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LOTKA-VOLTERRA TYPE PREDATOR-PREY MODELS:
COMPARISON OF HIDDEN AND EXPLICIT RESOURCES WITH
A TRANSMISSIBLE DISEASE IN THE PREDATOR SPECIES

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Abstract. The paper deals with two mathematical models of predator-prey type where a transmissible disease spreads among the predator species only. The proposed models are analyzed and compared in order to assess the influence of hidden and explicit alternative resource for predator. The analysis shows boundedness as well as local stability and trans-critical bifurcations for equilibria of systems. Numerical simulations support our theoretical analysis.

Keywords: hidden prey; explicit prey; bifurcation; predator-prey model

MSC 2010: 34A34, 92D25, 92D40

1. INTRODUCTION

Ecology is an area of biology that seeks to understand the relationships existing between living beings in a given environment and to ensure the maintenance of ecological balance. To protect species from extinction it is fundamental to understand the interaction dynamics between different populations, usually related through food links [11], [2], [9], [15]. Important tools used to investigate the dynamics among populations are mathematical models that seek to describe this type of interaction. As an instance we can cite the dynamics of predator-prey type biological systems [10], [16], [6], whose scientific foundations provide solid results that allow the expansion of research in the area [5], [14], [17], [1].

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In this work we extend the results of earlier investigations on predators feeding on a main resource and on an additional prey, when the latter is implicitly and explicitly modeled in the system [3]. For this case, two mathematical models were proposed and analyzed to elucidate the influence on a generalist predator of its hidden and explicit resources. Boundedness of the system's trajectories, feasibility, local and global stabilities of the equilibria for both models were established, as well as possible local bifurcations. The findings indicated that the relevant behaviour of the system, including switching of stability, extinction and persistence of the involved populations, depends mainly on the reproduction rate of the favorite prey. To achieve full ecosystem survival some balance between the respective grazing pressures exerted by the predator on the prey populations needs to be maintained, while higher grazing pressure just on one species always leads to its extinction.

In addition, we investigated also when the prey is subject to a transmissible disease [4]. In the same way, two mathematical models of predator-prey systems where a transmissible disease spreads only among the prey species were proposed, analyzed and compared in order to assess the influence of hidden or explicit resources for the predator. The predator is assumed to be a generalist one in the first model and a specialist one on two prey species in the second one. Existence and boundedness of the solutions of the models were established, as well as local and global stability and bifurcations. Comparison between the results of these models showed that the relevant ecosystem behaviour, including stability switching, extinction and persistence for any species depends on four important parameters, viz the reproduction rate and the infection rate of the main prey, the mortality rate of infected prey and the reproduction rate of the alternative prey. Again two models are here proposed to investigate a similar situation. However, now the epidemics affects the predators, as in [7], [8]. We investigate the dynamics between predator and prey in two different scenarios. In the first one, we consider a generalist predator that has two different prey for its own survival, the main prey and an alternative one which is not explicitly built in as a model variable. In the second scenario, the predator becomes a type of specialist with only two explicit preys. The results of [3] show that the grazing pressure on the preferred prey and carrying capacity of the predator determine the stable coexistence of prey and predator when the alternative resource is implicit.

The paper is organized as follows: the mathematical models are formulated in Section 2. The boundedness of both systems is discussed in Section 3. The existence of equilibria and the stability are examined in Section 4 and the theoretical results for bifurcations are discussed in Section 5. The numerical simulations of Section 6 give detailed results about the onset of bifurcations. In Sections 7 and 8 we compare the models and their results, respectively. Transcritical bifurcations present in both models are illustrated with help of numerical examples.

2. BASIC ASSUMPTIONS AND MODELS FORMULATION

This ecoepidemic model considers the following three populations: the prey X , the healthy predator population Z and the infected predators W . The model with the alternative food supply, in which the prey population is represented by Y , is denoted $[ep_hp]$, where “ ep ” denotes ecoepidemic in predator and “ hp ” denotes the hidden prey that substitutes resource not explicitly modeled in the equations [3]; it is well known in the literature, see Chapter 3 of [12]:

$$(2.1) \quad \begin{aligned} \frac{dX}{dt} &= rX \left(1 - \frac{X}{K}\right) - aZX - gXW, \\ \frac{dZ}{dt} &= uZ \left(1 - \frac{Z+W}{L}\right) + eX(aZ + gW) - \beta ZW, \\ \frac{dW}{dt} &= \beta ZW - \nu W. \end{aligned}$$

Now, we consider a disease-affected predator, which is specialist for two prey species. The model in this case is denoted by $[ep_ep]$ where the first “ ep ” denotes ecoepidemic in predator and the second denotes explicit prey:

$$(2.2) \quad \begin{aligned} \frac{dX}{dt} &= rX \left(1 - \frac{X}{K}\right) - aZX - gXW, \\ \frac{dY}{dt} &= sY \left(1 - \frac{Y}{H}\right) - bZY - \kappa YW, \\ \frac{dZ}{dt} &= -mZ^2 + eZ(aX + bY) + eW(gX + \kappa Y) - \beta ZW, \\ \frac{dW}{dt} &= \beta ZW - \nu W. \end{aligned}$$

In both models all the parameters are assumed to be nonnegative. Their biological meaning is rather obvious, as these are kind of standard models: r , u and s are growth rates, K , L , H denote carrying capacities, a , g , b and κ are hunting rates, β is the disease horizontal transmission rate, ν the natural plus disease-induced mortality, m is the predators’ mortality rate, e is the conversion factor, i.e., the fraction of captured prey that is used to produce new predators. In particular, note that for the latter, if the biomass is measured in kilograms and in any case taking into account that the whole prey is never entirely converted into predators’ mass, we take

$$(2.3) \quad e \leq 1.$$

The Jacobians are

$$(2.4) \quad J^{[ep_hp]} = \begin{pmatrix} J_{11}^{[ep_hp]} & -aX & -gX \\ aeZ + egW & J_{22}^{[ep_hp]} & -\frac{u}{L}Z + egX - \beta Z \\ 0 & \beta W & \beta Z - \nu \end{pmatrix}$$

with

$$J_{11}^{[ep-hp]} = r - \frac{2r}{K}X - aZ - gW, \quad J_{22}^{[ep-hp]} = u - \frac{2u}{L}Z - \frac{u}{L}W + aeX - \beta W$$

and

$$(2.5) \quad J^{[ep-ep]} = \begin{pmatrix} J_{11}^{[ep-ep]} & 0 & -aX & -gX \\ 0 & J_{22}^{[ep-ep]} & -bY & -\kappa Y \\ aeZ + egW & ebZ + e\kappa W & J_{33}^{[ep-ep]} & egX + e\kappa Y - \beta Z \\ 0 & 0 & \beta W & \beta Z - \nu \end{pmatrix}$$

with

$$J_{11}^{[ep-ep]} = r - \frac{2r}{K}X - aZ - gW, \quad J_{22}^{[ep-ep]} = s - \frac{2s}{H}Y - bZ - \kappa W, \\ J_{33}^{[ep-ep]} = -2mZ + eaX + ebY - \beta W,$$

respectively.

The first equation of model (2.1) describes the healthy prey population dynamics. The first term on the right-hand side expresses logistic growth with r being the per capita net reproduction rate and K the environment carrying capacity. The second and third terms describe the process, where the healthy individual is hunted by healthy predator Z and infected predator W , respectively. The second equation of model (2.1) contains the dynamics of the healthy predator, that in absence of prey X has an alternative resource, which is hidden in this model. It is implicitly represented in the model by the carrying capacity L , whereas the predators per capita net reproduction rate is u . The term $eX(aZ + gW)$ expresses the increase of the predator Z population due to successful hunting of the prey by healthy and infected predators, respectively. The term βZW models the infection process of susceptible predators by contact with other infected individuals. The third equation of model (2.1) describes the infected predator W evolution, recruited as explained in the previous equation and subject to disease-related mortality ν .

The first and fourth equations of model (2.2) represent the healthy prey X and infected predator W dynamics. They are the same as for model (2.1). The second equation of model (2.2) describes the alternative prey population dynamics which now becomes an explicit variable of the system.

The first term on the right-hand side expresses logistic growth with per capita net reproduction rate s and carrying capacity H . The second and third terms model the process, where the individual of population Y is hunted by healthy predator Z and infected predator W , respectively.

The third equation of model (2.2) describes the healthy predator population dynamics. In this equation, the first term on the right-hand side assumes mortality

in the quadratic form $-mZ^2$, since this term is related to the intraspecific competition term $-uL^{-1}Z^2$ of the system (2.1). Predators mortality clearly occurs in the absence of both their food resources X and Y , because in this model the predator is assumed to be a specialist on both of them. The term $eZ(aX + bY)$ corresponds to the population increase of predator Z due to hunting the prey X and Y . Finally, the term βZW accounts for individuals of the population Z that become infected.

3. BOUNDEDNESS OF MODELS

In order to have a well-posed model, the system's trajectories must be contained in a compact set.

First of all, note that the populations cannot become negative, because they start from positive initial values, for obvious biological reasons, and systems (2.1) and (2.2) are homogeneous, so that the coordinate subspaces are solution trajectories and, by the uniqueness theorem, they cannot be crossed by other trajectories. Indeed $\dot{X} = 0$ if $X(0) = 0$, $\dot{Y} = 0$ if $Y(0) = 0$, $\dot{Z} \geq 0$ if $Z(0) = 0$, $\dot{W} = 0$ if $W(0) = 0$ and when nonvanishing, the initial conditions should always be positive to make biological sense.

Proposition 3.1. *Consider the total environment population $\varphi(t) = X(t) + Z(t) + W(t)$, in model (2.1). Then there exists $\eta \in \mathbb{R}_+$ for which*

$$(3.1) \quad \varphi(t) \leq \left(\varphi(0) - \frac{M}{\eta} \right) e^{-\eta t} + \frac{M}{\eta} \leq \max \left\{ \varphi(0), \frac{M}{\eta} \right\}.$$

Thus for model (2.1) the solutions are always nonnegative.

Proof. Taking an arbitrary $0 < \eta < \nu$, summing the equations in model (2.1), we obtain

$$(3.2) \quad \begin{aligned} \frac{d\varphi(t)}{dt} = & rX \left(1 - \frac{X}{K} \right) + uZ \left(1 - \frac{Z+W}{L} \right) - \nu W \\ & + (e-1)(aXZ + gXW). \end{aligned}$$

Recalling (2.3), the last term in (3.2) can be dropped, as well as the term $-uL^{-1}WZ$, to obtain:

$$(3.3) \quad \frac{d\varphi(t)}{dt} \leq rX \left(1 - \frac{X}{K} \right) + uZ \left(1 - \frac{Z}{L} \right) - \nu W.$$

Then, adding $\eta\varphi(t)$ and using the definition of φ on both sides of the inequality (3.3) we find the estimate

$$\begin{aligned} \frac{d\varphi(t)}{dt} + \eta\varphi(t) &\leq rX\left(1 - \frac{X}{K} + \frac{\eta}{r}\right) + uZ\left(1 - \frac{Z}{L} + \frac{\eta}{u}\right) \\ &\quad + (\eta - \nu)W \leq p_1(X) + p_2(Z), \\ p_1(X) &= rX\left(1 - \frac{X}{K} + \frac{\nu}{r}\right), \\ p_2(Z) &= uZ\left(1 - \frac{Z}{L} + \frac{\nu}{u}\right). \end{aligned}$$

The functions $p_1(X)$ and $p_2(Z)$ are concave parabolae, with maxima located at X^* , Z^* , and corresponding maximum values

$$M_1 = p_1(X^*) = \frac{rK}{4}\left(1 + \frac{\nu}{r}\right)^2, \quad M_2 = p_2(Z^*) = \frac{uL}{4}\left(1 + \frac{\nu}{u}\right)^2.$$

Thus,

$$\frac{d\varphi(t)}{dt} + \eta\varphi(t) \leq M, \quad M_1 + M_2 = M.$$

Integrating the differential inequality, we find (3.1). From this result, since $0 \leq X, Z, W \leq \varphi$, the boundedness of the original ecosystem populations is immediate. From the nonnegativity of the trajectories, remarked before the proof, and this result, the solution of model (2.1) remains bounded and the trajectories remain nonnegative. \square

Proposition 3.2. *Consider the total environment population $\psi(t) = X(t) + Y(t) + Z(t) + W(t)$ in model (2.2). Then there exists $\eta_1 \in \mathbb{R}_+$ for which*

$$(3.4) \quad \psi(t) \leq \left(\varphi(0) - \frac{M}{\eta_1}\right)e^{-\eta_1 t} + \frac{M}{\eta_1} \leq \max\left\{\psi(0), \frac{M}{\eta_1}\right\}.$$

Thus for model (2.2) the solutions are always nonnegative.

Proof. We proceed in a way similar to that in the proof of Proposition 3.1.

Taking an arbitrary $0 < \eta_1 < \nu$, summing the equations in model (2.2), we obtain

$$(3.5) \quad \begin{aligned} \frac{d\psi(t)}{dt} &= rX\left(1 - \frac{X}{K}\right) + sY\left(1 - \frac{Y}{H}\right) - mZ^2 - \nu W \\ &\quad + (e - 1)(aXZ + bYZ + gXW + \kappa YW). \end{aligned}$$

Since $e \leq 1$ by (2.3), from (3.5) we can obtain

$$(3.6) \quad \frac{d\psi(t)}{dt} \leq rX\left(1 - \frac{X}{K}\right) + sY\left(1 - \frac{Y}{H}\right) - mZ^2 - \nu W.$$

Adding $\eta_1\psi(t)$ on both sides of inequality (3.3) we find the estimate

$$\begin{aligned} \frac{d\psi(t)}{dt} + \eta_1\psi(t) &\leq rX\left(1 - \frac{X}{K} + \frac{\eta_1}{r}\right) + sY\left(1 - \frac{Y}{H} + \frac{\eta_1}{s}\right) \\ &\quad + Z(\eta_1 - mZ) + (\eta_1 - \nu)W \leq q_1(X) + q_2(Y) + q_3(Z), \\ q_1(X) &= rX\left(1 - \frac{X}{K} + \frac{\nu}{r}\right), \\ q_2(Z) &= sY\left(1 - \frac{Y}{H} + \frac{\nu}{s}\right), \\ q_3(Z) &= Z(\nu - mZ). \end{aligned}$$

The functions $q_1(X)$, $q_2(Y)$ and $q_3(Z)$ are concave parabolae, with maxima located at X^* , Y^* , Z^* , and the corresponding maximum values

$$M_1 = q_1(X^*) = \frac{rK}{4}\left(1 + \frac{\nu}{r}\right)^2, \quad M_2 = q_2(Y^*) = \frac{sH}{4}\left(1 + \frac{\nu}{s}\right)^2, \quad M_3 = q_3(Z^*) = \frac{\nu^2}{4m}.$$

Thus,

$$\frac{d\psi(t)}{dt} + \eta_1\psi(t) \leq M, \quad M_1 + M_2 + M_3 = M.$$

Integrating the differential inequality, we find (3.4). From this result, since $0 \leq X, Y, Z, W \leq \psi$, the boundedness of the original ecosystem populations is immediate. \square

4. EQUILIBRIA AND STABILITY ANALYSIS

The purely demographic model (2.1). As illustrated in the following propositions, there are six equilibria for the model (2.1), two of which are unconditionally unstable while the remaining four are stable subject to suitable conditions on the system parameters. We are concerned with two main issues in this respect, namely feasibility and stability of these stationary points. The former refers to the fact that the population values are all nonnegative. This is a key issue for biological reasons. As for the latter, stability ensures that trajectories originating nearby an equilibrium, do indeed tend to it.

Proposition 4.1. *The trivial equilibrium point $P_1^{[ep-hp]} = (0, 0, 0)$ and the point $P_2^{[ep-hp]} = (K, 0, 0)$ are always feasible and unstable.*

Proof. Since the the system (2.1) is homogeneous, the origin $P_1^{[ep-hp]}$ is a solution. The eigenvalues of the Jacobian matrix (2.4) evaluated at $P_1^{[ep-hp]}$ are r , u , $-\nu$. As two eigenvalues are positive, the origin is unstable.

For $Z = W = 0$, the equilibrium equations of (2.1) give $X_2 = K$, i.e., the equilibrium $P_2^{[ep-hp]}$, which is always feasible. The eigenvalues of the Jacobian evaluated at $P_2^{[ep-hp]}$ are $-r$, $-\nu$, $u + aeK > 0$, again showing instability. \square

Proposition 4.2. *The healthy predator-only point $P_3^{[ep-hp]} = (0, L, 0)$ is always feasible. It is stable for*

$$(4.1) \quad r < aL, \quad \nu > \beta L.$$

Proof. For $X = W = 0$ in the system (2.1) we obtain the equilibrium $P_3^{[ep-hp]}$, which is always feasible. The Jacobian (2.4) at $P_3^{[ep-hp]}$ becomes

$$J_{P_3}^{[ep-hp]} = \begin{pmatrix} r - aL & 0 & 0 \\ aeL & -u & -(u + \beta L) \\ 0 & 0 & \beta L - \nu \end{pmatrix}$$

and provides explicitly the eigenvalues, one of which $-u$ is negative, while the remaining ones give conditions (4.1). \square

Proposition 4.3. *The disease-free point*

$$P_4^{[ep-hp]} = \left(\frac{urK - auKL}{a^2eKL + ur}, \frac{aerKL + urL}{a^2eKL + ur}, 0 \right)$$

is feasible for

$$(4.2) \quad r \geq aL,$$

and stable when the following condition holds:

$$(4.3) \quad \beta < \nu \frac{ur + a^2eKL}{urL + aerKL}.$$

Proof. The above equilibrium expression is easily obtained by setting $W = 0$ in the system (2.1). The inequality $X_4^{[ep-hp]} \geq 0$ provides the feasibility condition (4.2). The Jacobian matrix (2.4) evaluated at $P_4^{[ep-hp]}$ gives one explicit eigenvalue, from which (4.3) follows. In addition, since

$$-\text{tr}(\overline{J}_{P_4}^{[ep-hp]}) = \frac{r}{K} X_4^{[ep-hp]} + \frac{u}{L} Z_4^{[ep-hp]} > 0$$

and

$$\det(\overline{J}_{P_4}^{[ep-hp]}) = \left(\frac{ru}{KL} + a^2e \right) X_4^{[ep-hp]} Z_4^{[ep-hp]} > 0,$$

the Routh-Hurwitz conditions on the remaining minor

$$\overline{J}_{P_4}^{[ep-hp]} = \begin{pmatrix} -rK^{-1}X_4^{[ep-hp]} & -aX_4^{[ep-hp]} \\ aeZ_4^{[ep-hp]} & -uL^{-1}Z_4^{[ep-hp]} \end{pmatrix}$$

are always satisfied, and thus (4.3) is the only condition for stability. \square

Proposition 4.4. *The point*

$$P_5^{[ep-hp]} = \left(0, \frac{\nu}{\beta}, \frac{u\beta L - u\nu}{\beta u + \beta^2 L} \right)$$

is feasible if

$$(4.4) \quad \nu \leq \beta L$$

and stable for

$$(4.5) \quad wr\beta + r\beta^2 L + gu\nu < au\nu + a\nu\beta L + gu\beta L.$$

Proof. This equilibrium point is feasible for $W_5^{[ep-hp]} \geq 0$ which gives explicitly (4.4). One eigenvalue gives the stability condition (4.5), while for the remaining minor

$$\bar{J}_{P_5}^{[ep-hp]} = \begin{pmatrix} -\frac{u\nu}{\beta L} & -\frac{u\nu}{\beta L} - \nu \\ \frac{u\beta L - u\nu}{u + \beta L} & 0 \end{pmatrix}$$

the Routh-Hurwitz conditions are unconditionally satisfied:

$$-\text{tr}(\bar{J}_{P_5}^{[ep-hp]}) = \frac{u\nu}{\beta L} > 0, \quad \det(\bar{J}_{P_5}^{[ep-hp]}) = \beta \left(\frac{u}{L} + \beta \right) Z^{[ep-hp]} W^{[ep-hp]} > 0.$$

□

Proposition 4.5. *Coexistence, $P_6^{[ep-hp]} = (X_6^{[ep-hp]}, Z_6^{[ep-hp]}, W_6^{[ep-hp]})$, whose population values are given below (4.8), exists as a double equilibrium for (4.9), (4.10) and (4.11), or as a single point whenever (4.9) and (4.12) are satisfied, with the additional feasibility condition*

$$(4.6) \quad \beta \geq \frac{a\nu K + r\beta X_6^{[ep-hp]}}{rK},$$

and it is stable for

$$(4.7) \quad K > \frac{(a\nu\beta L + ug\beta L + au\nu)K + (aeg\beta KL + r\beta^2 L + ru\beta)X_6^{[ep-hp]}}{r\beta^2 L + 2gu\nu + ru\beta}.$$

Proof. Explicitly, the coordinates of $P_6^{[ep-hp]}$ are

$$(4.8) \quad Z_6^{[ep-hp]} = \frac{\nu}{\beta}, \quad W_6^{[ep-hp]} = \frac{r}{g} - \frac{a\nu}{g\beta} - \frac{r}{gK} X_6^{[ep-hp]},$$

where $X_6^{[ep-hp]}$ is a root of the quadratic function

$$\Phi(X_6^{[ep-hp]}) = \alpha_2(X_6^{[ep-hp]})^2 + \alpha_1 X_6^{[ep-hp]} + \alpha_0$$

with

$$\alpha_2 = -\frac{er}{K}, \quad \alpha_1 = er + \frac{ur\nu}{g\beta KL} + \frac{r\nu}{gK}, \quad \alpha_0 = \frac{u\nu}{\beta} - \frac{r\nu}{g} + \frac{a\nu^2}{g\beta^2 L} - \frac{u\nu^2}{\beta^2 L} - \frac{ur\nu}{g\beta L} + \frac{a\nu^2}{g\beta}.$$

Besides, $P_6^{[ep-hp]}$ is feasible if $W_6^{[ep-hp]} \geq 0$, i.e., (4.6), and for $X_6^{[ep-hp]} \geq 0$ we have conditions for two positive roots

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad -\alpha_1\alpha_2^{-1} > 0, \quad \alpha_0\alpha_2^{-1} > 0,$$

which are equivalent to

$$(4.9) \quad r\nu^2\beta^2 L + 4aeg\nu^2\beta KL^2 + 4eg^2uv\beta KL^2 + e^2g^2r\beta^2 K^2 L^2 + 2ruv^2\beta L \\ + 4aeg\nu^2 KL + ru^2\nu^2 > 2egr\nu\beta^2 KL^2 + 4eg^2\nu^2 KL + 2egr\nu\beta KL,$$

$$(4.10) \quad \frac{L(eg\beta K + \nu\beta) + uv}{eg\beta L} > 0$$

and

$$(4.11) \quad ur\beta + r\beta^2 L + gu\nu > au\nu + av\beta L + gu\beta L.$$

For one positive root we have the conditions

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad \alpha_0\alpha_2^{-1} < 0,$$

which correspond to (4.9) again, and

$$(4.12) \quad ur\beta + r\beta^2 L + gu\nu < au\nu + av\beta L + gu\beta L,$$

respectively. The Jacobian matrix of $P_6^{[ep-hp]}$ is

$$J_{P_6}^{[ep-hp]} = \begin{pmatrix} -rK^{-1}X_6^{[ep-hp]} & -aX_6^{[ep-hp]} & -gX_6^{[ep-hp]} \\ eav\beta^{-1} + egW_6^{[ep-hp]} & J_{22}^{[ep-hp]} & J_{23}^{[ep-hp]} \\ 0 & \beta W_6^{[ep-hp]} & 0 \end{pmatrix}$$

with

$$J_{22}^{[ep-hp]} = u - \frac{2u\nu}{\beta L} + eaX_6^{[ep-hp]} - \left(\frac{u}{L} + \beta\right)W_6^{[ep-hp]},$$

$$J_{23}^{[ep-hp]} = -\nu - \frac{u\nu}{\beta L} + egX_6^{[ep-hp]}.$$

Requiring the condition $J_{22}^{[ep-hp]} < 0$, that is, (4.7), the principal minors of $-J_{P_6}^{[ep-hp]}$ are all positive:

$$\begin{aligned} \frac{r}{K}X_6 > 0, \quad -\frac{r}{K}J_{22}^{[ep-hp]}X_6^{[ep-hp]} + aX_6^{[ep-hp]}\left(\frac{ea\nu}{\beta} + egW_6^{[ep-hp]}\right) > 0, \\ eag\nu X_6^{[ep-hp]}W_6^{[ep-hp]} + eg^2\beta X_6^{[ep-hp]}(W_6^{[ep-hp]})^2 \\ + \frac{ur\beta}{KL}X_6^{[ep-hp]}Z_6^{[ep-hp]}W_6^{[ep-hp]} + \frac{r}{K}\beta^2 X_6^{[ep-hp]}Z_6^{[ep-hp]}W_6^{[ep-hp]} \\ - \frac{egr\beta}{K}X_6^{[ep-hp]}W_6^{[ep-hp]} > 0. \end{aligned}$$

Thus, $P_6^{[ep-hp]}$ is feasible and stable, if (4.6), (4.9), (4.10), (4.11), (4.12), and (4.7) hold. \square

In Table 1 we summarize the equilibria of model (2.1).

Equilibria	Admissibility	Stability
$P_1^{[ep-hp]}$	always	unstable
$P_2^{[ep-hp]}$	always	unstable
$P_3^{[ep-hp]}$	always	$r < aL, \nu > \beta L$
$P_4^{[ep-hp]}$	$r \geq aL$	(4.3)
$P_5^{[ep-hp]}$	$\nu \leq \beta L$	(4.5)
$P_6^{[ep-hp]}$	(4.6), (4.9), (4.10), (4.11) – 2 positive roots	(4.7)
	(4.6), (4.9), (4.10), (4.12) – 1 positive root	

Table 1. Behaviour and conditions of feasibility and stability of equilibria for model (2.1).

Model (2.2). The local stability analysis of model (2.2) gives 11 equilibria, four of which are unconditionally unstable, one unfeasible and six are conditionally stable. The details follow.

Proposition 4.6. *The equilibria $P_1^{[ep-ep]} = (0, 0, 0, 0)$, $P_2^{[ep-ep]} = (K, 0, 0, 0)$, $P_3^{[ep-ep]} = (0, H, 0, 0)$, $P_4^{[ep-ep]} = (K, H, 0, 0)$ are feasible and unstable and the equilibrium $P_5^{[ep-ep]} = (0, 0, \nu\beta^{-1}, -m\nu\beta^{-2})$ is unfeasible.*

Proof. For $X = Y = Z = W = 0$ in the system (2.2) we obtain that the origin $P_1^{[ep-ep]}$ exists and is feasible. The eigenvalues of the Jacobian matrix (2.5) evaluated at $P_1^{[ep-ep]}$ are $-\nu, r, s, 0$. As two eigenvalues are positive, the origin is unstable.

For $Y = Z = W = 0$ in the system (2.2), we obtain the equilibrium $P_2^{[ep-ep]}$, which exists and is feasible. The eigenvalues of the Jacobian matrix (2.5) evaluated at $P_2^{[ep-ep]}$ are $-r, -\nu, s, eaK$. As two eigenvalues are positive, $P_2^{[ep-ep]}$ is unstable.

For $X = Z = W = 0$ in the system (2.2) we obtain the equilibrium $P_3^{[ep-ep]}$, which exists and is feasible. The eigenvalues of the Jacobian matrix (2.5) evaluated at $P_3^{[ep-ep]}$ are $-s, -\nu, r, ebH$. As two eigenvalues are positive, $P_3^{[ep-ep]}$ is unstable.

For $Z = W = 0$ in the system (2.2) we obtain the equilibrium $P_4^{[ep-ep]}$, which exists and is feasible. The eigenvalues of the Jacobian matrix (2.5) evaluated at $P_4^{[ep-ep]}$ are $-\nu, -s, -r, eaK + ebH$. As one eigenvalue is positive, $P_4^{[ep-ep]}$ is unstable.

Finally, for $X = Y = 0$ in the system (2.2) we obtain the equilibrium $P_5^{[ep-ep]} = (0, 0, \nu\beta^{-1}, -m\nu\beta^{-2})$ which is unfeasible. \square

Proposition 4.7. *The point*

$$P_6^{[ep-ep]} = \left(\frac{mrK}{a^2eK + mr}, 0, \frac{aerK}{a^2eK + mr}, 0 \right)$$

is always feasible and stable for

$$(4.13) \quad \beta < \frac{mr\nu + a^2e\nu K}{aerK}, \quad b > \frac{mrs + a^2esK}{aerK}.$$

Proof. Considering $Y = W = 0$ in the system (2.2), we obtain the equilibrium

$$P_6^{[ep-ep]} = \left(\frac{mrK}{a^2eK + mr}, 0, \frac{aerK}{a^2eK + mr}, 0 \right).$$

Two eigenvalues of the Jacobian (2.5) evaluated at $P_6^{[ep-ep]}$ are explicit, giving the stability conditions (4.13). No other conditions arise since $-\overline{J}_{P_6}^{[ep-ep]}$ with

$$\overline{J}_{P_6}^{[ep-ep]} = \begin{pmatrix} -\frac{r}{K}X_6^{[ep-ep]} & -aX_6^{[ep-ep]} \\ aeZ_6^{[ep-ep]} & -mZ_6^{[ep-ep]} \end{pmatrix},$$

is positive definite, because its principal minors are

$$\frac{r}{K}X_6^{[ep-ep]} > 0, \quad \frac{rm}{K}X_6^{[ep-ep]}Z_6^{[ep-ep]} + a^2eX_6^{[ep-ep]}Z_6^{[ep-ep]} > 0.$$

\square

Proposition 4.8. *The point*

$$P_7^{[ep-ep]} = \left(0, \frac{msH}{b^2eH + ms}, \frac{besH}{b^2eH + ms}, 0 \right)$$

is always feasible and stable whenever

$$(4.14) \quad \beta < \frac{ms\nu + b^2e\nu H}{besH}, \quad a > \frac{mrs + b^2erH}{besH}.$$

Proof. Substituting $X = W = 0$ in the system (2.2), we obtain the components of $P_7^{[ep-ep]}$ by solving the equilibrium equations. It is stable for the conditions (4.14), given by two explicit eigenvalues. Nothing else is required, because $-\overline{J}_{P_7}^{[ep-ep]}$ is positive definite with

$$\overline{J}_{P_7}^{[ep-ep]} = \begin{pmatrix} -\frac{s}{H}Y_7^{[ep-ep]} & -bY_7^{[ep-ep]} \\ ebZ_7^{[ep-ep]} & -mZ_7^{[ep-ep]} \end{pmatrix},$$

since its principal minors are

$$\frac{s}{H}Y_7^{[ep-ep]} > 0, \quad \frac{sm}{H}Y_7^{[ep-ep]}Z_7^{[ep-ep]} + b^2eY_7^{[ep-ep]}Z_7^{[ep-ep]} > 0.$$

□

Proposition 4.9. *The point $P_8^{[ep-ep]} = (X_8^{[ep-ep]}, Y_8^{[ep-ep]}, Z_8^{[ep-ep]}, 0)$ with*

$$X_8^{[ep-ep]} = \frac{b^2erHK + mrsK - abesHK}{a^2esK + b^2erH + mrs}, \quad Z_8^{[ep-ep]} = \frac{aersK + bersH}{a^2esK + b^2erH + mrs},$$

$$Y_8^{[ep-ep]} = \frac{a^2esHK + mrsH - aberHK}{a^2esK + b^2erH + mrs}$$

is feasible if

$$(4.15) \quad a \leq \frac{b^2erH + mrs}{besH},$$

$$(4.16) \quad b \leq \frac{a^2esK + mrs}{aerK},$$

and is conditionally stable for

$$(4.17) \quad \beta < \frac{a^2es\nu K + b^2er\nu H + mrs\nu}{aersK + bersH}.$$

Proof. $P_8^{[ep-ep]}$ is obtained by setting $W = 0$ in the system (2.2). It is feasible for $X_8^{[ep-ep]} \geq 0$, giving (4.15), and for $Y_8^{[ep-ep]} \geq 0$, giving (4.16). One explicit eigenvalue of the Jacobian matrix gives the stability condition (4.17), No further stability conditions arise, because $-\overline{J}_{P_8}^{[ep-ep]}$ is positive definite, where

$$\overline{J}_{P_8}^{[ep-ep]} = \begin{pmatrix} -\frac{r}{K}X_8^{[ep-ep]} & 0 & -aX_8^{[ep-ep]} \\ 0 & -\frac{s}{H}Y_8^{[ep-ep]} & -bY_8^{[ep-ep]} \\ aeZ_8 & ebZ_8^{[ep-ep]} & -mZ_8^{[ep-ep]} \end{pmatrix}.$$

Indeed, its principal minors are

$$\frac{r}{K}X_8^{[ep-ep]} > 0, \quad \frac{rs}{HK}X_8^{[ep-ep]}Y_8^{[ep-ep]} > 0, \quad \left(\frac{mrs}{HK} + \frac{a^2es}{H} + \frac{b^2er}{K}\right)X_8Y_8Z_8 > 0.$$

□

Proposition 4.10. *The main prey-free equilibrium point*

$$P_9^{[ep-ep]} = (0, Y_9^{[ep-ep]}, Z_9^{[ep-ep]}, W_9^{[ep-ep]})$$

is conditionally feasible, see (4.18), (4.20) below, and stable, (4.22).

Proof. We have explicitly

$$Z_9^{[ep-ep]} = \nu\beta^{-1}, \quad Y_9^{[ep-ep]} = H - \frac{b\nu H}{s\beta} - \frac{\kappa H}{s} W_9^{[ep-ep]},$$

and $W_9^{[ep-ep]}$ is given by the roots of the quadratic function

$$\Phi(W_9^{[ep-ep]}) = \alpha_2(W_9^{[ep-ep]})^2 + \alpha_1 W_9^{[ep-ep]} + \alpha_0$$

with

$$\alpha_2 = -\frac{e\kappa^2 H}{s}, \quad \alpha_1 = -\frac{2be\nu\kappa H}{s\beta} + e\kappa H - \nu, \quad \alpha_0 = -\frac{b^2 e\nu^2 H}{s\beta^2} + \frac{be\nu H}{\beta} - \frac{m\nu^2}{\beta^2}.$$

The point $P_9^{[ep-ep]}$ is feasible if $Y_9^{[ep-ep]} \geq 0$, which becomes

$$(4.18) \quad s \geq \frac{b\nu}{\beta} + \kappa W_9^{[ep-ep]},$$

and also, two positive values for $W_9^{[ep-ep]}$ are obtained if

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad -\alpha_1\alpha_2^{-1} > 0, \quad \alpha_0\alpha_2^{-1} > 0,$$

which are equivalent to

$$(4.19) \quad \nu < \frac{e^2 s \kappa^2 \beta^2 H^2 + 4be\nu^2 \beta \kappa H + \beta^2 s \nu^2}{4em\nu\kappa H + 2es\beta^2 \kappa H}$$

and

$$(4.20) \quad \nu < \frac{es\kappa\beta H}{s\beta + 2be\kappa H}, \quad \beta < \frac{b^2 e\nu H + ms\nu}{besH},$$

respectively. For one positive root $W_9^{[ep-ep]}$, instead of the above the following conditions must hold:

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad \alpha_0\alpha_2^{-1} < 0,$$

which are equivalent to the first condition (4.19) and

$$(4.21) \quad \beta > \frac{b^2 e \nu H + m s \nu}{b e s H}.$$

Besides, $P_9^{[ep-ep]}$ is stable for

$$(4.22) \quad r < \frac{a \nu}{\beta} + g W_9^{[ep-ep]}$$

given by an explicit eigenvalue of the Jacobian matrix.

In addition,

$$\bar{J}_{P_9}^{[ep-ep]} = \begin{pmatrix} -\frac{s}{H} Y_9^{[ep-ep]} & -b Y_9^{[ep-ep]} & -\kappa Y_9^{[ep-ep]} \\ \frac{b e \nu}{\beta} + e \kappa W_9^{[ep-ep]} & \bar{J}_{22}^{[ep-ep]} & \bar{J}_{23}^{[ep-ep]} \\ 0 & \beta W_9^{[ep-ep]} & 0 \end{pmatrix},$$

with

$$\bar{J}_{22}^{[ep-ep]} = J_{33}^{[ep-ep]}, \quad \bar{J}_{23}^{[ep-ep]} = J_{34}^{[ep-ep]},$$

is negative definite, if we require the conditions $J_{33}^{[ep-ep]} < 0$, $J_{34}^{[ep-ep]} < 0$, i.e.,

$$(4.23) \quad b < \frac{2m\nu}{e\beta H} + \frac{b^2\nu}{s\beta} + \left(\frac{b\kappa}{s} + \frac{\beta}{eH}\right) W_9^{[ep-ep]}$$

and

$$(4.24) \quad e < \frac{e b \nu}{s \beta} + \frac{\nu}{\kappa H} + \frac{e \kappa}{s} W_9^{[ep-ep]},$$

respectively. Indeed, in this way the principal minors of $-\bar{J}_{P_9}$ turn out to be all positive,

$$\begin{aligned} \frac{s}{H} Y_9^{[ep-ep]} > 0, \quad \frac{s}{H} \bar{J}_{22}^{[ep-ep]} Y_9^{[ep-ep]} + b Y_9^{[ep-ep]} \left(\frac{b e \nu}{\beta} + e \kappa W_9^{[ep-ep]} \right) > 0, \\ (\beta \kappa Y_9^{[ep-ep]} W_9^{[ep-ep]}) \bar{J}_{22}^{[ep-ep]} + \frac{s \beta}{H} Y_9^{[ep-ep]} W_9^{[ep-ep]} \bar{J}_{23}^{[ep-ep]} > 0. \end{aligned}$$

□

Proposition 4.11. *The equilibrium point*

$$P_{10}^{[ep-ep]} = (X_{10}^{[ep-ep]}, 0, Z_{10}^{[ep-ep]}, W_{10}^{[ep-ep]})$$

is unique and feasible if the conditions (4.25) and (4.28) hold; it is conditionally stable when (4.29), (4.30), and (4.31) hold.

P r o o f. Setting $Y = 0$ in the system (2.2), we obtain the population values

$$X_{10}^{[ep-ep]} = K - \frac{a\nu K}{r\beta} - \frac{gK}{r}W_{10}^{[ep-ep]}, \quad Z_{10}^{[ep-ep]} = \frac{\nu}{\beta},$$

where $W_{10}^{[ep-ep]}$ is a root of the quadratic function

$$\Phi(W_{10}^{[ep-ep]}) = \alpha_2(W_{10}^{[ep-ep]})^2 + \alpha_1W_{10}^{[ep-ep]} + \alpha_0$$

with

$$\alpha_2 = -\frac{eg^2K}{r}, \quad \alpha_1 = egK - \frac{2aeg\nu K}{r\beta} - \nu, \quad \alpha_0 = \frac{aevK}{\beta} - \frac{a^2e\nu^2K}{r\beta^2} - \frac{m\nu^2}{\beta^2}.$$

For feasibility we need to require $X_{10}^{[ep-ep]} \geq 0$, that is,

$$(4.25) \quad r \geq \frac{a\nu}{\beta} + gW_{10}^{[ep-ep]},$$

and $W_{10}^{[ep-ep]} \geq 0$. In this case, two positive roots arise if

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad -\alpha_1\alpha_2^{-1} > 0, \quad \alpha_0\alpha_2^{-1} > 0,$$

which are equivalent to

$$(4.26) \quad \nu < \frac{r\nu^2\beta^2 + 4aeg\nu^2\beta K + e^2g^2r\beta^2K^2}{4eg^2m\nu K + 2egr\beta^2K},$$

$$(4.27) \quad \beta > \frac{r\nu\beta + 2aeg\nu K}{egrK}, \quad \beta < \frac{mr\nu + a^2e\nu K}{aerK},$$

respectively. One positive root is found whenever the conditions

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad \alpha_0\alpha_2^{-1} < 0$$

hold, which are equivalent to (4.25) and

$$(4.28) \quad \beta > \frac{mr\nu + a^2e\nu K}{aerK}.$$

One explicit eigenvalue of the Jacobian at $P_{10}^{[ep-ep]}$ is $J_{22}^{[ep-ep]}$, which must be negative for stability, giving

$$(4.29) \quad s < \frac{b\nu}{\beta} + \kappa W_{10}^{[ep-ep]}$$

given by one explicit eigenvalue of $J_{P_{10}}^{[ep-ep]}$.

In addition,

$$\overline{J}_{P_{10}}^{[ep-ep]} = \begin{pmatrix} -\frac{r}{K}X_{10}^{[ep-ep]} & -aX_{10}^{[ep-ep]} & -gX_{10}^{[ep-ep]} \\ \frac{ae\nu}{\beta} + egW_{10}^{[ep-ep]} & J_{33}^{[ep-ep]} & egX_{10}^{[ep-ep]} - \nu \\ 0 & \beta W_{10}^{[ep-ep]} & 0 \end{pmatrix}$$

is negative definite, if we require the conditions $J_{33}^{[ep-ep]} < 0$ and $J_{34}^{[ep-ep]} < 0$, that is,

$$(4.30) \quad a < \frac{2m\nu}{e\beta K} + \frac{a^2\nu}{r\beta} + \left(\frac{ag}{r} - \beta\right)W_{10}^{[ep-ep]}$$

and

$$(4.31) \quad \nu > egX_{10}^{[ep-ep]},$$

because its principal minors become

$$\begin{aligned} \frac{r}{K}X_{10}^{[ep-ep]} &> 0, \quad \frac{r}{K}J_{33}^{[ep-ep]}X_{10} + aX_{10}^{[ep-ep]}\left(\frac{ae\nu}{\beta} + egW_{10}^{[ep-ep]}\right) > 0, \\ g\beta X_{10}^{[ep-ep]}W_{10}^{[ep-ep]}\left(\frac{ae\nu}{\beta} + egW_{10}^{[ep-ep]}\right) + \frac{r\beta}{K}X_{10}^{[ep-ep]}W_{10}^{[ep-ep]}(\nu - egX_{10}^{[ep-ep]}) &> 0. \end{aligned}$$

□

Proposition 4.12. *The coexistence*

$$P_{11}^{[ep-ep]} = (X_{11}^{[ep-ep]}, Y_{11}^{[ep-ep]}, Z_{11}^{[ep-ep]}, W_{11}^{[ep-ep]})$$

is unique if (4.32) and (4.35) hold and is conditionally stable for (4.36).

Proof. For the coexistence $P_{11}^{[ep-ep]}$ we have

$$\begin{aligned} Z_{11}^{[ep-ep]} &= \nu\beta^{-1}, \quad X_{11}^{[ep-ep]} = K - \frac{a\nu K}{r\beta} - \frac{gK}{r}W_{11}^{[ep-ep]}, \\ Y_{11}^{[ep-ep]} &= H - \frac{b\nu H}{s\beta} - \frac{\kappa H}{s}W_{11}^{[ep-ep]} \end{aligned}$$

with $W_{11}^{[ep-ep]}$ given by the root of the quadratic function

$$\Phi(W_{11}^{[ep-ep]}) = \alpha_2(W_{11}^{[ep-ep]})^2 + \alpha_1W_{11}^{[ep-ep]} + \alpha_0,$$

with

$$\alpha_2 = -\frac{eg^2K}{r} - \frac{e\kappa^2H}{s}, \quad \alpha_1 = e\kappa H + egK - \nu - \frac{2be\nu\kappa H}{s\beta} - \frac{2aeg\nu K}{r\beta},$$

$$\alpha_0 = \frac{be\nu H}{\beta} + \frac{ae\nu K}{\beta} - \frac{m\nu^2}{\beta^2} - \frac{a^2e\nu^2K}{r\beta^2} - \frac{b^2e\nu^2H}{s\beta^2}.$$

The equilibrium $P_{11}^{[ep-ep]}$ is feasible if $X_{11}^{[ep-ep]} \geq 0$ and $Y_{11}^{[ep-ep]} \geq 0$, i.e., for

$$(4.32) \quad r \geq \frac{a\nu}{\beta} + gW_{11}^{[ep-ep]}, \quad s \geq \frac{b\nu}{\beta} + \kappa W_{11}^{[ep-ep]},$$

respectively, and if $W_{11}^{[ep-ep]} \geq 0$. There are two positive roots if

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad -\alpha_1\alpha_2^{-1} > 0, \quad \alpha_0\alpha_2^{-1} > 0,$$

which are equivalent to

$$(4.33) \quad e^2rs\beta^2\kappa^2H^2 + 8abe^2g\nu^2\kappa KH + 4ber\nu^2\kappa\beta H + 4ae^2r\nu\kappa^2\beta KH$$

$$+ 4be^2g^2s\nu\beta KH + 2e^2grs\kappa\beta^2KH + 4aegs\nu^2\beta K + e^2g^2rs\beta^2K$$

$$+ rs\nu^2\beta^2 > 4a^2e^2\nu^2\kappa^2KH + 4b^2e^2g^2\nu^2KH + 4be^2gr\nu\kappa\beta KH$$

$$+ 4emr\nu^2\kappa^2H + 4ae^2gs\nu\kappa\beta KH$$

$$+ 2ers\nu\kappa\beta^2H + 4eg^2ms\nu^2K + 2egrsv\beta^2K,$$

$$(4.34) \quad \nu < \frac{ers\beta\kappa H + egrs\beta K}{2ber\kappa H + rs\beta + 2aegsK}, \quad \beta < \frac{b^2er\nu H + mrs\nu + a^2es\nu K}{bersH + aersK},$$

respectively. For one positive root the conditions are

$$\Delta = \alpha_1^2 - 4\alpha_2\alpha_0 > 0, \quad \alpha_0\alpha_2^{-1} < 0,$$

or, explicitly, (4.33) and

$$(4.35) \quad \beta > \frac{b^2er\nu H + mrs\nu + a^2es\nu K}{bersH + aersK}.$$

In addition, $J_{P_{11}}^{[ep-ep]}$ is negative definite if we require the condition $J_{34}^{[ep-ep]} < 0$ which explicitly becomes

$$(4.36) \quad egX_{11}^{[ep-ep]} + e\kappa Y_{11}^{[ep-ep]} < \nu.$$

Indeed, the Jacobian of $P_{11}^{[ep-ep]}$ simplifies to

$$J_{P_{11}}^{[ep-ep]} = \begin{pmatrix} -\frac{r}{K}X_{11}^{[ep-ep]} & 0 & -aX_{11}^{[sp-ep]} & -gX_{11}^{[ep-ep]} \\ 0 & -\frac{s}{H}Y_{11}^{[ep-ep]} & -bY_{11}^{[ep-ep]} & -\kappa Y_{11}^{[ep-ep]} \\ J_{31}^{[ep-ep]} & J_{32}^{[ep-ep]} & -\frac{m\nu}{\beta} & J_{34}^{[ep-ep]} \\ 0 & 0 & \beta W_{11}^{[ep-ep]} & 0 \end{pmatrix},$$

with

$$J_{31}^{[ep-ep]} = \frac{ae\nu}{\beta} + egW_{11}^{[ep-ep]}, \quad J_{32}^{[ep-ep]} = \frac{be\nu}{\beta} + e\kappa W_{11}^{[ep-ep]}, \\ J_{34}^{[ep-ep]} = egX_{11}^{[ep-ep]} + e\kappa Y_{11}^{[ep-ep]} - \nu.$$

The first three principal minors of $J_{P_{11}}^{[ep-ep]}$ are all positive:

$$\frac{r}{K}X_{11}^{[ep-ep]} > 0, \quad \frac{rs}{HK}X_{11}^{[ep-ep]}Y_{11}^{[ep-ep]} > 0, \\ X_{11}^{[ep-ep]}Y_{11}^{[ep-ep]} \left[\left(\frac{mrs}{HK} + \frac{a^2es}{H} + \frac{b^2er}{K} \right) \frac{\nu}{\beta} + \left(\frac{aegs}{H} + \frac{ber\kappa}{K} \right) W_{11}^{[ep-ep]} \right] > 0,$$

and also the determinant is, as it simplifies to

$$\frac{egs}{H} \left(\frac{a\nu}{\beta} + gW_{11}^{[ep-ep]} \right) + \frac{e\kappa r}{K} \left(\frac{b\nu}{\beta} + \kappa W_{11}^{[ep-ep]} \right) - \frac{rs}{HK} J_{34}^{[ep-ep]} > 0.$$

Thus, then being feasible, $P_{11}^{[ep-ep]}$ is stable if (4.36) holds. \square

In Table 2 we summarize the behaviour of the equilibria of model (2.2).

5. THEORETICAL RESULTS FOR BIFURCATIONS OF MODELS (2.1) AND (2.2)

The bifurcations presented in this section were found from the conditions of feasibility and stability of equilibria of the systems (2.1) and (2.2). These conditions are summarized in Tables 1 and 2. We do not claim that the bifurcations found are exhaustive.

To study the local bifurcations of the equilibria of models (2.1) and (2.2) we use the Sotomayor theorem [13].

Proposition 5.1. *Consider the continuously differentiable system (2.1), then:*

- (i) *There is a transcritical bifurcation between the equilibria $P_3^{[ep-hp]}$ and $P_4^{[ep-hp]}$ when r passes through the critical value $r^\dagger = aL$.*
- (ii) *There is a transcritical bifurcation between the equilibria $P_3^{[ep-hp]}$ and $P_5^{[ep-hp]}$ when ν passes through the critical value $\nu^\dagger = \beta L$.*

Equilibria	Admissibility	Stability
$P_1^{[ep-ep]}$	always	unstable
$P_2^{[ep-ep]}$	always	unstable
$P_3^{[ep-ep]}$	always	unstable
$P_4^{[ep-ep]}$	always	unstable
$P_5^{[ep-ep]}$	unfeasible	
$P_6^{[ep-ep]}$	always	(4.13)
$P_7^{[ep-ep]}$	always	(4.14)
$P_8^{[ep-ep]}$	(4.15), (4.16)	(4.17)
$P_9^{[ep-ep]}$	(4.18), (4.19), (4.20) – 2 positive roots (4.18), (4.19), (4.21) – 1 positive root	(4.22), (4.23), (4.24)
$P_{10}^{[ep-ep]}$	(4.25), (4.26), (4.27) – 2 positive roots (4.25), (4.26), (4.28) – 1 positive root	(4.29), (4.30), (4.31)
$P_{11}^{[ep-ep]}$	(4.32), (4.33), (4.34) – 2 positive roots (4.32), (4.33), (4.35) – 1 positive root	(4.36)

Table 2. Behaviour and conditions of feasibility and stability of equilibria for model (2.2).

P r o o f. (i) The equilibrium point $P_3^{[ep-hp]}$ coincides with the equilibrium $P_4^{[ep-hp]}$ at the parametric threshold $r^\dagger = aL$, compare the first stability condition (4.1) of $P_3^{[ep-hp]}$ and the feasibility condition (4.2) of $P_4^{[ep-hp]}$.

The Jacobian matrix of the system (2.1) evaluated at $P_3^{[ep-hp]}$ and at the parametric threshold $r^\dagger = aL$ becomes

$$J_{P_3}^{[ep-hp]}(r^\dagger) = \begin{pmatrix} 0 & 0 & 0 \\ aeL & -u & -u - \beta L \\ 0 & 0 & -\nu + \beta L \end{pmatrix}$$

and its right and left eigenvectors, corresponding to the zero eigenvalue, are given by $V_1 = \varphi_1(1, aeL/u, 0)^T$ and $Q_1 = \omega_1(1, 0, 0)^T$, where φ_1 and ω_1 are arbitrary nonzero real numbers. Differentiating with respect to r the right-hand sides of the system (2.1), we find

$$f_r = \begin{pmatrix} X_3^{[ep-hp]}(1 - X_3^{[ep-hp]}/K) \\ 0 \\ 0 \end{pmatrix}.$$

Its Jacobian matrix is

$$Df_r = \begin{pmatrix} 1 - \frac{2}{K}X_3^{[ep-hp]} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

Calculating D^2f , we find

$$D^2f(P, \psi)(V, V) = \begin{pmatrix} \frac{\partial^2 f_1}{\partial X^2} \xi_1^2 + \frac{\partial^2 f_1}{\partial Z^2} \xi_2^2 + \frac{\partial^2 f_1}{\partial W^2} \xi_3^2 + 2 \frac{\partial^2 f_1}{\partial X \partial Z} \xi_1 \xi_2 + 2 \frac{\partial^2 f_1}{\partial X \partial W} \xi_1 \xi_3 + 2 \frac{\partial^2 f_1}{\partial Z \partial W} \xi_2 \xi_3 \\ \frac{\partial^2 f_2}{\partial X^2} \xi_1^2 + \frac{\partial^2 f_2}{\partial Z^2} \xi_2^2 + \frac{\partial^2 f_2}{\partial W^2} \xi_3^2 + 2 \frac{\partial^2 f_2}{\partial X \partial Z} \xi_1 \xi_2 + 2 \frac{\partial^2 f_2}{\partial X \partial W} \xi_1 \xi_3 + 2 \frac{\partial^2 f_2}{\partial Z \partial W} \xi_2 \xi_3 \\ \frac{\partial^2 f_3}{\partial X^2} \xi_1^2 + \frac{\partial^2 f_3}{\partial Z^2} \xi_2^2 + \frac{\partial^2 f_3}{\partial W^2} \xi_3^2 + 2 \frac{\partial^2 f_3}{\partial X \partial Z} \xi_1 \xi_2 + 2 \frac{\partial^2 f_3}{\partial X \partial W} \xi_1 \xi_3 + 2 \frac{\partial^2 f_3}{\partial Z \partial W} \xi_2 \xi_3 \end{pmatrix},$$

where $P = (X, Z, W)^T$, while the components of $f = (f_1, f_2, f_3)^T$ are given by the right-hand sides of (2.1), ψ represents the parametric threshold and ξ_1, ξ_2, ξ_3 are the components of the eigenvector $V = (\xi_1, \xi_2, \xi_3)^T$ of the variations in X, Z , and W .

We can thus verify the following three conditions

$$Q_1^T f_r(P_3^{[ep-hp]}, r^\dagger) = 0, \quad Q_1^T [Df_r(P_3^{[ep-hp]}, r^\dagger)V_1] = \varphi_1 \omega_1 \neq 0, \\ Q_1^T [D^2f(P_3^{[ep-hp]}, r^\dagger)(V_1, V_1)] = -\omega_1 \varphi_1^2 \left(\frac{2aL}{K} + a^2 eL \right) \neq 0.$$

(ii) When the equilibrium point $P_3^{[ep-hp]}$ coincides with the equilibrium $P_5^{[ep-hp]}$ at the threshold $\nu^\dagger = \beta L$ (compare the second stability condition (4.1) of $P_3^{[ep-hp]}$ and the feasibility condition (4.4) of equilibrium $P_5^{[ep-hp]}$), the Jacobian matrix of the system (2.1) evaluated at $P_3^{[ep-hp]}$ and at the parametric threshold ν^\dagger becomes

$$J_{P_3}^{[ep-hp]}(\nu^\dagger) = \begin{pmatrix} r - aL & 0 & 0 \\ aeL & -u & -u - \beta L \\ 0 & 0 & 0 \end{pmatrix}.$$

Its right and left eigenvectors, corresponding to the zero eigenvalue, are given by $V_2 = \varphi_2(0, 1, -u/(u + \beta L))^T$ and $Q_2 = \omega_2(0, 0, 1)^T$, where φ_2 and ω_2 are any nonzero real numbers. Differentiating with respect to ν^\dagger the right-hand sides of (2.1), we find

$$f_\nu = \begin{pmatrix} 0 \\ 0 \\ -W_3^{[ep-hp]} \end{pmatrix},$$

and calculating its Jacobian matrix, we get

$$Df_\nu = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -1 \end{pmatrix}.$$

From D^2f we can finally verify the following three conditions:

$$Q_2^T f_\nu(P_3^{[ep-hp]}, \nu^\dagger) = 0, \quad Q_2^T [Df_\nu(P_3^{[ep-hp]}, \nu^\dagger) V_2] = \varphi_2 \omega_2 \frac{u}{u + \beta L} \neq 0,$$

$$Q_2^T [D^2f(P_3^{[ep-hp]}, \nu^\dagger)(V_2, V_2)] = -\omega_2 \varphi_2^2 \frac{2u\beta}{u + \beta L} \neq 0.$$

Hence all conditions for transcritical bifurcation are satisfied. \square

Proposition 5.2. *Consider the continuously differentiable system of equations (2.2), then:*

- (i) *There is a transcritical bifurcation between the equilibria $P_8^{[ep-ep]}$ and $P_6^{[ep-ep]}$ when b crosses the critical value $b^\dagger = (mrs + a^2esK)/(aerK)$.*
- (ii) *There is a transcritical bifurcation between the equilibria $P_8^{[ep-ep]}$ and $P_7^{[ep-ep]}$ when a passes through the critical value $a^\dagger = (mrs + b^2erH)/(besH)$.*

Proof. (i) When the equilibria $P_8^{[ep-ep]}$ and $P_6^{[ep-ep]}$ coincide at the parametric threshold $b^\dagger = (mrs + a^2esK)/(aerK)$ (compare the second condition of (4.13) and the condition (4.16)), the Jacobian of the system (2.1) evaluated at $P_8^{[ep-ep]}$ and at the parametric threshold b^\dagger is

$$J_{P_8}^{[ep-ep]}(b^\dagger) = \begin{pmatrix} -\frac{mr^2}{mr + a^2eK} & 0 & -\frac{amrK}{mr + a^2eK} & -\frac{gmrK}{mr + a^2eK} \\ 0 & 0 & 0 & 0 \\ \frac{a^2e^2rK}{mr + a^2eK} & es & -\frac{aemrK}{mr + a^2eK} & \frac{egmrK - aer\beta K}{mr + a^2eK} \\ 0 & 0 & 0 & \frac{-mr\nu - a^2e\nu K + aer\beta K}{mr + a^2eK} \end{pmatrix}$$

and its right and left eigenvectors, corresponding to the zero eigenvalue are given by $V_3 = \varphi_3(1, -r/s, -r/(aK), 0)^T$ and $Q_3 = \omega_3(0, 1, 0, 0)^T$, where φ_3 and ω_3 are any nonzero real numbers. Differentiating partially the right-hand sides of the system of equations (2.2) with respect to b , we find

$$f_b = \begin{pmatrix} 0 \\ -Y_8^{[ep-ep]} Z_8^{[ep-ep]} \\ eY_8^{[ep-ep]} Z_8^{[ep-ep]} \\ 0 \end{pmatrix},$$

and calculating its Jacobian matrix, we get

$$Df_b = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & -Z_8^{[ep-ep]} & -Y_8^{[ep-ep]} & 0 \\ 0 & eZ_8^{[ep-ep]} & eZ_8^{[ep-ep]} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

From the calculation of D^2f the following three conditions are verified:

$$\begin{aligned} Q_3^T f_b(P_8^{[ep-ep]}, b^\dagger) &= 0, \quad Q_3^T [Df_b(P_8^{[ep-ep]}, b^\dagger)V_3] = \varphi_3\omega_3\varrho \neq 0, \\ Q_3^T [D^2f_b(P_8^{[ep-ep]}, b^\dagger)(V_3, V_3)] &= -2\omega_3\varphi_3^2 \frac{mr^2H + a^2erHK + a^2er^2K}{a^2esHK} \neq 0, \end{aligned}$$

Since the feasibility condition of $P_8^{[ep-ep]}$ for $Y_8^{[ep-ep]}$ is given by (4.16), and

$$\varrho = \frac{r(a^2esHK - aberHK + mrsH)}{aK} + \frac{r(arrK + berH)}{a^2esK + b^2erH + mrs},$$

we have

$$\frac{r(a^2esHK - aberHK + mrsH)}{aK} \geq 0$$

and thus $\varrho \neq 0$.

(ii) For the equilibrium point $P_8^{[ep-ep]} = P_7^{[ep-ep]}$ at the threshold $a^\dagger = (mrs + b^2erH)/(besH)$ (compare the second condition of (4.14) and the condition (4.15)), the Jacobian of (2.2) evaluated at $P_8^{[ep-ep]}$ and at the parametric threshold a^\dagger , is

$$J_{P_8}^{[ep-ep]}(a^\dagger) = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & -\frac{ms^2}{ms + b^2eH} & -\frac{bmsH}{ms + b^2eH} & 0 \\ er & \frac{b^2e^2sH}{ms + b^2eH} & -\frac{bemsh}{ms + b^2eH} & \frac{(em\kappa - eb\beta)sH}{ms + b^2eH} \\ 0 & 0 & 0 & \frac{-b^2e\nu H + bes\beta H - ms\nu}{ms + b^2eH} \end{pmatrix}$$

and its right and left eigenvectors, corresponding to the zero eigenvalue, are given by $V_4 = \varphi_4(1, -r/s, r/(bH), 0)^T$ and $Q_4 = \omega_4(1, 0, 0, 0)^T$, where φ_4 and ω_4 are any nonzero real numbers. Differentiating partially with respect to a^\dagger the right-hand sides of (2.2), we find

$$f_a = \begin{pmatrix} -X_8^{[ep-ep]} Z_8^{[ep-ep]} \\ 0 \\ eX_8^{[ep-ep]} Z_8^{[ep-ep]} \\ 0 \end{pmatrix},$$

and calculating its Jacobian, we get

$$Df_a = \begin{pmatrix} -Z_8^{[ep-ep]} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ eZ_8^{[ep-ep]} & 0 & eX_8^{[ep-ep]} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

Evaluation of D^2f verifies the following three conditions:

$$Q_4^T f_a(P_8^{[ep-ep]}, a^\dagger) = 0, \quad Q_4^T [Df_a(P_8^{[ep-ep]}, a^\dagger)V_4] = -\varphi_4\omega_4 \frac{besH}{ms + b^2eH} \neq 0$$

$$Q_4^T [D^2f_a(P_8^{[ep-ep]}, a^\dagger)(V_4, V_4)] = -2\omega_4\varphi_4^2 \frac{b^2ersH^2 + b^2er^2K + mr^2sK}{b^2esH^2K} \neq 0.$$

Hence all conditions for a transcritical bifurcation are satisfied. The computation of $D^2f(P, \psi)(V, V)$ of (2.2) is analogous to the formula for the model (2.1). \square

6. NUMERICAL RESULTS FOR BIFURCATIONS OF MODELS (2.1) AND (2.2)

In Section 5 we performed theoretical analysis for transcritical bifurcation of models (2.1) and (2.2). In this section, we illustrate these transcritical bifurcations and further investigate the possibilities for transcritical bifurcations about other equilibria of the systems by means of numerical simulations, by suitably adapting the standard ode45 Matlab routine for our purposes.

Numerical results for model (2.1). Here, we perform the investigation for transcritical bifurcations in terms of the bifurcation parameters ν and r . Considering ν as the bifurcation parameter we find transcritical bifurcations between the equilibria: $P_3^{[ep-hp]}$ and $P_5^{[ep-hp]}$ for $\nu^\dagger = \beta L = 1.6$ as well as between $P_5^{[ep-hp]}$ and $P_6^{[ep-hp]}$ for

$$\nu^\dagger = \frac{\beta(ur + r\beta L - guL)}{au + a\beta L - gu} = 0.4009,$$

see Figure 1 frames (a) and (b), respectively.

The frames (a) and (b) of Figure 2 illustrate the transcritical bifurcation between $P_3^{[ep-hp]}$ and $P_4^{[ep-hp]}$ taking r as a bifurcation parameter with threshold $r^\dagger = aL = 0.5$, and between $P_6^{[ep-hp]}$ and $P_4^{[ep-hp]}$ for the threshold

$$\nu^\dagger = \frac{\beta(urL + aerK)}{ur + a^2eKL} = 0.9747,$$

respectively.

Table 3 presents a summary of all bifurcation results in our numerical simulations.

Behaviour of the model (2.1)	Equilibria involved	Parameter threshold
Transcritical bifurcation	$P_3^{[ep-hp]} - P_5^{[ep-hp]}$	$\nu^\dagger = 1.6$
Transcritical bifurcation	$P_5^{[ep-hp]} - P_6^{[ep-hp]}$	$\nu^\dagger = 0.4009$
Transcritical bifurcation	$P_3^{[ep-hp]} - P_4^{[ep-hp]}$	$r^\dagger = 0.5$
Transcritical bifurcation	$P_4^{[ep-hp]} - P_6^{[ep-hp]}$	$\nu^\dagger = 0.9747$

Table 3. Behaviour of equilibria of model (2.1) considering ν and r as variation parameters.

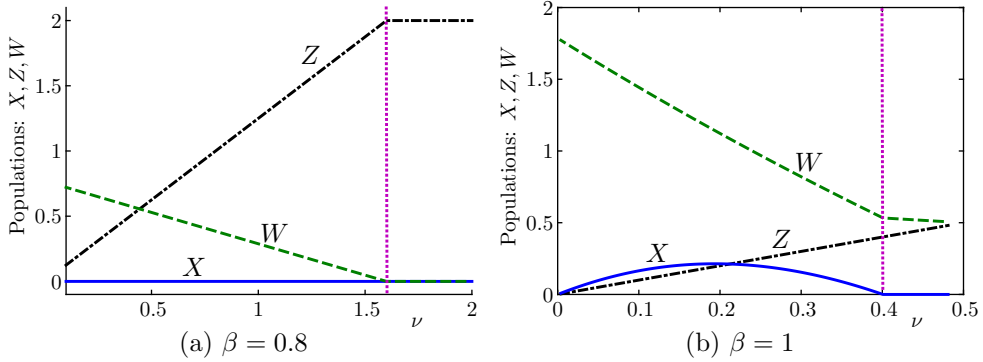


Figure 1. (a) Transcritical bifurcation between $P_3^{[ep-hp]}$ and $P_5^{[ep-hp]}$. The equilibrium $P_5^{[ep-hp]}$ is stable for $0.1 < \nu < 1.6$ and $P_3^{[ep-hp]}$ is stable for $\nu > 1.6$. The vertical line corresponds to the transcritical bifurcation threshold $\nu^\dagger = 1.6$ between the equilibria.

(b) Transcritical bifurcation between $P_5^{[ep-hp]}$ and $P_6^{[ep-hp]}$. The equilibrium $P_6^{[ep-hp]}$ is stable for $0.1 < \nu < 0.4009$ and $P_5^{[ep-hp]}$ is stable for $\nu > 0.4009$. The vertical line corresponds to the transcritical bifurcation threshold $\nu^\dagger = 0.4009$. The parameter values for (a) and (b) are $r = u = 1$, $L = 2$, $K = 10$, $e = 0.75$, $g = 0.56$, $a = 1.75$.

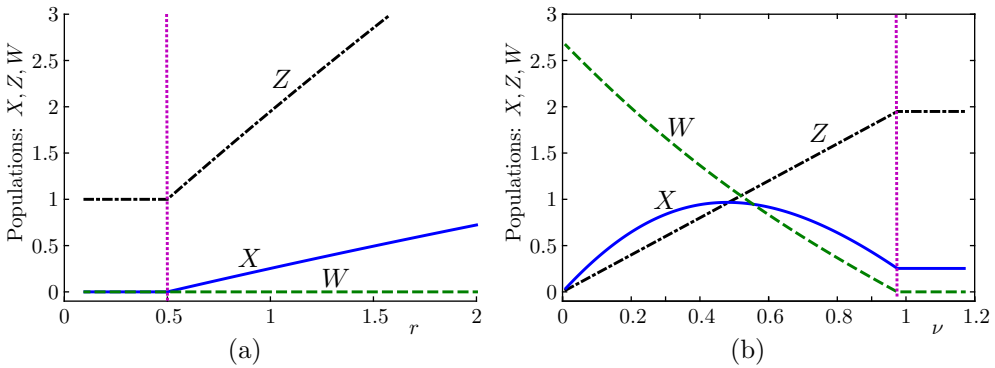


Figure 2. (a) Transcritical bifurcation between $P_3^{[ep-hp]}$ and $P_4^{[ep-hp]}$. The equilibrium $P_3^{[ep-hp]}$ is stable for $0.1 < r < 0.5$ and $P_4^{[ep-hp]}$ is stable for $r > 0.5$. The vertical line corresponds to the transcritical bifurcation threshold $r^\dagger = 0.5$ with $\nu = 0.9747$.

(b) Transcritical bifurcation between $P_6^{[ep-hp]}$ and $P_4^{[ep-hp]}$. The equilibrium $P_6^{[ep-hp]}$ is stable for $0.1 < \nu < 0.9747$ and $P_4^{[ep-hp]}$ is stable for $\nu > 0.9747$. The vertical line corresponds to the transcritical bifurcation threshold $\nu^\dagger = 0.9747$ between the equilibria and $r = 1$.

The parameter values for (a) and (b) are: $L = 1$, $K = 10$, $e = 0.75$, $a = \beta = 0.5$, $u = 0.1$, $g = 0.37$.

▷ Numerical results for model (2.2)

Here we take β , a , and b as bifurcation parameters in model (2.2). Figures 3, 4, 5 illustrate all the possibilities that we have found. All the different behaviours of the system are summarized in Table 4.

Behaviour of the model (2.2)	Equilibria involved	Parameter threshold
Transcritical bifurcation	$P_7^{[ep-ep]} - P_9^{[ep-ep]}$	$\beta^\dagger = 0.5667$
Transcritical bifurcation	$P_6^{[ep-ep]} - P_{10}^{[ep-ep]}$	$\beta^\dagger = 0.1826$
Transcritical bifurcation	$P_{11}^{[ep-ep]} - P_8^{[ep-ep]}$	$\beta^\dagger = 0.3884$
Transcritical bifurcation	$P_6^{[ep-ep]} - P_8^{[ep-ep]}$	$b^\dagger = 1.5$
Transcritical bifurcation	$P_7^{[ep-ep]} - P_8^{[ep-ep]}$	$a^\dagger = 2.17$

Table 4. Behaviour of equilibria of model (2.2) considering β , b , and a as bifurcation parameters.

Note that considering β as the bifurcation parameter the system has several possible different behaviours.

Figure 3 (a) illustrates the transcritical bifurcation between $P_6^{[ep-ep]}$ and $P_{10}^{[ep-ep]}$ and (b) illustrates a transcritical bifurcation between $P_7^{[ep-ep]}$ and $P_9^{[ep-ep]}$ for

$$\beta^\dagger = \frac{\nu(mr + a^2eK)}{aerK} = 0.1826, \quad \beta^\dagger = \frac{ms\nu + b^2e\nu H}{besH} = 0.5667,$$

respectively.

Figure 4 illustrates the transcritical bifurcation between $P_8^{[ep-hp]}$ and $P_{11}^{[ep-ep]}$ with critical threshold

$$\beta^\dagger = \frac{\nu(a^2esK + b^2erH + mrs)}{aersK + bersH} = 0.3884.$$

Figure 5 (a), (b) illustrates numerical simulations when we consider b and a as bifurcation parameters. There is a transcritical bifurcation between $P_6^{[ep-ep]}$ and $P_8^{[ep-ep]}$ and another one between $P_7^{[ep-ep]}$ and $P_8^{[ep-ep]}$ for

$$b^\dagger = \frac{mrs + a^2esK}{aerK} = 1.5, \quad a^\dagger = \frac{mrs + b^2erH}{besH} = 2.17,$$

respectively.

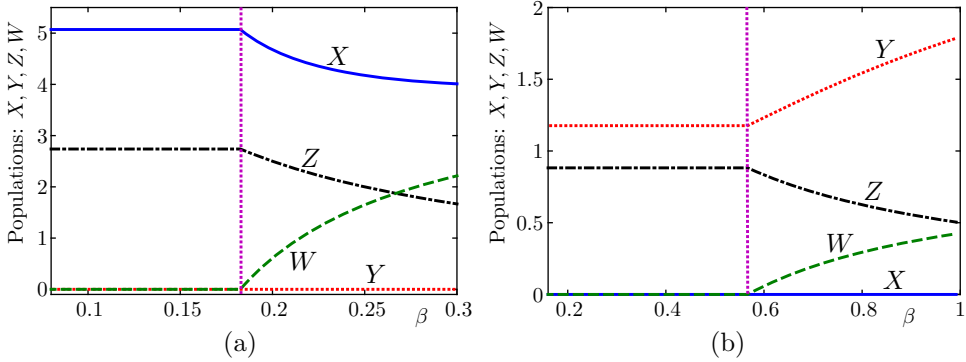


Figure 3. The common parameter values for both (a) and (b) are: $r = 1$, $K = 10$, $e = 0.75$, $\nu = 0.5$, $g = 0.937$, $m = s = b = 0.25$, $H = 10$, $\kappa = 0.187$.

(a) Transcritical bifurcation between $P_6^{[ep-hp]}$ and $P_{10}^{[ep-ep]}$. The equilibrium $P_6^{[ep-hp]}$ is stable for $0.1 < \beta < 0.1826$ and $P_{10}^{[ep-ep]}$ is stable for $\beta > 0.1826$. The vertical line corresponds to the transcritical bifurcation threshold $\beta^\dagger = 0.1826$ between the equilibria. Here we have $a = 0.18$.

(b) Transcritical bifurcation between $P_7^{[ep-hp]}$ and $P_9^{[ep-ep]}$. The equilibrium $P_7^{[ep-hp]}$ is obtained for $0.1 < \beta < 0.5667$ while $P_9^{[ep-ep]}$ is found for $\beta > 0.5667$. The vertical line corresponds to the transcritical bifurcation threshold $\beta^\dagger = 0.5667$ between the equilibria. In this case we take $a = 1.25$.

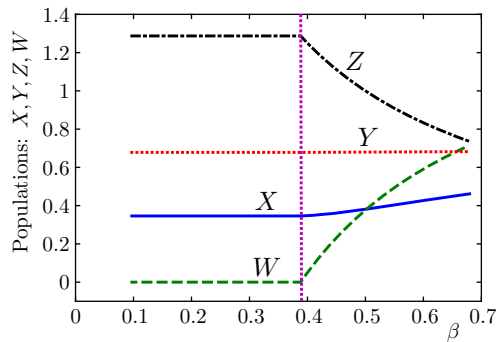


Figure 4. Transcritical bifurcation between $P_8^{[ep-hp]}$ and $P_{11}^{[ep-ep]}$. The equilibrium $P_8^{[ep-hp]}$ is stable for $0.1 < \beta < 0.3884$ while $P_{11}^{[ep-ep]}$ is obtained for $0.3884 < \beta < 0.67$. The vertical line corresponds to the transcritical bifurcation threshold $\beta^\dagger = 0.3884$. The remaining parameter values are $r = 1$, $K = 10$, $e = 0.75$, $\nu = 0.5$, $g = 0.5625$, $m = b = 0.25$, $\kappa = 0.187$, $a = 0.75$, $s = H = 1$.

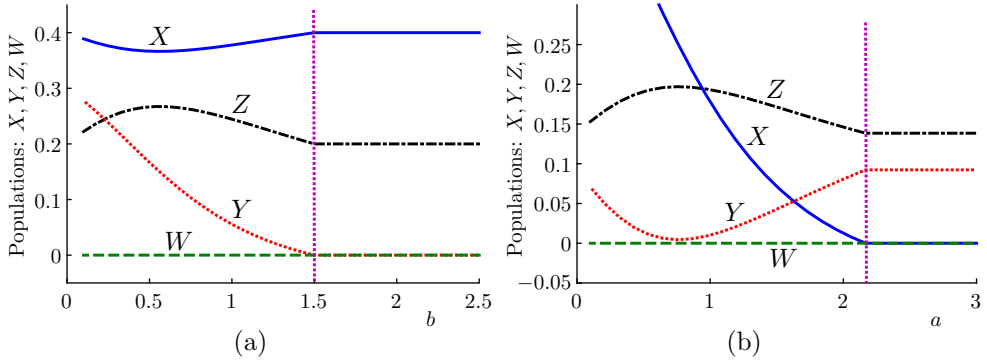


Figure 5. (a) Transcritical bifurcation between $P_8^{[ep-ep]}$ and $P_6^{[ep-ep]}$ for the parameter values $r = K = a = e = m = 0.5$, $g = 0.8$, $s = H = \beta = 0.3$ and $\nu = \kappa = 0.9$. Initial conditions $X_0 = Z_0 = W_0 = 0.01$. The equilibrium $P_8^{[ep-ep]}$ is found for $0.1 \leq b < 1.5$ and $P_6^{[ep-ep]}$ arises for $b > 1.5$. The vertical line corresponds to the transcritical bifurcation threshold $b^\dagger = 1.5$. (b) Transcritical bifurcation between $P_8^{[ep-ep]}$ and $P_7^{[ep-ep]}$ for the parameter values $K = e = m = 0.5$, $g = 0.8$, $r = s = H = \beta = 0.3$, $b = 1.5$ and $\nu = \kappa = 0.9$. Initial conditions and populations are the same. The equilibrium $P_8^{[ep-ep]}$ is found for $0.1 \leq a < 2.17$ while $P_7^{[ep-ep]}$ exists in the range $a > 2.17$. The vertical line corresponds to the transcritical bifurcation threshold $a^\dagger = 2.17$.

7. COMPARING ANALYTICAL FINDINGS FOR MODELS (2.1) AND (2.2)

In this section, we compare the behaviour of the models (2.1) and (2.2), summarizing in Table 5 all the possibilities.

As we can see in Table 5, both ecosystems cannot completely disappear. Note that to the origin $P_1^{[ep-hp]}$ in model (2.1) corresponds also the point $P_3^{[ep-ep]}$ of model (2.2), in which only the alternative prey thrives. The prey-only equilibria $P_2^{[ep-hp]}$ and $P_2^{[ep-ep]}$, $P_3^{[ep-ep]}$ and $P_4^{[ep-ep]}$ are all unstable.

The healthy-predator-only equilibrium $P_3^{[ep-hp]}$ has its counterpart in the point $P_7^{[ep-ep]}$. The equilibrium $P_3^{[ep-hp]}$ can be achieved stably in the simpler model provided (4.1) is satisfied, and $P_7^{[ep-ep]}$ can also be stably attained, if the stability condition (4.14) holds.

The disease-free equilibrium point in model (2.1) is $P_4^{[ep-hp]}$. Three points of model (2.2) could be related to it, namely $P_6^{[ep-ep]}$, $P_7^{[ep-ep]}$ and $P_8^{[ep-ep]}$, differing in that either the extra source or the main prey are absent, or that both preys thrive, together with the healthy predators.

The main-prey-free point $P_5^{[ep-hp]}$ in model (2.1) cannot be compared with the equilibrium $P_5^{[ep-ep]}$ of model (2.2), because $P_5^{[ep-ep]}$ does not contain the alternative

Equilibrium – model (2.1)	Equilibrium – model (2.2)	Interpretation
$P_1^{[ep-hp]} = (0, 0, 0)$ (u)	$P_1^{[ep-ep]} = (0, 0, 0, 0)$ (u)	ecosystem collapse
$P_2^{[ep-hp]} = (\cdot, 0, 0)$ (u)	$P_3^{[ep-ep]} = (0, \cdot, 0, 0)$ (u)	prey-only
	$P_2^{[ep-ep]} = (\cdot, 0, 0, 0)$ (u)	
$P_3^{[ep-hp]} = (0, \cdot, 0)$ (cs)	$P_3^{[ep-ep]} = (0, \cdot, 0, 0)$ (u)	healthy-predator-only
	$P_4^{[ep-ep]} = (\cdot, \cdot, 0, 0)$ (u)	
$P_4^{[ep-hp]} = (\cdot, \cdot, 0)$ (cs)	$P_7^{[ep-ep]} = (0, \cdot, \cdot, 0)$ (cs)	disease-free
	$P_6^{[ep-ep]} = (\cdot, 0, \cdot, 0)$ (cs)	
$P_5^{[ep-hp]} = (0, \cdot, \cdot)$ (cs)	$P_7^{[ep-ep]} = (0, \cdot, \cdot, 0)$ (cs)	main-prey-free
	$P_8^{[ep-ep]} = (\cdot, \cdot, \cdot, 0)$ (cs)	
$P_6^{[ep-hp]} = (\cdot, \cdot, \cdot)$ (cs)	$P_5^{[ep-ep]} = (0, 0, \cdot, \cdot)$ (u)	coexistence
	$P_9^{[ep-ep]} = (0, \cdot, \cdot, \cdot)$ (cs)	
	$P_{10}^{[ep-ep]} = (\cdot, 0, \cdot, \cdot)$ (cs)	
	$P_{11}^{[ep-ep]} = (\cdot, \cdot, \cdot, \cdot)$ (cs)	

Table 5. Possibilities of comparison between equilibria of systems (2.1) and (2.2) that have the same biological behaviour. Notation: u = unstable, s = stable, cs = conditionally stable, uf = unstable if feasible, sf = stable if feasible. Note that the second and third components of system (2.1) correspond to the third and fourth components of system (2.2), respectively, while in this latter system the second component represents the explicit resource that was hidden in the model (2.1).

resource and the predator can only survive if the alternative prey thrives in the absence of the main prey. Its counterpart is thus just the equilibrium $P_9^{[ep-ep]}$.

Finally, the coexistence equilibria in both models are conditionally stable. Table 5 shows that the $P_6^{[ep-hp]}$ in model (2.1) can be related with equilibria $P_{10}^{[ep-ep]}$ and $P_{11}^{[ep-ep]}$ of model (2.2). Thus, for both models there is a possibility of survival of all predators and preys.

8. RESULTS

In this paper, we have compared the dynamics between two predator-prey models where a transmissible disease spreads among the predators. The alternative prey for the predator is implicit in the first model, but in the second we have made it explicit.

The most important parameters determining the type of possible changes in the system behaviour, leading to transcritical bifurcations, are the growth rate r of the prey population X and the mortality of the infected predator ν . In the case where the mortality rate ν of the infected predator exceeds the infection rate β of healthy predator Z , the environment becomes infection-free due to the extinction of the infected predators W . However, two distinct scenarios arise: in the first, if the growth

rate of the prey X is smaller than the predator efficiency Z in converting the resource into new predators as well as its carrying capacity L (see Proposition 4.2), the resulting dynamics is composed only of healthy predators Z ; their survival is guaranteed by the existence of an alternative resource. However, if the growth rate of the prey X exceeds the predator efficiency as well as the carrying capacity of the healthy predator Z , the main prey survives in the environment. This result is guaranteed by the existence of a transcritical bifurcation between the equilibria $P_3^{[ep-hp]}$ and $P_4^{[ep-hp]}$. Continuing along the same lines, the study of transcritical bifurcation between the equilibria $P_3^{[ep-hp]}$ and $P_5^{[ep-hp]}$ shows that if the mortality rate ν of the infected predator W is smaller than the infection rate β and the carrying capacity L of the healthy-predator, the ecosystem will be composed just of the populations of healthy predators Z and infected predators W ; their survival is in this case guaranteed by the available alternative resource (see the feasibility and stability conditions (4.4) and (4.5)).

For the second model (2.2), where the alternative resource is explicit, the main parameters defining the system dynamics are the predation rates a and b on the main prey X and on the alternative prey Y as well as the infection rate β of the healthy predator Z , respectively. In an infection-free scenario, the analysis of the transcritical bifurcation between equilibria $P_6^{[ep-ep]}$ and $P_8^{[ep-ep]}$ indicates the predation rate b as an important factor to guarantee the survival of the predator, i.e., b determines if the predator will feed only on the main prey or on both main and alternative prey, see the second condition of (4.13) and (4.16). Similarly, the transcritical bifurcation between $P_7^{[ep-ep]}$ and $P_8^{[ep-ep]}$ indicates that the mortality a characterizes the predator survival only. The second condition of (4.14) shows that the healthy predator Z has only the alternative prey Y as the source of food represented by the stable equilibrium point $P_7^{[ep-ep]}$. But, when a transcritical bifurcation occurs with the equilibrium point $P_8^{[ep-ep]}$, considering the same value of the bifurcation parameter a (see condition (4.15)), the healthy predator Z has two sources of food, i.e., the main prey X and the alternative prey Y . Thus, the predator thrives on both resources.

Our numerical analysis indicates that the disease transmission rate β plays a fundamental role for obtaining an environment with persistent disease, see Section 6.

Table 6 illustrates the comparison between models with hidden and explicit prey for the predator, considering an environment with and without the possibility of a transmissible disease among the predators.

There is no possibility of a scenario where in the ecoepidemic model (2.2) the infected predators thrive without the presence of the main and of the alternative prey, because $P_5^{[ep-ep]}$ is unstable. However, healthy and infected predators survive without the presence of the main prey in both systems (2.1) and (2.2). In this case, the alternative prey provides the food for predators in both models. This situation is represented by the main-prey-free equilibria $P_5^{[ep-hp]}$ and $P_9^{[ep-ep]}$.

Biological interpretation	Environment <i>with</i> disease transmission in predator Z	Environment <i>without</i> disease transmission in predator Z , [3]
ecosystem collapse	not possible	not possible
prey-only	not possible	not possible
healthy-predator-only	possible	possible
disease-free	possible	possible
main-prey-free/predator-only	possible	possible
coexistence	possible	possible

Table 6. Systems dynamics considering an environment with and without a transmissible disease among the predator population Z . The column representing the biological interpretation in the table refers to the equilibrium points obtained in both models (2.1) and (2.2) which are biologically equivalent.

The environment in which only the healthy predator Z survives in the absence of the main prey is possible in both scenarios, i.e., at the equilibria $P_3^{[ep-hp]}$ and $P_7^{[ep-ep]}$. The disease-free equilibrium points represented by $P_4^{[ep-hp]}$ and $P_8^{[ep-ep]}$ when represented in the same dynamics but without a transmissible disease among individuals Z , [3], clearly can represent the coexistence between X and Z populations. In this situation, investigated in [3], the same feasibility conditions for these equilibria hold. The coexistence also has the same behaviour in both environments, i.e., with and without a transmissible disease among the predator population Z .

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References

- [1] *K. Chakraborty, S. S. Das*: Biological conservation of a prey-predator system incorporating constant prey refuge through provision of alternative food to predators: A theoretical study. *Acta Biotheoretica* 62 (2014), 183–205. [doi](#)
- [2] *C. W. Clark*: *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. Wiley-Interscience Publication, John Wiley & Sons, New York, 1990. [zbl](#) [MR](#)
- [3] *L. M. E. de Assis, M. Banerjee, E. Venturino*: Comparing predator-prey models with hidden and explicit resources. *Ann. Univ. Ferrara, Sez. VII, Sci. Mat.* 64 (2018), 259–283. [MR](#) [doi](#)
- [4] *L. M. E. de Assis, M. Banerjee, E. Venturino*: Comparison of hidden and explicit resources in ecoepidemic models of predator-prey type. To appear in *Comput. Appl. Math.*
- [5] *H. I. Freedman*: *Deterministic Mathematical Models in Population Ecology*. Monographs and Textbooks in Pure and Applied Mathematics 57, Marcel Dekker, New York, 1980. [zbl](#) [MR](#) [doi](#)
- [6] *N. S. Goel, S. C. Maitra, E. W. Montroll*: On the Volterra and other nonlinear models of interacting populations. *Rev. Mod. Phys.* 43 (1971), 231–276. [MR](#) [doi](#)
- [7] *M. Haque, B. L. Li, M. S. Rahman, E. Venturino*: Effect of a functional response-dependent prey refuge in a predator-prey model. *Ecological Complexity* 20 (2014), 248–256. [doi](#)
- [8] *M. Haque, M. S. Rahman, E. Venturino*: Comparing functional responses in predator-infected eco-epidemics models. *BioSystems* 114 (2013), 98–117. [doi](#)

- [9] *M. A. Hixon*: Species diversity: Prey refuges modify the interactive effects of predation and competition. *Theor. Popul. Biol.* *39* (1991), 178–200. [doi](#)
- [10] *A. J. Lotka*: Contribution to the theory of periodic reactions. *J. Phys. Chem.* *14* (1910), 271–274. [doi](#)
- [11] *A. J. Lotka*: Analytical note on certain rhythmic relations in organic systems. *Proc. Natl. Acad. Sci. USA* *6* (1920), 410–415. [doi](#)
- [12] *J. D. Murray*: *Mathematical Biology*. *Biomathematics* 19, Springer, Berlin, 1989. [MR](#) [zbl](#) [doi](#)
- [13] *L. Perko*: *Differential Equations and Dynamical Systems*. *Texts in Applied Mathematics* 7, Springer, New York, 2001. [zbl](#) [MR](#) [doi](#)
- [14] *E. Venturino*: The influence of diseases on Lotka-Volterra systems. *Rocky Mt. J. Math.* *24* (1994), 381–402. [zbl](#) [MR](#) [doi](#)
- [15] *E. Venturino*: Ecoepidemiology: a more comprehensive view of population interactions. *Math. Model. Nat. Phenom.* *11* (2016), 49–90. [zbl](#) [MR](#) [doi](#)
- [16] *V. Volterra*: Variazioni e fluttuazioni del numero d’individui in specie animali conviventi. *Memorie Acad. d. L. Roma* *2* (1927), 31–113. (In Italian.) [zbl](#)
- [17] *V. Volterra*: Variations and fluctuations of the number of individuals in animal species living together. *ICES Journal of Marine Science* *3* (1928), 3–5. [doi](#)

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