle, as seen in the following result.

Theorem 6.2. Assume that (H1)–(H4) are satisfied, together with (S) and (D), and there are $x_L, x_R, y_L, y_R, x^* \in (x_L, x_R), y_2^* \in (y_L, y_R)$ such that the inequalities

$$n(x) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)} \right) - n(x^*) \left(1 - \frac{\omega(x^*, y_2)}{\omega(x, y_2)} \right) \leq 0 \quad (12)$$

and

$$\frac{\omega(x, y_2)}{\omega(x, y_2^*)} - \frac{d(y_2)}{d(y_2^*)} + \frac{\omega(x^*, y_2^*)}{\omega(x^*, y_2)} \frac{d(y_2)}{d(y_2^*)} - 1 \leq 0 \quad (13)$$

hold for all $x \in (x_L, x_R), y_2 \in (y_L, y_R)$. Define

$$\alpha = \min (U_2(x_L, y_1^*, y_2^*), U_2(x_R, y_1^*, y_2^*), U_2(x^*, y_1^*, y_L), U_2(x^*, y_1^*, y_R)).$$

Then (x^*, y_1^*, y_2^*) is locally asymptotically stable and its domain of attraction includes the set

$$S_\alpha = \{(x, y_1, y_2) \in Q_2; U_2(x, y_1, y_2) < \alpha\}.$$

Proof. Let $k < \alpha$ arbitrary and $\Omega_k = \{(x, y_1, y_2) \in Q_2; U_2(x, y_1, y_2) \leq k\}$. Since $U_2(x, y_1, y_2) \geq U_2(x, y_1^*, y_2^*)$ and $U_2(x, y_1, y_2) \geq U_2(x^*, y_1^*, y_2)$, it follows that all $(x, y_1, y_2) \in \Omega_k$ have the property that $x_L < x < x_R, y_L < y_2 < y_R$. Obviously, $\dot{U}_2 \leq 0$ in Ω_k and the equality holds if and only if the equalities in (11), (12) and (13) also hold. It now remains to find the invariant set \tilde{E}_2 within the set

$$E_2 = \{(x, y_1, y_2) \in \Omega_k; \dot{U}_2(x, y_1, y_2) = 0\}.$$

First of all, one deduces from the last relation in (11) and the sign conditions that $x = x^*$. Substituting in the first part of (11), one obtains that $\frac{m(y_1)}{m(y_1^*)} = \frac{\omega(x^*, y_2)}{\omega(x^*, y_2^*)}$. Since $x = x^*$ on \tilde{E}_2 , it follows that $n(x^*) = \omega(x^*, y_2)$ on \tilde{E}_2 , so $\frac{m(y_1)}{m(y_1^*)} = \frac{\omega(x^*, y_2)}{\omega(x^*, y_2^*)} = 1$ on \tilde{E}_2 , and from the sign conditions we obtain that $y_1 = y_1^*$. This implies that $\omega(x^*, y_2) = \omega(x^*, y_2^*)$ and consequently one gets from the sign conditions that $y_2 = y_2^*$. It follows from LaSalle's invariance principle that all solutions $(x(t), y_1(t), y_2(t))$ of (1) starting in Ω_k tend to (x^*, y_1^*, y_2^*) as $t \rightarrow \infty$. Since $k < \alpha$ was arbitrary, the conclusion follows. \square

A few comments on the feasibility of (12) and (13) are perhaps in order. First of all, if $\omega(x, y_2) = f(x)g(y_2)$ and $d(y_2) = cy_2$, then (13) reduces to

$$\left(\frac{g(y_2)}{g(y_2^*)} - \frac{y_2}{y_2^*}\right) \left(1 - \frac{g(y_2)}{g(y_2^*)}\right) \leq 0. \tag{14}$$

If $g(y_2) = y_2$, as is the case for Examples 1 and 2,

$$\left(\frac{g(y_2)}{g(y_2^*)} - \frac{y_2}{y_2^*}\right) \left(1 - \frac{g(y_2)}{g(y_2^*)}\right) \equiv 0,$$

so (13) is trivially satisfied. If $g(y_2) = y_2e^{-my_2}$, as is the case for Example 3, then (14) reduces to

$$\frac{e^{my_2}}{y_2^*} \left(\frac{y_2}{e^{my_2}} - \frac{y_2^*}{e^{my_2^*}}\right) \left(\frac{e^{my_2}}{e^{my_2}} - 1\right) \leq 0,$$

which is satisfied if y_2, y_2^* belong to the interval $(0, \frac{1}{m})$ on which g increases.

However, (12) has less chances to be satisfied, at least for models describing predator–prey interactions. This happens since putting $y_2 = y_2^*$ in (12) yields

$$(n(x) - n(x^*)) \left(1 - \frac{\omega(x^*, y_2^*)}{\omega(x, y_2^*)}\right) \leq 0. \tag{15}$$

Since $\text{sgn}(\omega(x, y_2^*) - \omega(x^*, y_2^*)) = \text{sgn}(x - x^*)$ from (S), it follows that necessarily

$$(n(x) - n(x^*))(x - x^*) \leq 0, \tag{16}$$

which in some situations may not hold even locally (if x^* belongs to an interval on which n increases, for instance). However, (16) holds if x belongs to an interval on which n decreases. This is always the case if $n(x) = \lambda - dx$, as in Example 2, which leads to global stability properties, but if $n(x) = x(r - ax)$, as in Example 1, one needs to restrict the domain of attraction in order to ensure that the x -coordinate belongs to $(\frac{r}{2a}, +\infty)$ (to assume that the persistency constant for x is larger than $\frac{r}{2a}$, that is). The following stability results may then be obtained as consequences of Theorem 6.2.

Corollary 6.3. *If $R_0 > 1$ and $\liminf_{t \rightarrow \infty} x(t) > \frac{r}{2a}$, then the positive equilibrium of (2) is unique and globally asymptotically stable on $(0, \infty)^3$.*

Corollary 6.4. *If $R_0 > 1$, then the positive equilibrium of (3) is unique and globally asymptotically stable on $(0, \infty)^3$.*

Corollary 6.5. *If $R_0 > 1$, $\liminf_{t \rightarrow \infty} x(t) > \frac{K}{2}$ and $\liminf_{t \rightarrow \infty} y_2(t) < \frac{1}{m}$, then the positive equilibrium of (4) is unique and globally asymptotically stable on $(0, \infty)^3$.*

As a side effect, note that Corollary 6.5 implies that the positive (endemic) equilibrium of (4) has less chances to be stable if the media coverage m is large, that is, media coverage is a positive factor towards the containment of a disease.

Finally let us now finally consider the case of ratio-dependent predation, that is, the case in which $\omega(x, y_2) = \frac{bxy_2}{my_2 + x}$, for $d(y_2) = d_2y_2$ and $n(x) = x(r - ax)$. In this situation, (13) reduces to

$$\frac{m(y_2 - y_2^*)(xy_2^* - x^*y_2)}{y_2^*(my_2 + x)(my_2^* + x^*)} \leq 0, \tag{17}$$

while (12) reduces to

$$\frac{m(x - x^*)}{x} \left[\frac{x(r - ax)y_2^*}{my_2^* + x^*} - \frac{x^*(r - ax^*)y_2}{my_2 + x^*} \right] \leq 0. \tag{18}$$

However, for $x = x^* + \varepsilon_1, y_2 = y_2^* + \varepsilon_2$, (17) reduces to

$$\frac{m\varepsilon_2(\varepsilon_1y_2^* - \varepsilon_2x^*)}{y_2^*(my_2 + x)(my_2^* + x^*)} \leq 0,$$

which has no chance to be satisfied for all $\varepsilon_1, \varepsilon_2 \in (-\epsilon, \epsilon)$, where ϵ is a small parameter. Consequently, ratio-dependent predation does not seem to fit into our theoretical framework.

7. Discussion and concluding remarks

In the previous sections, we have analyzed the stability of the equilibria and the persistence of the general stage-structured system,

$$\begin{aligned}x' &= n(x) - \omega(x, y_2), \\y_1' &= k\omega(x, y_2) - c_1 m(y_1), \\y_2' &= c_2 m(y_1) - d(y_2),\end{aligned}$$

in terms of conditions (H1)–(H8), (E1), (E2), (S) and (D), whose biological significance has also been discussed. It has been found that the basic reproduction number of the predator population, defined as

$$R_0 = k \frac{\partial \omega}{\partial y_2}(x_0, 0) \frac{c_2}{c_1} \frac{1}{d'(0)}$$

is a threshold parameter for the stability of the system and the local stability of the positive equilibrium can be obtained under two feasible conditions (12) and (13) which involve n , ω and d . One may also associate a transparent biological interpretation with R_0 . Specifically, the first term $k \frac{\partial \omega}{\partial y_2}(x_0, 0)$ represents the average number of newborn immature predators per mature predator introduced in a predator-free environment and per unit time, while the second term $\frac{c_2}{c_1}$ represents the probability that an immature predator will survive to adulthood. The third term, $\frac{1}{d'(0)}$, has no direct interpretation for the initial system, as the equation $y_2'(t) = -d(y_2(t))$ cannot be integrated explicitly for general d 's, but it represents the average time spent by a predator in the mature stage if the third equation is replaced with its linearization near $y_2 = 0$, namely with $y_2' = m(y_1) - d'(0)y_2$. Consequently, R_0 approximates the mean number of offsprings per every mature predator. Note that the basic reproduction number R_0 does not depend upon m .

The practical applicability of this theoretical framework has also been discussed and it has been observed that, for certain particular but significant cases, our analysis yields global stability results, although ratio-dependent predation does not fall within the scope of our results.

The Lyapunov functional U_2 which is used to study the stability of the positive equilibrium is a generalisation of the functional $V(x, y) = d_x(x - x^* - \ln \frac{x}{x^*}) + d_y(y - y^* - \ln \frac{y}{y^*})$ used by Volterra in [1]. Note that if $\omega(x, y) = bxy$ and $m(y_1) = y_1$, then

$$U_2 = x - x^* - x^* \ln \frac{x}{x^*} + \frac{1}{k} \left(y_1 - y_1^* - y_1^* \ln \frac{y_1}{y_1^*} \right) + \frac{1}{k} \frac{c_1}{c_2} \left(y_2 - y_2^* - y_2^* \ln \frac{y_2}{y_2^*} \right).$$

Note also the difference between the Lyapunov functional U_1 used to study the stability of the x -only equilibrium and the corresponding functional used by Korobeinikov in [9]. It is easy to see that our considerations can be extended to models in which predators pass through $p > 2$ life stages, as long as prey consumption occurs in the last stage, or to disease propagation models in which the exposed individuals pass through $p > 2$ latent stages.

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