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Unsustainable zip-bifurcation in a predator–prey model involving discrete delay

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A third-order system of ordinary differential equations, modelling two predators competing for a single prey species, is analysed in this paper. A delay term modelling the delayed logistic growth of the prey is included. Fixed points of the system are identified, and a linearized stability analysis is carried out. For some parameter regime, there exists a continuum of equilibria and these equilibria may undergo a zip bifurcation. The main results presented herein are that this zip bifurcation is 'unsustainable' for certain ranges of values of the time-delay parameter. Finally, spatial diffusion is incorporated in the delay differential equation model, and it is shown that the zip bifurcation remains unsustainable.

1. Introduction

In a recent study of a model describing the interactions of two predator species competing for one prey [6], under certain natural assumptions, it was observed that the system admits a one-dimensional continuum of equilibria, leading to what is described as a zip bifurcation phenomenon. In this model, a predator that has relatively low growth rate and survives at low carrying capacity K is identified as a K-strategist, while the other predator, which exhibits high growth rate, is identified as an r-strategist. Clearly, the model is not structurally stable. However, it serves as an illustration of the intuitively evident fact that at low values of the carrying capacity K both predators might survive, but as K grows the K-strategist loses ground and only the r-strategist may survive with the prey. Subsequently, a whole class of models that show this phenomenon were proposed and analysed in the literature (see [2, 10, 11, 13, 18]). Interestingly enough, in all the above studies the zip bifurcation is sustainable even in the presence of diffusion. Also, as observed in the earlier studies, for low values of the carrying capacity K both predators may coexist with the prey, but if K increases only the r-strategist may survive. This

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fact may seem against the biological considerations, as coexistence of species is a common phenomenon. Thus, a switch in the stability behaviour of the continuum of the equilibria is highly desirable, as it will facilitate coexistence among the species, especially when the K-strategist loses ground. Also, time delays are natural in any biological process. Accordingly, in this paper we consider the system of ordinary differential equations involving a discrete time delay given by

$$\left.\begin{aligned} S'(t) &= \gamma\left(1-\frac{S(t-\tau)}{K}\right)S(t) - m_1\frac{S(t)}{a_1+S(t)}x_1(t) - m_2\frac{S(t)}{a_2+S(t)}x_2(t),\\ x_1'(t) &= \frac{m_1S(t)}{a_1+S(t)}x_1(t) - d_1x_1(t),\\ x_2'(t) &= \frac{m_2S(t)}{a_2+S(t)}x_2(t) - d_2x_2(t) \end{aligned}\right\} \tag{1.1}$$

as a model to describe the dynamical interactions of two predators competing for a single regenerating resource. In (1.1) x_1, x_2 and S are the population sizes of the two predators and a single prey species, respectively. In this model $K > 0$ denotes the carrying capacity of the environment with respect to the prey, $\gamma > 0$ is the intrinsic growth rate of the prey, m_i, d_i, a_i for $i = 1, 2$ are non-negative parameters and represent the maximum birth rate, the death rate and the 'half saturation constant', respectively, of the ith predator. The predator functional response is saturating according to Michaelis–Menten kinetics.

A delayed logistic growth of prey is assumed when no predators are present and $\tau \geqslant 0$ represents the time delay. It has been suggested by Hutchinson that a delay logistic equation (the first equation of (1.1) when $x_1 = x_2 = 0$) can be used to model the dynamics of a population growing towards a saturation level K with a constant reproduction rate γ. The term $(1 - S(t - \tau)/K)$ denotes a density-dependent feedback mechanism, which takes τ units of time to respond to changes in the population density represented by S in this equation. There are a number of articles on these delayed single species population models (see [15, 17] and the references therein).

The model (1.1) when $\tau = 0$ has been a focus of extensive investigations in the last few years and there is a large literature on this subject. For a detailed account of these results we refer the reader to [19]. In [6, 7] Farkas observed that at low values of the carrying capacity K of the ecosystem (1.1), when $\tau = 0$ with respect to the prey, a line of equilibria exists, which is an attractor of the system representing stable coexistence of the three species. If K is increased, the equilibria are continuously destabilized, and above a certain value of K the system has no stable equilibria representing coexistence. In [18], Sáez *et al*. considered a three-dimensional competition model with a generalized Holling type III functional response and established that the system admits a one-dimensional continuum of equilibria leading to zip bifurcation. In subsequent studies, variants of these models, with and without diffusion, have been studied by several researchers and in all these situations the occurrence of the phenomenon of zip bifurcation has been confirmed (see [6–10, 12, 13]).

This paper has the following structure. In § 2 we discuss the equilibria and local stability analysis following the linearization procedure. In § 3 we study the linearized problem and establish conditions for the unsustainability of zip bifurcation in the model. Generally, diffusion is a process that helps maintain the state of dynamics of a system. In § 4 we consider a model where time delays render the zip bifurcation unsustainable, and the effect of the introduction of diffusion in such time-delay models. A discussion follows in § 5.

2. Equilibria and local stability analysis

In this section, we determine the equilibria of system (1.1) and study the local stability analysis. The equilibria of (1.1) satisfy the equations

$$\left.\begin{aligned}\gamma\left(1-\frac{S(t-\tau)}{K}\right)S(t)-m_1\frac{S(t)}{a_1+S(t)}x_1(t)-m_2\frac{S(t)}{a_2+S(t)}x_2(t)=0,\\ \frac{m_1S(t)}{a_1+S(t)}x_1(t)-d_1x_1(t)=0,\\ \frac{m_2S(t)}{a_2+S(t)}x_2(t)-d_2x_2(t)=0.\end{aligned}\right\}\tag{2.1}$$

Following the arguments given in [6,7,12,13], we conclude that the equilibria of (1.1) are

$$(S,x_1,x_2)=(0,0,0),\qquad (S,x_1,x_2)=(K,0,0)$$

and the points on the straight line segment

$$L_K=\left\{(S,x_1,x_2)\in\mathbb{R}^3;\ S=\lambda,\ x_1\geqslant 0,\ x_2\geqslant 0 \text{ and } m_1\frac{S}{a_1+S}x_1+m_2\frac{S}{a_2+S}x_2=\gamma\left(1-\frac{\lambda}{K}\right)\right\}\tag{2.2}$$

in the positive octant of (S,x_1,x_2)-space, provided we assume that

$$m_i>d_i\quad\text{for } i=1,2\qquad\text{and}\qquad\frac{a_1d_1}{m_1-d_1}=\frac{a_2d_2}{m_2-d_2}.\tag{2.3}$$

With the previous hypotheses and the notation

$$\lambda=\frac{a_1d_1}{m_1-d_1}=\frac{a_2d_2}{m_2-d_2},$$

system (1.1) can be written as

$$\left.\begin{aligned}S'(t)&=\gamma\left(1-\frac{S(t-\tau)}{K}\right)S(t)-m_1\frac{S(t)}{a_1+S(t)}x_1(t)-m_2\frac{S(t)}{a_2+S(t)}x_2(t),\\ x_1'(t)&=\beta_1\frac{S(t)-\lambda}{a_1+S(t)}x_1(t),\\ x_2'(t)&=\beta_2\frac{S(t)-\lambda}{a_2+S(t)}x_2(t),\end{aligned}\right\}\tag{2.4}$$

where $\beta_i=m_i-d_i$, $i=1,2$.

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In what follows, we assume that (2.3) holds. The numbers $a_1d_1/(m_1-d_1)$ and $a_2d_2/(m_2-d_2)$ correspond to the threshold quantities of the prey species for the predators x_1 and x_2, respectively. If $a_1d_1/(m_1-d_1)\neq a_2d_2/(m_2-d_2)$, it follows that (2.1) has only the axial equilibria given by $(S,x_1,x_2)=(0,0,0)$, $(S,x_1,x_2)=(K,0,0)$.

We now study the stability of the equilibria for system (1.1), that is, $(S,x_1,x_2)=(0,0,0)$, $(S,x_1,x_2)=(K,0,0)$ and equilibria on L_K and of the set L_K, where $\lambda=a_1d_1/(m_1-d_1)=a_2d_2/(m_2-d_2)$. To study the local stability of those equilibria, we let $E=(S^*,x_1^*,x_2^*)$ be an equilibrium solution of system (2.4).

The variational system of (2.4) corresponding to E is given by

$$\begin{bmatrix} S(t)\\ x_1(t)\\ x_2(t)\end{bmatrix}' = \begin{bmatrix} \gamma-\dfrac{\gamma}{K}S^*-\dfrac{m_1a_1}{(a_1+S^*)^2}x_1^*-\dfrac{m_2a_2}{(a_2+S^*)^2}x_2^* & -\dfrac{m_1}{a_1+S^*}S^* & -\dfrac{m_2}{a_2+S^*}S^* \\ \dfrac{\beta_1a_1}{(a_1+S^*)^2}x_1^*+\dfrac{\beta_1\lambda}{(a_1+S^*)^2}x_1^* & \beta_1\dfrac{S^*-\lambda}{a_1+S^*} & 0 \\ \dfrac{\beta_2a_2}{(a_2+S^*)^2}x_2^*+\dfrac{\beta_2\lambda}{(a_2+S^*)^2}x_2^* & 0 & \beta_2\dfrac{S^*-\lambda}{a_2+S^*} \end{bmatrix} \times \begin{bmatrix} S(t)\\ x_1(t)\\ x_2(t)\end{bmatrix} + \begin{bmatrix} -\dfrac{\gamma}{K}S^* & 0 & 0\\ 0 & 0 & 0\\ 0 & 0 & 0\end{bmatrix}\begin{bmatrix} S(t-\tau)\\ x_1(t-\tau)\\ x_2(t-\tau)\end{bmatrix}. \tag{2.5}$$

For the equilibrium $E=(0,0,0)$, we have from (2.5) that

$$\begin{bmatrix} S(t)\\ x_1(t)\\ x_2(t)\end{bmatrix}' = \begin{bmatrix} \gamma & 0 & 0\\ 0 & -\beta_1\dfrac{\lambda}{a_1} & 0\\ 0 & 0 & -\beta_2\dfrac{\lambda}{a_2}\end{bmatrix}\begin{bmatrix} S(t)\\ x_1(t)\\ x_2(t)\end{bmatrix} + \begin{bmatrix} 0 & 0 & 0\\ 0 & 0 & 0\\ 0 & 0 & 0\end{bmatrix}\begin{bmatrix} S(t-\tau)\\ x_1(t-\tau)\\ x_2(t-\tau)\end{bmatrix}. \tag{2.6}$$

The characteristic equation associated with (2.6) is given by

$$(\mu-\gamma)\left(\mu+\beta_1\frac{\lambda}{a_1}\right)\left(\mu+\beta_2\frac{\lambda}{a_2}\right)=0,$$

and it is easy to see that the equilibrium is unstable, since γ is a positive root of the above equation.

When $E=(K,0,0)$ we have that

$$\begin{bmatrix} S(t)\\ x_1(t)\\ x_2(t)\end{bmatrix}' = \begin{bmatrix} 0 & -\dfrac{m_1K}{a_1+K} & -\dfrac{m_2K}{a_2+K}\\ 0 & \beta_1\dfrac{K-\lambda}{a_1+K} & 0\\ 0 & 0 & \beta_2\dfrac{K-\lambda}{a_2+K}\end{bmatrix}\begin{bmatrix} S(t)\\ x_1(t)\\ x_2(t)\end{bmatrix} + \begin{bmatrix} -\gamma & 0 & 0\\ 0 & 0 & 0\\ 0 & 0 & 0\end{bmatrix}\begin{bmatrix} S(t-\tau)\\ x_1(t-\tau)\\ x_2(t-\tau)\end{bmatrix}. \tag{2.7}$$

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Thus, the characteristic equation of (2.7) is given by

$$(\mu + \gamma \mathrm{e}^{-\mu\tau})\left(\beta_1 \frac{K-\lambda}{a_1+K} - \mu\right)\left(\beta_2 \frac{K-\lambda}{a_2+K} - \mu\right) = 0,$$

or, equivalently,

$$\mu^3 + \alpha\mu^2 + \beta\mu = H\mathrm{e}^{-\mu\tau}[\mu^2 + \alpha\mu + \beta], \tag{2.8}$$

where

$$a = \beta_1 \frac{K-\lambda}{a_1+K}, \quad b = \beta_2 \frac{K-\lambda}{a_2+K}, \quad \alpha = -(a+b), \quad \beta = ab \quad \text{and} \quad H = -\gamma. \tag{2.9}$$

We can write (2.8) in the form

$$P(\mu) + \mathrm{e}^{-\mu\tau} Q(\mu) = 0,$$

where $P(\mu) = \mu^3 + \alpha\mu^2 + \beta\mu$ and $Q(\mu) = -H(\mu^2 + \alpha\mu + \beta)$.

We now set $\mu = \delta + \mathrm{i}\nu$ in (2.8). Separating real and imaginary parts, we have that

$$\left.\begin{aligned} &\delta^3 - 3\delta\nu^2 + \alpha(\delta^2 - \nu^2) + \beta\delta \\ &\qquad = H\mathrm{e}^{-\delta\tau}[(\beta + \alpha\delta + \delta^2 - \nu^2)\cos(\nu\tau) + (\alpha\nu + 2\delta\nu)\sin(\nu\tau)], \\ &-\nu^3 + 3\delta^2\nu + 2\alpha\delta\nu + \beta\nu \\ &\qquad = H\mathrm{e}^{-\delta\tau}[(2\delta\nu + \alpha\nu)\cos(\nu\tau) - (\delta^2 - \nu^2 + \alpha\delta + \beta)\sin(\nu\tau)]. \end{aligned}\right\} \tag{2.10}$$

Remark 2.1. It is important to note that when $\tau = 0$ both predator species may survive only if $0 < \lambda < K$ (see [6]). Hence, when $\tau = 0$ it is easy to see that E is unstable for system (1.1) since the characteristic equation associated with the linearized system of (1.1) has two positive roots (see [6] for details). Clearly, all these characteristic roots will continue to have positive real parts for sufficiently small $\tau > 0$.

We now study the possibility of a stability switch for E, examining the sign of the derivative of the real parts of the eigenvalues associated with the characteristic equation (2.8) with respect to τ, as the roots cross zero. That is, we analyse $\mathrm{d}\delta(\hat\tau)/\mathrm{d}\tau$ where $\delta(\hat\tau) = 0$. If the derivative is positive (negative), then clearly stabilization (destabilization) cannot take place at that value of $\hat\tau$ (see [14]).

At $\tau = \hat\tau$, $\mu(\hat\tau) = \delta(\hat\tau) + \mathrm{i}\hat\nu(\hat\tau) = \mathrm{i}\hat\nu(\hat\tau)$ since $\delta(\hat\tau) = 0$, and (2.10) becomes

$$\left.\begin{aligned} \alpha\hat\nu^2 &= H(\hat\nu^2 - \beta)\cos(\hat\nu\hat\tau) - H\alpha\hat\nu\sin(\hat\nu\hat\tau), \\ -\hat\nu^3 + \beta\hat\nu &= H\alpha\hat\nu\cos(\hat\nu\hat\tau) + H(\hat\nu^2 - \beta)\sin(\hat\nu\hat\tau). \end{aligned}\right\} \tag{2.11}$$

Squaring and adding the equations in (2.11), we have that

$$\nu^6 + (\alpha^2 - 2\beta - H^2)\nu^4 + (\beta^2 + 2H^2\beta - H^2\alpha^2)\nu^2 - H^2\beta^2 = 0. \tag{2.12}$$

Differentiating system (2.10) with respect to τ, substituting $\tau = \hat\tau$, $\delta = 0$, $\nu = \hat\nu$ and using (2.11), we get the equations for $\mathrm{d}\delta(\hat\tau)/\mathrm{d}\tau$ and $\mathrm{d}\nu(\hat\tau)/\mathrm{d}\tau$ as

$$\left.\begin{aligned} A\frac{\mathrm{d}\delta}{\mathrm{d}\tau}(\hat\tau) + B\frac{\mathrm{d}\nu}{\mathrm{d}\tau}(\hat\tau) &= C, \\ -B\frac{\mathrm{d}\delta}{\mathrm{d}\tau}(\hat\tau) + A\frac{\mathrm{d}\nu}{\mathrm{d}\tau}(\hat\tau) &= D, \end{aligned}\right\} \tag{2.13}$$

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where

$$\left.\begin{aligned}A &= -3\hat{\nu}^2 + \beta - \hat{\tau}\alpha\hat{\nu}^2 - H\alpha\cos(\hat{\nu}\hat{\tau}) - 2H\hat{\nu}\sin(\hat{\nu}\hat{\tau}),\\ B &= -2\alpha\hat{\nu} + 2H\hat{\nu}\cos(\hat{\nu}\hat{\tau}) + \hat{\tau}(\hat{\nu}^3 - \beta\hat{\nu}) - H\alpha\sin(\hat{\nu}\hat{\tau}),\\ C &= \hat{\nu}(-\hat{\nu}^3 + \beta\hat{\nu}),\\ D &= \alpha\hat{\nu}^3.\end{aligned}\right\} \tag{2.14}$$

Solving the equations in (2.13), we get that

$$\frac{\mathrm{d}\delta}{\mathrm{d}\tau}(\hat{\tau}) = \frac{AC - BD}{A^2 + B^2} \tag{2.15}$$

and the sign of $\mathrm{d}\delta(\hat{\tau})/\mathrm{d}\tau$ depends upon the sign of $AC - BD$. From (2.14), after some simplifications, we obtain

$$AC - BD = \hat{\nu}^2(3\hat{\nu}^4 - 4\beta\hat{\nu} + \beta + 2\alpha\hat{\nu}^2 - H^2\alpha^2 - 2\hat{\nu}^2H^2 + 2H^2\beta).$$

So, stabilization (destabilization) cannot take place if $AC - BD > 0$ ($AC - BD < 0$).

Let

$$F(z) = z^3 + (\alpha^2 - 2\beta - H^2)z^2 + (\beta^2 + 2H^2\beta - H^2\alpha^2)z - H^2\beta^2,$$

which is the left-hand side of (2.12) with $\hat{\nu}^2 = z$. Then, $F(\hat{\nu}^2) = 0$ and we note that

$$\frac{\mathrm{d}F}{\mathrm{d}z}(\hat{\nu}^2) = \frac{A^2 + B^2}{\hat{\nu}^2}\frac{\mathrm{d}\mu}{\mathrm{d}\tau}(\hat{\tau}).$$

We write $F(z)$ as

$$F(z) = z^3 + A_1z^2 + A_2z + A_3, \tag{2.16}$$

where

$$\left.\begin{aligned}A_1 &= \alpha^2 - 2\beta - H^2,\\ A_2 &= \beta^2 + 2H^2\beta - H^2\alpha^2,\\ A_3 &= -H^2\beta^2.\end{aligned}\right\} \tag{2.17}$$

We note that the real roots of (2.12), which are precisely the positive roots of (2.16), are of interest to us, as these roots determine the change in the stability of E.

Note that from (2.9) we have that

$$\left.\begin{aligned}A_1 &= \beta_1^2\frac{(K-\lambda)^2}{(a_1+K)^2} + \beta_2^2\frac{(K-\lambda)^2}{(a_2+K)^2} - \gamma,\\ A_2 &= \beta_1^2\beta_2^2\frac{(K-\lambda)^4}{(a_1+K)^2(a_2+K)^2} - \gamma^2\left(\beta_1^2\frac{(K-\lambda)^2}{(a_1+K)^2} + \beta_2^2\frac{(K-\lambda)^2}{(a_2+K)^2}\right),\\ A_3 &= -\gamma^2\beta_1^2\beta_2^2\frac{(K-\lambda)^4}{(a_1+K)^2(a_2+K)^2}.\end{aligned}\right\} \tag{2.18}$$

Letting

$$N = 18A_1A_2A_3 - 4A_1^3A_3 + A_1^2A_2^2 - 4A_2^3 - 27A_3^2,$$

we observe that $A_3 < 0$. Thus, using Descartes's rule of signs, we see that (2.16) has one positive root if any of the following conditions holds:

(H1) (i) $A_1 \geqslant 0$, $A_2 \geqslant 0$,

(ii) $A_1 \geqslant 0$, $A_2 \leqslant 0$,

(iii) $A_1 \leqslant 0$, $A_2 \leqslant 0$,

(iv) $A_1 < 0$, $A_2 > 0$ and $N < 0$.

We observe that (2.16) has three positive roots if any of the following conditions holds:

(H2) $A_1 < 0$, $A_2 > 0$ and $N > 0$.

We summarize the above discussion in the following theorem.

THEOREM 2.2.

(i) *Assume that the conditions in (H1) hold. If the equilibrium* $E = (K, 0, 0)$ *is unstable for* $\tau = 0$*, then it remains unstable for all* $\tau \geqslant 0$.

(ii) *Assume that the conditions in (H2) hold. Then, stability of* $E = (K, 0, 0)$ *cannot be preserved. As* τ *increases, stability switches may occur and, furthermore, there exists a* τ^* *such that* E *is unstable for all* $\tau > \tau^*$. *As* τ *varies from* 0 *to* τ^**, at most a finite number of stability switches may occur.*

We now study the stability of the equilibria $E = (\lambda, \xi_1, \xi_2)$ on L_K. Observe that, in view of (2.2), we have that

$$\gamma\left(1-\frac{\lambda}{K}\right)-\sum_{i=1}^{2}\frac{m_i a_1}{(a_i+\lambda)^2}\xi_i=\sum_{i=1}^{2}\frac{m_i a_1}{a_i+\lambda}\xi_i-\sum_{i=1}^{2}\frac{m_i a_1}{(a_i+\lambda)^2}\xi_i=\lambda\sum_{i=1}^{2}\frac{m_i}{(a_i+\lambda)^2}\xi_i,$$

and hence the characteristic equation associated with (2.5) at (λ, ξ_1, ξ_2) is given by

$$\begin{vmatrix} \mu-\lambda\displaystyle\sum_{i=1}^{2}\frac{m_i}{(a_i+\lambda)^2}\xi_i+\frac{\gamma\lambda}{K}\mathrm{e}^{-\tau\mu} & \dfrac{m_1\lambda}{a_1+\lambda} & \dfrac{m_2\lambda}{a_2+\lambda} \\ -\dfrac{\beta_1\xi_1}{a_1+\lambda} & \mu & 0 \\ -\dfrac{\beta_2\xi_2}{a_2+\lambda} & 0 & \mu \end{vmatrix}=0.$$

Thus, the characteristic polynomial is given by

$$P(\mu)=\mu\left[\mu^2-\lambda\sum_{i=1}^{2}\frac{m_i}{(a_i+\lambda)^2}\xi_i\mu+\lambda\sum_{i=1}^{2}\frac{m_i\beta_i}{(a_i+\lambda)^2}\xi_i+\frac{\lambda\gamma}{K}\mathrm{e}^{-\mu\tau}\mu\right]. \tag{2.19}$$

We defer the study of the stability of the equilibria on the line L_K and of the set L_K where $\lambda = a_1 d_1/(m_1 - d_1) = a_2 d_2/(m_2 - d_2)$ to the next section.

3. Stability analysis of non-isolated equilibria

In this section we discuss the stability analysis of the non-isolated equilibria, which in the present case lie on the line L_K. We first discuss the case for $\tau = 0$ in system (1.1). For $\tau = 0$, system (1.1) reduces to

$$\left.\begin{aligned} \dot{S} &= \gamma\left(1-\frac{S}{K}\right)S - m_1\frac{S}{a_1+S}x_1 - m_2\frac{S}{a_2+S}x_2, \\ \dot{x_1} &= m_1\frac{S}{a_1+S}x_1 - d_1x_1, \\ \dot{x_2} &= m_2\frac{S}{a_2+S}x_2 - d_2x_2. \end{aligned}\right\} \tag{3.1}$$

The system (3.1) describes the competition of an 'r-strategist' and a 'K-strategist' for a single regenerating prey species. We note that an *r-strategist* is a species that tries to ensure its survival by having a relatively high growth rate and a *K-strategist* is a species that consumes less, has a lower growth rate and is able to raise its offspring on a scarce supply of food. The parameters in (3.1) have the same meaning as in (1.1). In the following we present a very brief summary of the results in [6] for system (3.1). System (3.1) admits the following equilibria: $(S, x_1, x_2) = (0, 0, 0)$, $(S, x_1, x_2) = (K, 0, 0)$ and the points on the straight line L_K. It is easy to see that the trivial equilibria $(0, 0, 0)$ and $(K, 0, 0)$ are unstable provided that $0 < \lambda < K$ (see [6,8] for details). It is clear that all equilibria on L_K are stable for all K that satisfy the inequality $\lambda < K \leqslant a_2 + 2\lambda$. This means that if food is scarce, both the r- and K-strategists may live together in the long run in a steady state that depends on the initial values of the species. When $a_2 + 2\lambda < K < a_1 + 2\lambda$ (i.e. when $a_1 > a_2$) the family of equilibria on the line L_K undergoes a split and a part of L_K is unstable, that is, there exists a point $(\lambda, \xi_1(K), \xi_2(K))$ on L_K such that the equilibria on

$$L_{\mathrm{U}} = \{(\lambda, \xi_1, \xi_2) \text{ on } L_K : \xi_1 < \xi_1(K)\}$$

are unstable for the flow of (3.1), and the equilibria on

$$L_{\mathrm{S}} = \{(\lambda, \xi_1, \xi_2) \text{ on } L_K : \xi_1 > \xi_1(K)\}$$

are stable. The point $(\xi_1(K), \xi_2(K))$ is obtained by solving the system

$$\left.\begin{aligned} \frac{m_1\xi_1}{a_1+\lambda} + \frac{m_2\xi_2}{a_2+\lambda} &= \frac{\gamma(K-\lambda)}{K}, \\ \frac{m_1\xi_1}{(a_1+\lambda)^2} + \frac{m_2\xi_2}{(a_2+\lambda)^2} &= \frac{\gamma}{K}. \end{aligned}\right\} \tag{3.2}$$

As K takes on the value $a_1 + 2\lambda$, the equilibrium that exists in the (S, x_1)-plane is stable, while all other equilibria on L_K lose stability. When $K > a_1 + 2\lambda$ all equilibria on L_K become unstable.

Note that as K increases from $a_2 + 2\lambda$ to $a_1 + 2\lambda$ the point $(\lambda, \xi_1(K), \xi_2(K))$ moves along L_K continuously from $(\lambda, 0, \xi_2(K))$ to $(\lambda, \xi_1(K), 0)$, so the points left behind become unstable. This phenomenon has been termed *zip bifurcation* (see [6, 8]). From the point of view of the competition, as the quantity of available food increases, the K-strategist loses ground and those equilibria where the relative growth of the K-strategist is high compared with the growth of the r-strategist are the first to be destabilized. When K reaches the value $a_1 + 2\lambda$ all interior equilibria become destabilized and the only stable equilibrium remaining is the endpoint of L in the (S, x_1)-plane. This means that at this value of the carrying capacity the K-strategist dies out. One may prove that if K is increased further, then even the equilibrium in the (S, x_1)-plane gets destabilized, but the prey and the r-strategist continue to coexist in a periodic manner due to the occurrence of Andronov–Hopf bifurcation.

It is interesting to observe that the line L_K (grey line in figure 1) represents the line of non-isolated equilibria in the positive octant of $\mathbb{R}^3$. This line connects the points P_K in the (S, x_2)-plane and Q_K in the (S, x_1)-plane. Note that there exists a point M_K on L_K with the property that the equilibria on L_K between P_K and M_K are unstable, while those between M_K and Q_K are stable in the case where $a_1 > a_2$, or vice versa in the case where $a_1 < a_2$ (figure 1(a)).

Also, when $a_1 = a_2$ it is clear that all equilibria on L_K are stable for all K that satisfy the inequality $\lambda < K \leqslant a_2 + 2\lambda$. Furthermore, when K crosses $a + 2\lambda$ all equilibria on L_K lose stability, and at $K = a + 2\lambda$ the segment L_K bifurcates into a cylinder, that is, there exists a $\delta > 0$ such that, for $a + 2\lambda < K < a + 2\lambda + \delta$, system (3.1) has an invariant topological cylinder C that is the union of closed paths and is an attractor of the system. Furthermore, it has a 'neighbourhood' in which the trajectories with initial condition in this 'neighbourhood' tend to C as t tends to ∞ (figure 1(b)). In other words, we observe that the zip bifurcation that shows up for all $a_1 \neq a_2$ vanishes when $a_1 = a_2$. This is an interesting scenario in the dynamics of system (3.1), and henceforth we term this phenomenon a *degenerate zip bifurcation*.

We simulate system (3.1) with the following values of the parameters (figure 2(a)): $m_1 = 0.6$, $m_2 = 0.7$, $d_1 = 0.3$, $d_2 = 0.2$, $\beta_1 = 0.3$, $\beta_2 = 0.5$, $\gamma = 0.8$, $a_1 = 0.16$, $a_2 = 0.4$, $\lambda = 0.16$ and $K = 0.6$. Clearly, figure 2(a) explains the occurrence of zip bifurcation of the equilibria on the line L_K with the unstable part initiating near the (S, x_1)-plane, and also on the line L_K (the straight grey line) and directed towards the (S, x_2)-plane with the stable part lying near this plane. We note that the transition from instability to stability occurs at $(\lambda, \xi_1(K), \xi_2(K)) = (0.16, 0.1137777778, 0.2986666667)$ on L_K.

Similarly, choosing the parameter values $m_1 = 0.6$, $m_2 = 0.7$, $d_1 = 0.2$, $d_2 = 0.4$, $\beta_1 = 0.4$, $\beta_2 = 0.3$, $\gamma = 0.8$, $a_1 = 0.8$, $a_2 = 0.4$, $\lambda = 0.4$ and $K = 1.35$ leads to figure 2(b), which explains the occurrence of zip bifurcation of the equilibria on the line L_K with stable part initiating near the (S, x_1)-plane, and also on the line L_K (the straight grey line) and directed towards the (S, x_2)-plane with the unstable part lying near this plane. We note that the transition from instability to stability occurs at $(\lambda, \xi_1(K), \xi_2(K)) = (0.3, 0.4909090909, 0.2545454546)$ on L_K (figure 2(b)).

In what follows, we consider model (1.1) in the case $\tau \neq 0$. The characteristic equation associated with (2.5) at $(\lambda, \xi_1, \xi_2) \in L_K$ is given by

$$\mu\left[\mu^2 - \lambda \sum_{i=1}^{2} \frac{m_i}{(a_i + \lambda)^2} \xi_i \mu + \lambda \sum_{i=1}^{2} \frac{m_i \beta_i}{(a_i + \lambda)^2} \xi_i + \frac{\lambda\gamma}{K} \mathrm{e}^{-\mu\tau} \mu\right] = 0$$

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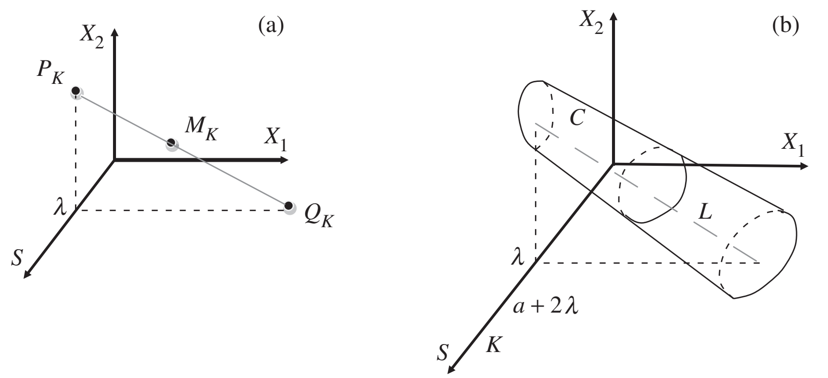

Figure 1. (a) Zip bifurcation for the case $a_1 \neq a_2$: the part of L_K between P_K and M_K is unstable and that between M_K and Q_K is stable if $a_1 > a_2$, or vice versa if $a_1 < a_2$. (b) Degenerate zip bifurcation for the case $a_1 = a_2$: in this case $a + 2\lambda < K < a + 2\lambda + \delta$ and all equilibria on L_K are unstable with an invariant topological cylinder around L_K, which is a local attractor for system (3.1).

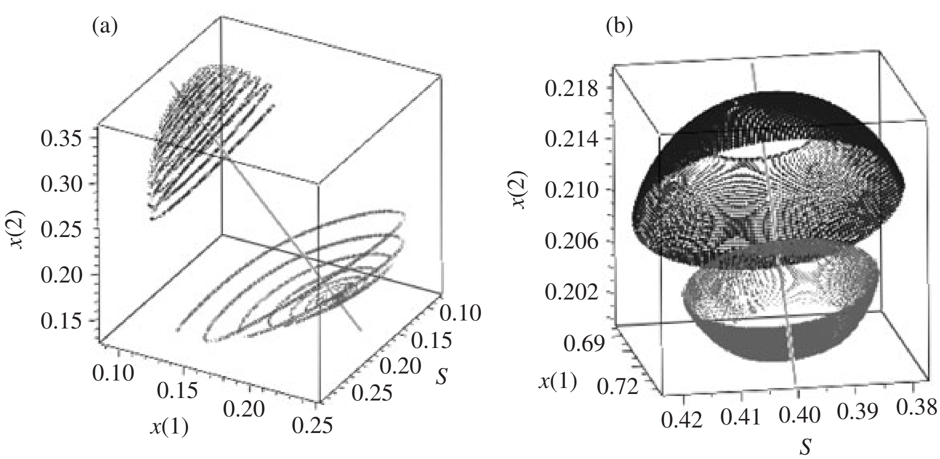

Figure 2. Phase portrait where (a) the grey curve is an unstable orbit initiating near the $(S,\ x_1)$-plane and the line L_K, directed towards the $(S,\ x_2)$-plane with the stable part lying in it, and the black curve is a stable orbit initiating near the $(S,\ x_2)$-plane and the line L_K, directed towards the $(S,\ x_1)$-plane with the unstable part lying in it, and (b) the phase portrait has the same meaning as in (a), but with directions reversed.

or, equivalently,

$$\mu[\mu^2 - a\mu + c + be^{-\mu\tau}\mu] = 0, \tag{3.3}$$

where

$$a = \lambda \sum_{i=1}^{2} \frac{m_i}{(a_i + \lambda)^2}\xi_i, \quad b = \frac{\lambda\gamma}{K} \quad \text{and} \quad c = \lambda \sum_{i=1}^{2} \frac{m_i\beta_i}{(a_i + \lambda)^2}\xi_i.$$

We now study the stability of the equilibria (λ, ξ_1, ξ_2) on L_K for a fixed K in the interval $(a_2 + 2\lambda, a_2 + 2\lambda)$. In this case, the family of equilibria on L_K undergoes a

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split and there exists a point $(\lambda, \xi_1(K), \xi_2(K))$ on L_K such that the equilibria on L_{U} are unstable for the flow of (3.1) and the equilibria on L_{S} are stable in view of the case when $\tau = 0$. It is important to observe that, for $\tau = 0$, an equilibrium point is stable (respectively, unstable) for the flow of system (3.1) if the following condition is satisfied (see [6, p. 1301]):

$$a + b > 0 \quad (\text{respectively, } a + b < 0). \tag{3.4}$$

In the remainder of this section, we confine ourselves to the study of the possible *stability switches* for those equilibria (λ, ξ_1, ξ_2) on L_{U} or L_{S} when τ varies, since a stability switch leads to the unsustainability of the *zip bifurcation* for system (1.1).

Equation (3.3) for $\tau \neq 0$ has infinitely many roots. By Rouche's theorem and continuity in τ, the expression in the brackets of (3.3) has roots with negative real parts if and only if no pure imaginary root exists. Therefore, to obtain a stability switch one needs to have a pure imaginary root for

$$G(\mu, \tau) = \mu^2 - a\mu + c + b\mathrm{e}^{-\mu\tau}\mu = 0. \tag{3.5}$$

In the following, we investigate the existence of pure imaginary roots $\mu = \mathrm{i}\omega$ $(\omega > 0)$ for (3.5).

Defining

$$P_1(\mu) = \mu^2 - a\mu + c \tag{3.6}$$

and

$$Q_1(\mu) = b\mu, \tag{3.7}$$

the characteristic equation (3.5) is equivalent to

$$P_1(\mu) + Q_1(\mu)\mathrm{e}^{-\mu\tau} = 0. \tag{3.8}$$

We now have the following.

PROPOSITION 3.1. *The functions $P_1(\mu)$ and $Q_1(\mu)$ are analytic functions of μ in a right half-plane* $\mathrm{Re}\, z > -\delta$, $\delta > 0$, *and satisfy the following.*

(i) $P_1(0) + Q_1(0) = c \neq 0$, *that is, $\mu = 0$ is not a root of the characteristic equation (3.8).*

(ii) *If $\mu = \mathrm{i}\omega$, $\omega > 0$, then*

$$P_1(\mathrm{i}\omega) + Q_1(\mathrm{i}\omega) \neq 0, \quad \tau \in R. \tag{3.9}$$

This implies that $P_1(\mu)$ and $Q_1(\mu)$ have no common imaginary roots.

(iii) *We have that*

$$\limsup \left\{ \left| \frac{Q_1(\mu)}{P_1(\mu)} \right|;\ |\mu| \to \infty,\ \mathrm{Re}\, \mu \geqslant 0 \right\} < 1,$$

that is, there are no roots bifurcating from infinity.

Proof. Clearly, the functions $P_1(\mu)$ and $Q_1(\mu)$, being polynomials, are analytic function of μ. Thus, part (i) of the proposition is obvious.

To prove part (ii), note that $P_1(\mathrm{i}\omega)+Q_1(\mathrm{i}\omega)=\omega^2-c+\mathrm{i}[b-a]\omega\neq 0$. Evidently, (λ,ξ_1,ξ_2) is stable (unstable) in view of (3.4).

To prove part (iii), observe that

$$\frac{|Q_1(\mu)|}{|P_1(\mu)|}=\frac{|b\mu|}{|\mu^2-a\mu+c|}=\frac{|b|}{|\mu-a+c/\mu|}\leqslant\frac{|b|}{|\mu|-|a|-|c/\mu|}$$

for $|\mu|$ large. So, $|Q_1(\mu)|/|P_1(\mu)|\to 0$ when $|\mu|\to\infty$ and $\operatorname{Re}\mu\geqslant 0$. □

Define the auxiliary function $F(\omega)=|P_1(\mathrm{i}\omega)|^2-|Q_1(\mathrm{i}\omega)|^2$, that is,

$$F(\omega)=\omega^4-[b^2+2c-a^2]\omega^2+c^2. \tag{3.10}$$

Observe that $F(\omega)=0$ has at most a finite number of real zeros, so there are only a finite number of 'places' for roots to cross the imaginary axis.

From now on, we drop the index 1 from P_1 and Q_1; furthermore, we denote by P_R, Q_R the real parts of P and Q, respectively, and by P_I, Q_I the imaginary parts of P and Q, respectively.

A necessary condition for the change in stability of each equilibrium (λ,ξ_1,ξ_2) on L_K is the existence of $\omega_0>0$ such that $F(\omega_0)=0$.

We examine the possibility that $\mu=\mathrm{i}\omega$ $(\omega>0)$ is a root of the characteristic equation (3.5). Observe that ω is a root of (3.5) if and only if $|P(\mathrm{i}\omega)|=|Q(\mathrm{i}\omega)|$ and

$$\left.\begin{aligned}\sin(\omega\tau)&=\frac{P_\mathrm{I}(\mathrm{i}\omega)Q_\mathrm{R}(\mathrm{i}\omega)-P_\mathrm{R}(\mathrm{i}\omega)Q_\mathrm{I}(\mathrm{i}\omega)}{|Q(\mathrm{i}\omega)|^2},\\ \cos(\omega\tau)&=-\frac{P_\mathrm{I}(\mathrm{i}\omega)Q_\mathrm{I}(\mathrm{i}\omega)+P_\mathrm{R}(\mathrm{i}\omega)Q_\mathrm{R}(\mathrm{i}\omega)}{|Q(\mathrm{i}\omega)|^2},\end{aligned}\right\} \tag{3.11}$$

where $P(\mathrm{i}\omega)=P_\mathrm{R}(\mathrm{i}\omega)+\mathrm{i}P_\mathrm{I}(\mathrm{i}\omega)$, $Q(\mathrm{i}\omega)=Q_\mathrm{I}(\mathrm{i}\omega)+\mathrm{i}Q_\mathrm{I}(\mathrm{i}\omega)$ and $|Q(\mathrm{i}\omega)|^2\neq 0$ in view of assumption (ii) of proposition 3.1 (since $G(\mathrm{i}\omega,\tau)=Q(\mathrm{i}\omega,\tau)=0$ together imply that $P(\mathrm{i}\omega,\tau)=0$). Equation (3.11) can be written in the equivalent form as

$$\sin(\omega\tau)=\frac{\omega^2-c}{\omega b},\qquad \cos(\omega\tau)=\frac{a}{b}. \tag{3.12}$$

If ω satisfies (3.12), and consequently (3.5), then ω must satisfy

$$|P(\mathrm{i}\omega)|^2=|Q(\mathrm{i}\omega)|^2, \tag{3.13}$$

that is, ω must be a positive root of

$$F(\omega)=|P(\mathrm{i}\omega)|^2-|Q(\mathrm{i}\omega)|^2=0. \tag{3.14}$$

The zeros of $F(\omega)$ are roots of the equation

$$\omega^4-[b^2+2c-a^2]\omega^2+c^2=0$$

and are given by

$$\left.\begin{aligned}\omega_-^2&=\tfrac{1}{2}[(b^2+2c-a^2)-\sqrt{(b^2+2c-a^2)^2-4c^2}],\\ \omega_+^2&=\tfrac{1}{2}[(b^2+2c-a^2)+\sqrt{(b^2+2c-a^2)^2-4c^2}].\end{aligned}\right\} \tag{3.15}$$

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We now have the following.

PROPOSITION 3.2. *The number of different imaginary roots of (3.5) with positive (negative) imaginary parts can be zero, one or two only.*

Proof. If $a^2 = b^2$, the equation $F(\omega) = 0$ has only one positive root. But this is not possible since we are considering equilibria on L_{U} or on L_{S}, which implies that $a^2 + b^2 \neq 0$.

On the other hand, the following cases arise.

(I) Since $4c^2 > 0$, the equation $F(\omega) = 0$ has two positive roots ω_- and ω_+, with $0 < \omega_- < \omega_+$, provided that the following inequalities hold:

(i) $b^2 + 2c - a^2 > 0$,

(ii) $(b^2 + 2c - a^2)^2 > 4c^2$.

In this case, (3.5) has two imaginary roots.

(II) The equation $F(\omega) = 0$ has two negative roots, $\omega_- < \omega_+ < 0$, provided that the following conditions are true:

(i) $b^2 + 2c - a^2 < 0$,

(ii) $(b^2 + 2c - a^2)^2 > 4c^2$.

In this case, (3.5) has no imaginary roots with positive imaginary part.

(III) The equation $F(\omega) = 0$ has no roots if the following condition holds:

$$(b^2 + 2c - a^2)^2 < 4c^2.$$

In this case, (3.5) has no imaginary roots.

□

Thus, applying [17, theorem 3.1, p. 77], we have the following.

THEOREM 3.3. *The number of different imaginary roots with positive (negative) imaginary parts of (3.5) can be zero, one or two only.*

(I) *If there are no such roots, then the stability of each equilibrium (λ, ξ_1, ξ_2) on L_K does not switch for any $\tau \geqslant 0$.*

(II) *If there is one imaginary root of (3.5) with positive imaginary part, an unstable solution (λ, ξ_1, ξ_2) on L_K never becomes stable for any $\tau \geqslant 0$. If the solution is asymptotically stable for $\tau = 0$, then there exists a $\tau_0 > 0$ such that for all $\tau < \tau_0$ this solution is uniformly asymptotically stable, and is unstable for all $\tau > \tau_0$.*

(III) *If there are two imaginary roots with positive imaginary part, ω_+, ω_-, such that $0 < \omega_- < \omega_+$, then the stability of each equilibrium (λ, ξ_1, ξ_2) on L_K can change at most a finite number of times, as τ increases, and eventually becomes unstable.*

Proof. Since the first statement is proved in proposition 3.2 we need only prove the statements (II) and (III).

(I) Observe that if condition (III)(ii) of proposition 3.2 is satisfied, then (3.5) has no imaginary roots. Hence, there is no switch in stability of any equilibrium (λ, ξ_1, ξ_2) on L_K.

(II) Note that if $a^2 = b^2$, then, from proposition 3.2, (3.5) has only one imaginary root $\mu = \mathrm{i}\omega_0$, where ω_0 is the only positive root of (3.10); therefore, the only crossing of the imaginary axis at $\mathrm{i}\omega_0$ is from the left to the right as τ increases and passes through τ_0, where

$$\tau_0 = \frac{1}{\omega_0} \tan^{-1}\left(\frac{\omega_0^2 - c}{\omega_0 a}\right).$$

Clearly, this is not possible since $a \neq b$.

(III) Finally, from (I)(i) and (I)(ii) of proposition 3.2, the equation $F(\omega) = 0$ has two positive real roots, such that $0 < \omega_- < \omega_+$ only if conditions given in (I)(i) and (I)(ii) are satisfied. Therefore, (3.5) has two pure imaginary roots $\mu = \mathrm{i}\omega_-$ and $\mu = \mathrm{i}\omega_+$. Thus, in view of [17, theorem 3.1, p. 77] the stability of each equilibrium point (λ, ξ_1, ξ_2) on L_K can change at most a finite number of times as τ increases, and eventually becomes unstable. □

We now present a few corollaries of theorem 3.3.

COROLLARY 3.4. *Suppose that $E = (\lambda, \xi_1, \xi_2)$ on L_K is an equilibrium point of system (1.1) or, equivalently, of system (3.1). The following statements then hold.*

(i) *If E is stable (or unstable) for system (1.1) when $\tau = 0$, then stability switches may not occur for all $\tau \geqslant 0$.*

(ii) *If E is stable for system (1.1) when $\tau = 0$, we may have a $\tau_0 > 0$ such that E loses its stability when τ passes through τ_0.*

(iii) *If E is stable (or unstable) for system (1.1) when $\tau = 0$, we may have a finite number of stability switches for E as τ increases.*

Proof. The proof is an immediate consequence of theorem 3.3. □

COROLLARY 3.5. *For any fixed K satisfying $a_2 + 2\lambda \leqslant K \leqslant a_1 + 2\lambda$ there exists an equilibrium point $(\lambda, \xi_1(K), \xi_2(K))$, which splits L_K into two parts L_K^{U} and L_K^{S} (one of which may be empty); for $\tau = 0$, the equilibria of (1.1) on the set*

$$L_K^{\mathrm{U}} = \{(\lambda, \xi_1, \xi_2) \text{ on } L_K : \xi_1 < \xi_1(K)\}$$

are unstable and the equilibria on the set

$$L_K^{\mathrm{S}} = \{(\lambda, \xi_1, \xi_2) \text{ on } L_K : \xi_1 > \xi_1(K)\}$$

are stable. Furthermore, depending on the values of the parameters of system (1.1), the zip bifurcation phenomenon may or may not be preserved. In other words, the zip bifurcation is unsustainable.

Proof. Suppose that corollary 3.4(i) holds. In this case the *zip bifurcation phenomenon* is preserved, since for $a_2 + 2\lambda < K < a_1 + 2\lambda$ neither the stable part nor the unstable part of the line of equilibria L_K changes for all $\tau \geqslant 0$. On the other hand, if corollary 3.4(ii) holds, then the *zip bifurcation* is not sustained since for $a_2+2\lambda < K < a_1+2\lambda$ the unstable part of the line of equilibria L_K remains unstable for all $\tau \geqslant 0$, whereas the stable part becomes unstable for $\tau \geqslant \tau_0$. Furthermore, if corollary 3.4(iii) holds, a similar argument shows that the zip bifurcation is not sustained and in this case the switch can be from instability to stability. □

Remark 3.6. The above result is surprising since it shows that the zip bifurcation phenomenon cannot be sustained in the presence of a discrete delay in system (3.1). In [10,13] it was concluded that in a delay-free system the sustainability of the zip bifurcation is achieved in the presence of diffusion.

Remark 3.7. From the results of § 3 we know that if $a_1 > a_2$ and $\lambda < K < a_2+2\lambda$, all points on L_K are stable for system (3.1), and this means that both the r- and K-strategists may coexist. If time delay is introduced in this system for a fixed K, then, in view of corollary 3.4, there exists a $\tau_0 > 0$ such that for $\tau \geqslant \tau_0$ all stable points on L_K become unstable. On the other hand, if $K > a_1+2\lambda$ all points on L_K are unstable for system (3.1) and these points may become stable as τ increases from zero. This means that if the delay increases, the r- and K-strategists may live together again in the long run near a steady state, which is quite natural. Also, if $a_1 > a_2$ and $a_2+2\lambda < K < a_1+2\lambda$, the family of equilibria for system (3.1) on the line L_K undergoes a split resulting in unstable and stable parts. In this case, if time delay is introduced in the system for a fixed K, then corollary 3.4 guarantees that there exists a $\tau_0 > 0$ such that the stable part of L_K may become unstable for $\tau \geqslant \tau_0$, and hence all points on L_K are unstable. On the other hand, the unstable part of L_K may become stable as τ increases from zero, and hence all points on L_K are stable. This implies that if the time delay increases, the r- and K-strategists may come back to live together again. Finally, we know that if $K = a_1+2\lambda$, then all interior equilibria are unstable for system (3.1) and the only stable equilibrium is the endpoint of L_K in the (S, x_1)-plane, which means that at this value of the carrying capacity the K-strategist dies out. However, increasing τ from zero may yield that the unstable part of L_K becomes stable, implying that the r- and K-strategists may come back to coexistence again.

Theorem 3.8. *Suppose that (3.5) has a pair of simple and conjugate pure imaginary roots $\mu = \pm \mathrm{i}\omega(\tau_0)$, $\omega(\tau_0)$ real, for $\tau_0 \in R$, where*

$$\tau_0 = \frac{1}{\omega_0}\tan^{-1}\left(\frac{\omega_0^2 - c}{\omega_0 a}\right). \tag{3.16}$$

(i) *If $\omega(\tau_0) = \omega_+(\tau_0)$, then*

$$\frac{\mathrm{d}}{\mathrm{d}\tau}\operatorname{Re}\mu\bigg|_{\mu=\omega_+(\tau_0)} > 0,$$

since

$$2\omega_0^2 + a^2 + b^2 - 2c = 2b^2 + \sqrt{(b^2-a^2)^2 + 4c(b^2-a^2)} > 0.$$

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(i) *If* $\omega(\tau_0) = \omega_-(\tau_0)$, *then*

$$\frac{\mathrm{d}}{\mathrm{d}\tau}\operatorname{Re}\mu\bigg|_{\mu=\omega_+(\tau_0)} > 0 \quad \text{if } b^2 > \tfrac{1}{2}\sqrt{(b^2-a^2)^2+4c(b^2-a^2)}$$

and

$$\frac{\mathrm{d}}{\mathrm{d}\tau}\operatorname{Re}\mu\bigg|_{\mu=\omega_+(\tau_0)} < 0 \quad \text{if } b^2 < \tfrac{1}{2}\sqrt{(b^2-a^2)^2+4c(b^2-a^2)}.$$

Proof. To calculate $\mathrm{d}\operatorname{Re}\mu/\mathrm{d}\tau$, where $\mu(\tau) = \eta(\tau) + \mathrm{i}\omega(\tau)$, we use the implicit function theorem to determine the derivative of the function $\mu(\tau)$. Let $\mu = \mu(\tau)$ and consider that $G(\mu,\tau) = \mu^2 - a\mu + c + b\mathrm{e}^{-\mu\tau}\mu$. Thus, we have that

$$\frac{\mathrm{d}\mu}{\mathrm{d}\tau} = -\frac{\partial G(\mu,\tau)/\partial\tau}{\partial G(\mu,\tau)/\partial\mu} = \frac{b\mu(\tau)^2\mathrm{e}^{-\mu(\tau)\tau}}{(1-\mu(\tau)\tau)b\mathrm{e}^{-\mu(\tau)\tau} + 2\mu(\tau) - a} \tag{3.17}$$

or, similarly,

$$\begin{aligned}\frac{\mathrm{d}\mu}{\mathrm{d}\tau} &= \frac{b\omega^2\cos(\omega\tau)(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2} \\ &\quad - \frac{b\omega^2\sin(\omega\tau)(2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2} \\ &\quad + \mathrm{i}\bigg[\frac{b\omega^2\cos(\omega\tau)(2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2} \\ &\qquad - \frac{b\omega^2\sin(\omega\tau)(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2}\bigg].\end{aligned} \tag{3.18}$$

Therefore,

$$\begin{aligned}\eta'(\tau) &= \frac{b\omega^2(b - a\cos(\omega\tau) - 2\omega\sin(\omega\tau))}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2} \\ &= \frac{(a^2+b^2)/b - 2(c-\omega_0^2)/b}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2} \\ &= \frac{1}{b}\frac{2\omega^2 + a^2 + b^2 - 2c}{(b\cos(\omega\tau) - b\tau\omega\sin(\omega\tau) - a)^2 + (2\omega - b\sin(\omega\tau) - b\tau\omega\cos(\omega\tau))^2},\end{aligned} \tag{3.19}$$

where the last equality follows from (3.12).

Using (3.15) in (3.19) we see that $\eta'(\tau_{0_+}) > 0$, since

$$2\omega_0^2 + a^2 + b^2 - 2c = 2b^2 + \sqrt{(b^2-a^2)^2 + 4c(b^2-a^2)} > 0.$$

On the other hand, $\eta'(\tau_{0_-}) > 0$ if

$$b^2 > \tfrac{1}{2}\sqrt{(b^2-a^2)^2+4c(b^2-a^2)} \tag{3.20}$$

and $\eta'(\tau_{0_-}) < 0$ if

$$b^2 < \tfrac{1}{2}\sqrt{(b^2-a^2)^2+4c(b^2-a^2)}. \tag{3.21}$$

□

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REMARK 3.9. We can define the angle $\theta(\tau) \in [0, 2\pi)$ as the solution of (3.12):

$$\sin\theta(\tau) = \frac{\omega^2 - c}{\omega b}, \qquad \cos\theta(\tau) = \frac{a}{b}. \tag{3.22}$$

Also, the relation between the arguments $\theta(\tau)$ in (3.22) and $\tau\omega(\tau)$ in (3.12) must be

$$\tau\omega(\tau) = \theta(\tau) + 2n\pi,$$

and then we obtain the following two sets of values of τ, for which there are imaginary roots:

$$\tau_{n,1} = \frac{\theta_1}{\omega_+} + \frac{2n\pi}{\omega_+} \quad \text{and} \quad \tau_{n,2} = \frac{\theta_2}{\omega_-} + \frac{2n\pi}{\omega_-}, \tag{3.23}$$

with $\theta_1, \theta_2 \in [0, 2\pi)$, $n = 0, 1, 2, \dots$.

REMARK 3.10. In part (II) of theorem 3.3, only $\tau_{0,1}$ need be considered, since the equilibrium (λ, ξ_1, ξ_2) on L_K that is stable for $\tau = 0$ remains stable up to $\tau_{0,1}$ and is unstable thereafter.

REMARK 3.11. In part (III) of theorem 3.3 if the equilibrium (λ, ξ_1, ξ_2) on L_K is stable for $\tau = 0$, then it follows that $\tau_{0,1} < \tau_{0,2}$, that is, the multiplicity of roots with positive real parts cannot become negative, since $\eta'(\tau_0) > 0$.

REMARK 3.12. With the notation $\tau_{0_+} = \tau_{0,1}$ and $\tau_{0_-} = \tau_{0,2}$, if (3.5) has a pair of simple and conjugate pure imaginary roots $\mu = \pm i\omega(\tau_{0_\pm})$, $\omega(\tau_{0_\pm})$ real, at $\tau_{0_\pm} \in R$, then crossing from left to right as τ increases occurs at $\tau = \tau_{0_+}$, and crossing from right to left occurs at $\tau = \tau_{0_-}$, corresponding to ω_- if inequality (3.20) (respectively, for left to right, (3.21)) is satisfied, in view of [1, theorem 4.1, p. 1157]. Furthermore, if we treat (λ, ξ_1, ξ_2) on L_K as an isolated equilibrium, then each such equilibrium in L_K undergoes a Hopf-like bifurcation at $\tau_{0_\pm}$.

REMARK 3.13. Observe that

$$\tau_{n+1,1} - \tau_{n,1} = \frac{2\pi}{\omega_+} < \frac{2\pi}{\omega_-}\tau_{n+1,2} - \tau_{n,2}. \tag{3.24}$$

Therefore, if the equilibrium (λ, ξ_1, ξ_2) on L_K is stable for $\tau = 0$, there can be only a finite number of switches between stability and instability. However, there exists a value of τ, say $\tau = \hat{\tau}$, such that at $\tau = \hat{\tau}$ a stability switch occurs from stability to instability, and for $\tau > \hat{\tau}$ the solution remains unstable. On the other hand, if the equilibrium (λ, ξ_1, ξ_2) on L_K is unstable for $\tau = 0$, then a similar argument as before can be made. As τ increases, the multiplicity of roots for which $\operatorname{Re}\mu > 0$ increases by two whenever τ passes through a value $\tau_{n,1}$, and decreases by two whenever τ passes through a value $\tau_{n,2}$.

REMARK 3.14. When the equilibrium (λ, ξ_1, ξ_2) on L_K is stable for $\tau = 0$, k switches from stability to instability, and vice versa, can occur when the parameters satisfy the inequality

$$\tau_{0,1} < \tau_{0,2} < \tau_{1,1} < \cdots < \tau_{k-1,1} < \tau_{k-1,2} < \tau_{k,1} < \tau_{k+1,1} < \tau_{k,2} \cdots,$$

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or k switches from instability to stability, and vice versa, *may* occur when the parameters are such that

$$\tau_{0,2} < \tau_{0,1} < \tau_{1,2} < \cdots < \tau_{k-1,2} < \tau_{k-1,1} < \tau_{k,1} < \tau_{k,2} \cdots .$$

Remark 3.15. Consider system (1.1) restricted to the (S, x_1)-plane, which we denote by

$$\Omega_1 = \{(S, x_1, x_2) \in \mathbb{R}^3 \mid x_2 = 0\}.$$

Let $E_1 = (\lambda, \xi_1, 0)$ on L_K be an *isolated* equilibrium solution of system (2.4) on Ω_1. Note that $(\lambda, \xi_1, 0)$ satisfies the equation

$$\frac{m_1 a_1}{a_1 + \lambda}\xi_1 = \gamma\left(1 - \frac{\lambda}{K}\right). \tag{3.25}$$

In view of (3.25), the variational system that corresponds to (E_1) is given by

$$\begin{bmatrix} S(t) \\ x_1(t) \end{bmatrix}' = \begin{bmatrix} \lambda\dfrac{m_1}{(a_1+\lambda)^2}\xi_1 & -\dfrac{m_1}{a_1+\lambda}\lambda \\ \dfrac{\beta_1\xi_1}{a_1+\lambda} & 0 \end{bmatrix} \begin{bmatrix} S(t) \\ x_1(t) \end{bmatrix} + \begin{bmatrix} -\dfrac{\gamma}{K}\lambda & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} S(t-\tau) \\ x_1(t-\tau) \end{bmatrix}$$

and the characteristic equation associated with the isolated equilibrium (E_1) on L_K is

$$\mu^2 - \lambda\frac{m_1\xi_1}{(a_1+\lambda)^2}\mu + \lambda\frac{m_1\beta_1\xi_1}{(a_1+\lambda)^2} + \frac{\lambda\gamma}{K}\mathrm{e}^{-\mu\tau}\mu = 0$$

or, equivalently,

$$\mu^2 - a\mu + c + b\mathrm{e}^{-\mu\tau}\mu = 0, \tag{3.26}$$

in which

$$a = \lambda\frac{m_1\xi_1}{(a_1+\lambda)^2}, \qquad b = \frac{\lambda\gamma}{K} \quad \text{and} \quad c = \lambda\frac{m_1\beta_1\xi_1}{(a_1+\lambda)^2}.$$

Analysing (3.26), as has been done in § 4, one can obtain similar results for the isolated equilibrium $E_1 = (\lambda, \xi_1, 0)$ on L_K. Accordingly, we may conclude that the equilibrium E_1 undergoes a Hopf bifurcation when τ increases and passes through $\tau_{0_\pm}$. Similar results can also be derived with respect to the equilibrium $E_2 = (\lambda, 0, \xi_2)$ on L_K belonging to the set

$$\Omega_2 = \{(S, x_1, x_2) \in \mathbb{R}^3 \mid x_1 = 0\}.$$

The following simulations conducted in Matlab highlight the analytical results obtained for system (1.1) in the case where the zip bifurcation is unsustainable.

We first present a few simulations that illustrate the dynamics of the time-delay system (1.1). We choose the following values for the parameters in system (1.1): $m_1 = 0.6$, $m_2 = 0.3$, $d_1 = 0.3$, $d_2 = 0.2$, $\beta_1 = 0.3$, $\beta_2 = 0.1$, $\gamma = 46$, $a_2 = 1$, $a_1 = 2$, $\lambda = 2$ and $K = 5.5$. Using (3.16) and corollary 3.5, we find that the stable equilibrium (λ, ξ_1, ξ_2) on the line L_K is stable for all values of τ satisfying $0 \leqslant \tau \leqslant \tau_1 = 0.04163939054$ and is unstable for $\tau > \tau_1$ (figure 3). This confirms the unsustainability of the zip bifurcation when $\tau > \tau_1$. It is clear from figure 3 that $\tau = 0.03$ (black line) represents the stable behaviour of S and that for $\tau = 0.04$

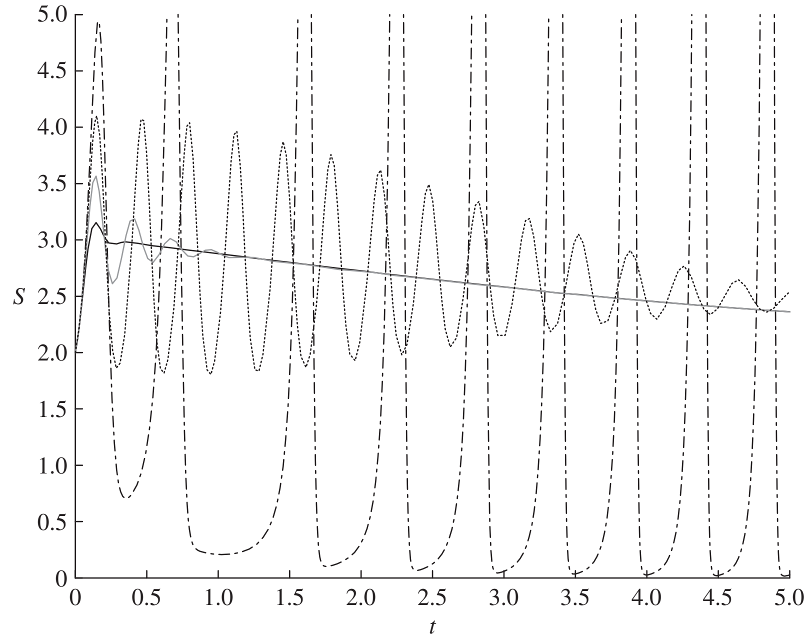

Figure 3. Unsustainable zip bifurcation.

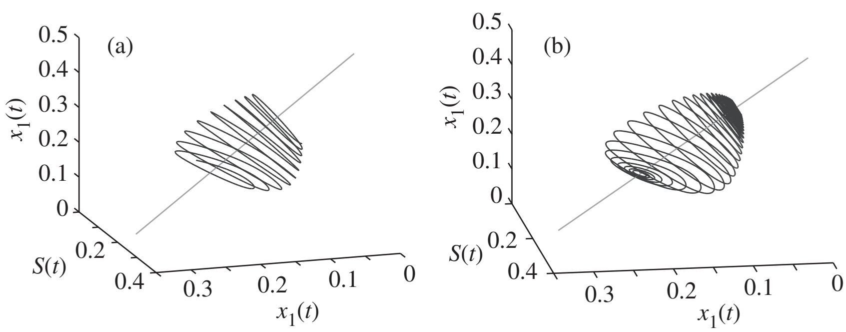

Figure 4. Hopf-like bifurcation: there exists an $\varepsilon > 0$ such that any solution (black line) that stays in an ε-neighbourhood of the equilibrium line L_K (grey line) for all positive or negative times (or possibly both) converges to a single equilibrium on L_K.

(grey line) S loses stability, since this value of τ is nearer to τ_1. Also, for $\tau = 0.05$ and 0.06, S increasingly tends towards instability (dotted and dash-dotted lines, respectively).

Remark 3.16. We remark that, for $\tau = 0.01$, the choice of $m_1 = 0.6$, $m_2 = 0.7$, $d_1 = 0.3$, $d_2 = 0.2$, $\beta_1 = 0.3$, $\beta_2 = 0.5$, $\gamma = 0.8$, $a_1 = 0.16$, $a_2 = 0.4$, $\lambda = 0.16$ and $K = 0.6$ leads us to figure 4, in which all non-equilibrium trajectories starting sufficiently close to the equilibrium line L_K (grey line) are heteroclinic between equilibria on opposite sides of $(\lambda, \xi_1(K), \xi_2(K))$. From figure 4 it is clear that Hopf bifurcation takes place, that is, there exists an $\varepsilon > 0$ such that any solution (black

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line) that stays in an ε-neighbourhood of the equilibrium line L_K (grey line) for all positive or negative times (or possibly both) converges to a single equilibrium on L_K. This numerical experiment confirms the presence of another interesting phenomenon not discussed earlier for this model. Accordingly we have the following.

Conjecture 3.17. *In view of remark 3.16, we conjecture that for system (1.1) when* $\tau = 0.01$ *the equilibria on the line* L_K *undergo a Hopf-type bifurcation. That is, all non-equilibrium trajectories starting sufficiently close to* L_k *are heteroclinic between the equilibria on the stable and unstable parts of* L_K.

In figure 4 we see that the orbits emanating from the unstable part of the line L_K move to the stable part. It appears that the K-strategist loses its ground during the competition and this strengthens the survival of the r-strategist.

4. The model with diffusion

Spatial ecology addresses the fundamental effects of space on the dynamics of individual species and on the structure, dynamics, diversity and stability of multi-species communities. Essentially, this subject is designed to highlight the importance of space in the areas of stability, patterns of diversity, invasions, coexistence and pattern generation. The mathematical formulation of the ideas dealing with the spacial aspect of species leads to reaction–diffusion models. For a more interesting account of various aspects and examples in population ecology we refer the reader to [20]. We are particularly interested in the study of the stability of isolated equilibrium populations, wherein we assume that the prey and predators are diffusing in a domain $\Omega \subset \mathbb{R}^N$ $(N = 1, 2, 3)$, an open, connected and bounded set with smooth boundary $\partial\Omega$. So as to ensure that the equilibrium is isolated and corresponds to that of the related ordinary differential equation model, we invoke the Neumann boundary conditions. Due to the limited resources, the growth rate of population will slow down, and the population may saturate to a maximum level. Thus, it is natural to use a density-dependent growth rate per capita, that is, the logistic growth rate. Other studies for this kind of model can be found in [3–5, 16, 21]. Together with the diffusion of the species, the reaction–diffusion model studied in this section is represented by the following partial differential equation (PDE) system:

$$\left.\begin{aligned} \frac{\partial S}{\partial t}(x,t) &= \delta_0 \Delta S(t,x) + \gamma\left(1 - \frac{S(t-\tau,x)}{K}\right)S(t,x) \\ &\qquad - \sum_{i=1}^{2} m_i f_i(S(t,x))u_i(t,x) \quad \text{on } \Omega \times (0,\infty), \\ \frac{\partial u_i}{\partial t}(x,t) &= \delta_i \Delta u_i(t,x) + (m_i f_i(S(t,x)) - d_i)u_i(t,x), \\ &\qquad i = 1,2, \quad \text{on } \Omega \times (0,\infty), \end{aligned}\right\} \tag{4.1}$$

where we assume that the functions S and u_i satisfy the Neumann boundary conditions

$$\frac{\partial S}{\partial \nu} = 0, \quad \frac{\partial u_i}{\partial \nu} = 0, \quad i = 1,2, \text{ on } \partial\Omega \times (0,\infty), \tag{4.2}$$

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$\nu = \boldsymbol{\nu}(x)$ denotes the outer unit normal to $\partial\Omega$, $\Delta = \sum_{j=1}^{N}\partial/\partial x_j$ is the Laplacian operator, S is the population density of the prey, u_i, $i = 1, 2$, are the population densities of the ith predator competing for prey and $\delta_i > 0$, $i = 1, 2$, are the diffusion rates. Here, K represents the carrying capacity of the environment that depends on the state x. In this case the environment is regarded as homogeneous. The remaining parameters are the same as in system (1.1). Positivity and global existence of the solutions for (4.1) and (4.2), when $\tau = 0$, have been studied in [13].

Following the arguments of § 2, we may conclude that the constant solutions of (4.1) and (4.2) are

$$(S, u_1, u_2) = (0, 0, 0), \qquad (S, u_1, u_2) = (K, 0, 0),$$

and the points on the straight line segment

$$L_K = \biggl\{(S, u_1, u_2) \in \mathbb{R}^3;\ S = \lambda, u_1 \geqslant 0, u_2 \geqslant 0 \text{ and } m_1\frac{S}{a_1 + S}u_1 + m_2\frac{S}{a_2 + S}u_2 = \gamma\biggl(1 - \frac{\lambda}{K}\biggr)\biggr\} \tag{4.3}$$

in the positive octant of (S, u_1, u_2)-space are equilibria, provided we assume that

$$m_i > d_i \quad \text{for } i = 1, 2 \qquad \text{and} \qquad \frac{a_1 d_1}{m_1 - d_1} = \frac{a_2 d_2}{m_2 - d_2}.$$

To study the stability of these equilibria, let $E = (S^*, u_1^*, u_2^*)$ be a constant solution of (4.1) and (4.2). Thus, the variational system of (4.1) and (4.2) corresponding to E is given by

$$\left.\begin{aligned} \frac{\partial S(x,t)}{\partial t} &= \delta_0\Delta S + \biggl[\gamma\biggl(1 - \frac{S^*}{K}\biggr) - \sum_{i=1}^{n} m_i\frac{a_i}{(a_i + S^*)^2}u_i^*\biggr]S(t,x) \\ &\qquad - \sum_{i=1}^{2}\frac{m_i S^*}{a_i + S^*}u_i(t,x) - \frac{\gamma\lambda}{K}S(t - \tau, x), \\ \frac{\partial u_i(x,t)}{\partial t} &= \delta_i\Delta u_i + \frac{\beta_i u_i^*}{a_i + S^*}u_i(t,x), \quad i = 1, 2, \text{ on } \Omega \times (0, \infty). \end{aligned}\right\} \tag{4.4}$$

Let $0 = \mu_0 < \mu_1 < \mu_2 < \cdots \to \infty$ and $\{\psi_k\}_{k=0}^{\infty}$ be the eigenvalues and eigenfunctions, respectively, of the Laplacian operator in Ω with Neumann boundary conditions on $\partial\Omega$:

$$\left.\begin{aligned} \Delta\psi_k &= \lambda_k\psi_k \quad \text{in } \Omega, \\ \frac{\partial\psi_k}{\partial\nu} &= 0 \qquad \text{on } \partial\Omega. \end{aligned}\right\} \tag{4.5}$$

Without loss of generality, we suppose that $\{\psi_k\}_{k=0}^{\infty}$ is an orthonormal basis for $L^2(\Omega)$.

Let $w = (S, u_1, u_2)$, let $D = \operatorname{diag}(\delta_0, \delta_1, \delta_2)$ and let J be the matrix

$$J = \begin{pmatrix} \lambda \sum_{i=1}^{2} \dfrac{m_i}{(a_i + S^*)^2} u_i^* - \dfrac{\gamma S^*}{K} \mathrm{e}^{-\tau\nu} & -\dfrac{m_1 S^*}{a_1 + S^*} & -\dfrac{m_2 S^*}{a_2 + S^*} \\ \dfrac{\beta_1 u_1^*}{a_1 + S^*} & 0 & 0 \\ \dfrac{\beta_2 u_2^*}{a_2 + S^*} & 0 & 0 \end{pmatrix}.$$

Then, (4.4) can be written as

$$\frac{\partial w}{\partial t} = D\Delta w + Jw;$$

hence, the solution of (4.2) and (4.4) with initial condition $w(\cdot, 0) = w_0$ is given by

$$w(x,t) = \sum_{k=0}^{\infty} \mathrm{e}^{(J - \mu_k D)t} \langle w_0, \psi_k \rangle \psi_k(x), \tag{4.6}$$

where

$$\langle w_0, \psi_k \rangle = \int_{\Omega} w_0(x) \psi_k(x) \, \mathrm{d}x.$$

It follows from the linearization principle that a 'non-trivial' homogeneous solution of (4.1) and (4.2) is asymptotically stable if all the eigenvalues of the matrix $J - \mu_k D$ have negative real parts, and if there exists a $k \geqslant 0$ such that $J - \mu_k D$ has an eigenvalue with positive real part, then the solution is unstable.

(1) At $E = (0, 0, 0)$ the linearized system has the form

$$\left.\begin{aligned} \frac{\partial S(x,t)}{\partial t} &= \delta_0 \Delta S(t,x) + \gamma S(t,x), \\ \frac{\partial u_1(x,t)}{\partial t} &= \delta_1 \Delta u_1(t,x) - \beta_1 \frac{\lambda}{a_1} u_1(t,x), \\ \frac{\partial u_2(x,t)}{\partial t} &= \delta_2 \Delta u_2(t,x) - \beta_2 \frac{\lambda}{a_2} u_2(t,x) \quad \text{on } \Omega \times (0, \infty), \end{aligned}\right\} \tag{4.7}$$

with boundary conditions (4.2).

Thus, the characteristic equation is given by

$$(\nu - \gamma + \mu_k \delta_0) \left(\mu + \beta_1 \frac{\lambda}{a_1} + \mu_k \delta_1 \right) \left(\mu + \beta_1 \frac{\lambda}{a_1} + \mu_k \delta_2 \right) = 0.$$

Note that for $k = 0$ we have $\mu_0 = 0$; therefore, system (4.4) has the same coefficient matrix at $(0, 0, 0)$ as system (2.5), which has an eigenvalue with positive real part. Hence, the equilibrium $(0, 0, 0)$ is unstable.

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(2) At $E = (K, 0, 0)$ the linearized system has the form

$$\left.\begin{aligned}\frac{\partial S(x,t)}{\partial t} &= \delta_0 \Delta S(t,x) - \frac{m_1 K}{a_1 + K} u_1(t,x) - \frac{m_2 K}{a_2 + K} u_2(t,x) - \gamma S(t-\tau),\\ \frac{\partial u_1(x,t)}{\partial t} &= \delta_1 \Delta u_1(t,x) + \beta_1 \frac{K-\lambda}{a_1+K} u_1(t,x),\\ \frac{\partial u_2(x,t)}{\partial t} &= \delta_2 \Delta u_2(t,x) + \beta_2 \frac{K-\lambda}{a_2+K} u_2(t,x) \quad \text{on } \Omega \times (0,\infty),\end{aligned}\right\} \tag{4.8}$$

with boundary conditions (4.2).

Thus, the characteristic equation is given by

$$(\upsilon + \gamma \mathrm{e}^{-\upsilon\tau} + \mu_k \delta_0)\left(\beta_1 \frac{K-\lambda}{a_1+K} - \mu_k \delta_1 - \upsilon\right)\left(\beta_2 \frac{K-\lambda}{a_2+K} - \mu_k \delta_2 - \upsilon\right) = 0$$

or, equivalently,

$$\upsilon^3 + (\alpha - \mu_k \delta_0)\upsilon^2 + (\beta - \alpha\mu_k\delta_0)\upsilon - \mu_k\delta_0\beta = H\mathrm{e}^{-\upsilon\tau}[\upsilon^2 + \alpha\upsilon + \beta]. \tag{4.9}$$

Now, proceeding as in § 2, we find the following coefficients for $F(z)$ given by (2.16):

$$\left.\begin{aligned}A_1 &= (\alpha - \mu_k\delta_0)^2 - 2(\beta - \alpha\mu_k\delta_0) - H^2,\\ A_2 &= (\beta - \alpha\mu_k\delta_0)^2 + 2H^2(\beta - \alpha\mu_k\delta_0) - H^2(\beta - \alpha\mu_k\delta_0)^2,\\ A_3 &= -\mu_k\delta_0 - H^2\beta^2.\end{aligned}\right\} \tag{4.10}$$

Letting $N = 18A_1A_2A_3 - 4A_1^3A_3 + A_1^2A_2^2 - 4A_2^3 - 27A_3^2$, consider the following hypotheses:

($\bar{\mathrm{H}}$1) (i) $A_1 \geqslant 0$, $A_2 \geqslant 0$, $A_3 > 0$,

(ii) $A_1 > 0$, $A_2 < 0$, $A_3 > 0$ and $\kappa > 2\rho^{3/2}$,

(iii) $A_1 \leqslant 0$, $A_2 \leqslant 0$,

(iv) $A_3 > 0$ and $N < 0$,

here $\kappa = 2A_1^3 - 9A_1A_2 + 27A_3$ and $\rho = A_1^2 - 3A_2$. Note that ($\bar{\mathrm{H}}$1) gives conditions for no change in the stability of $E = (K, 0, 0)$, that is, if E is stable (unstable) at $\tau = 0$, then it remains stable (unstable) for all values of $\tau \geqslant 0$ whenever ($\bar{\mathrm{H}}$1) holds.

Consider the following:

($\bar{\mathrm{H}}$2) (i) $A_1 \geqslant 0$, $A_2 \geqslant 0$, $A_3 < 0$,

(ii) $A_1 \geqslant 0$, $A_2 \leqslant 0$, $A_3 < 0$,

(iii) $A_1 \leqslant 0$, $A_2 \leqslant 0$, $A_3 < 0$,

(iv) $A_1 < 0$, $A_2 > 0$ and $N < 0$.

These conditions imply that, if $E = (K, 0, 0)$ is unstable for any $\tau = \tau^* \geqslant 0$, then it will be unstable for all $\tau \geqslant \tau^*$.

Consider the equation

$$z^3 + A_1z^2 + A_2z + A_3 = 0,$$

when $N > 0$ and any of the following conditions hold:

($\bar{\text{H}}3$) (i) $A_1 \geqslant 0$, $A_2 < 0$ and $A_3 > 0$,
(ii) $A_1 < 0$, $A_2 \geqslant 0$ and $A_3 > 0$,
(iii) $A_1 \leqslant 0$, $A_2 \leqslant 0$,
(iv) $A_1 < 0$, $A_2 < 0$ and $A_3 > 0$ and

($\bar{\text{H}}4$) (i) $A_1 < 0$, $A_2 < 0$, $A_3 < 0$ and $N > 0$.

If either ($\bar{\text{H}}3$) or ($\bar{\text{H}}4$) holds, following the arguments in [14], we see that the stability of $E = (K, 0, 0)$ cannot be preserved. Thus, we have the following theorem.

Theorem 4.1.

(i) *Assume that the conditions in* ($\bar{\text{H}}1$) *hold. If the equilibrium* $E = (K, 0, 0)$ *is stable (unstable) at* $\tau = 0$*, then* E *remains stable (unstable) for all* $\tau \geqslant 0$*.*

(ii) *Assume that the conditions in* ($\bar{\text{H}}2$) *hold. Then* $E = (K, 0, 0)$ *is unstable for all* $\tau \geqslant 0$*.*

(iii) *Assume that the conditions in either* ($\bar{\text{H}}3$) *or* ($\bar{\text{H}}4$) *hold. As* τ *increases, stability switches may occur.*

(3) At $E = (\lambda, \xi_1, \xi_2)$ on L_K the linearized system has the form

$$\left.\begin{aligned} \frac{\partial S(x,t)}{\partial t} &= \delta_0 \Delta S + \left[\gamma\left(1 - \frac{\lambda}{K}\right) - \sum_{i=1}^{n} m_i \frac{a_i}{(a_i+\lambda)^2}\xi_i\right] S(t,x) \\ &\qquad - \sum_{i=1}^{2} \frac{m_i \lambda}{a_i + \lambda} u_i(t,x) - \frac{\gamma\lambda}{K} S(t-\tau, x), \\ \frac{\partial u_i(x,t)}{\partial t} &= \delta_i \Delta u_i + \frac{\beta_i \xi_i}{a_i + \lambda} u_i(t,x), \quad i = 1,2, \text{ on } \Omega \times (0,\infty), \end{aligned}\right\} \tag{4.11}$$

with boundary conditions (4.2). In the following we study the stability of $E = (\lambda, \xi_1, \xi_2)$, when $\tau = 0$ and $\tau > 0$.

4.1. Stability of the equilibrium points in the case $\tau = 0$

Note that in the case of no delay the corresponding PDE model with different diffusion coefficients was first studied in [13], and it is described by the system

$$\left.\begin{aligned} \frac{\partial S}{\partial t}(x,t) &= \delta_0 \Delta S + \gamma\left(1 - \frac{S(t,x)}{K}\right) S(t,x) - \sum_{i=1}^{2} m_i f_i(S(t,x)) u_i(t,x) \\ &\qquad\qquad \text{on } \Omega \times (0,\infty), \\ \frac{\partial u_i}{\partial t}(x,t) &= \delta_i \Delta u_i + (m_i f_i(S(t,x)) - d_i) u_i, \quad i = 1,2, \text{ on } \Omega \times (0,\infty). \end{aligned}\right\} \tag{4.12}$$

The characteristic polynomial $P_k(\nu)$ of $J - \mu_k D$, where J is the Jacobian matrix of (4.12) evaluated at $E = (\lambda, \xi_1, \xi_2)$, is given by

$$P_k(\nu) = \nu^3 + \bar{A}_k \nu^2 + \bar{B}_k \nu + \bar{C}_k, \tag{4.13}$$

where

$$\bar{A}_k = \mu_k(\delta_0+\delta_1+\delta_2) - \bar{a},$$
$$\bar{B}_k = \mu_k^2(\delta_0\delta_1+\delta_0\delta_2+\delta_1\delta_2) - \bar{a}\mu_k(\delta_1+\delta_2) - \bar{b}d - e\bar{c},$$
$$\bar{C}_k = \mu_k^3\delta_0\delta_1\delta_2 - \bar{a}\mu_k^2\delta_1\delta_2 - \mu_k(e\bar{c}\delta_1 + \bar{b}d\delta_2),$$
$$\bar{a} = \lambda\sum_{i=1}^{2}\frac{m_i\xi_i}{(a_i+\lambda)^2} - \frac{\gamma\lambda}{K}, \qquad \bar{b} = \frac{\beta_1\xi_1}{a_1+\lambda}, \qquad \bar{c} = \frac{\beta_2\xi_2}{a_2+\lambda},$$
$$d = -\frac{m_1\lambda}{a_1+\lambda}, \qquad e = -\frac{m_2\lambda}{a_2+\lambda}.$$

If $\lambda < K < a_2 + 2\lambda$, $\bar{a} < 0$, $\bar{b}d < 0$ and $e\bar{c} < 0$, then $\bar{A}_k > 0$, $\bar{B}_k > 0$ and $\bar{C}_k \geqslant 0$ for all $k \geqslant 0$. Hence, the polynomial $P_k(\nu)$ is stable independently of the diffusion matrix $D = \operatorname{diag}(\delta_0, \delta_1, \delta_2)$. The following result may be found in [13].

THEOREM 4.2. *Suppose that E is an equilibrium of (4.2)–(4.12) independent of x. If E is stable for the flow of (3.1), then E is stable for the flow of (4.2)–(4.12) independently of $D = \operatorname{diag}(\delta_0, \delta_1, \delta_2)$.*

As a consequence, if $\lambda < K < a_2 + 2\lambda$, the line of equilibrium points L_K of (3.1) is asymptotically stable for the flow of (4.2)–(4.12). If $a_2 + 2\lambda < K < a_1 + 2\lambda$, let $(\xi_1(K), \xi_2(K))$ be the unique solution of the system consisting of [6, (3.1), (3.4)]. Then, the following theorem due to Ferreira and Oliveira [13] also holds.

THEOREM 4.3. *For any K satisfying $a_2 + 2\lambda \leqslant K \leqslant a_1 + 2\lambda$, the point given by $(\lambda, \xi_1(K), \xi_2(K))$ splits L_K into two parts L_K^{U} and L_K^{S}; the equilibria of (4.2)–(4.12) in the set*

$$L_K^{\mathrm{U}} = \{(\lambda, \xi_1, \xi_2) \text{ on } L_K : \xi_1 < \xi_1(K)\}$$

are unstable, and those in the set

$$L_K^{\mathrm{S}} = \{(\lambda, \xi_1, \xi_2) \text{ on } L_K : \xi_1 > \xi_1(K)\}$$

are stable, independently of the diffusion matrix $D = \operatorname{diag}(\delta_0, \delta_1, \delta_2)$.

Therefore, the result given in theorem 4.2 shows that the zip bifurcation phenomenon may be preserved by the introduction of a diagonal diffusion matrix D in model (3.1), independent of the domain Ω.

4.2. Stability of the equilibrium points in the case $\tau \neq 0$

To study the stability of the equilibria on L_K, we consider $\lambda < K < a_2 + 2\lambda$, with a fixed K. The quasi-polynomial for E has a similar structure to that given by (4.13) for the case $\tau \neq 0$ and, accordingly, we have that

$$P(\nu) = \tilde{P}_3(\nu, \tau) + \tilde{Q}_2(\nu, \tau)\mathrm{e}^{-\tau\nu}, \tag{4.14}$$

where

$$\tilde{P}_3(\nu, \tau) = P_k(\nu) = \nu^3 + \bar{D}_k\nu^2 + \bar{E}_k\nu + \bar{G}_k \tag{4.15}$$

and

$$\tilde{Q}_2(\nu,\tau) = \frac{\gamma\lambda}{K}(\nu^2 + [\delta_1+\delta_2]\nu + \delta_1\delta_2\mu_k) \tag{4.16}$$

are analytic functions in the right half-plane and satisfy the following conditions:

(1) $\tilde{P}_3(0,\tau) + \tilde{Q}_2(0,\tau) \neq 0$ for all $\tau \in R$,

(2) If $\nu = \mathrm{i}\omega$, $\omega > 0$, then $\tilde{P}_3(\mathrm{i}\omega,\tau) + \tilde{Q}_2(\mathrm{i}\omega,\tau) \neq 0$, $\tau \in R$,

(3) $\limsup\{|\tilde{Q}_2(\nu,\tau)/\tilde{P}_3(\nu,\tau)|;\ |\nu| \to \infty,\ \mathrm{Re}\,\nu \geqslant 0\} < 1$,

(4) $\tilde{F}(\omega,\tau) = |\tilde{P}_3(\mathrm{i}\omega,\tau)|^2 - |\tilde{Q}_2(\mathrm{i}\omega,\tau)|^2$ has a finite number of zeros.

As we know from § 3, for a stability switch one needs to examine the existence of real roots of the equation $\tilde{F}(\omega,\tau) = 0$, in which

$$\left.\begin{aligned} \tilde{F}(\omega,\tau) &= |\tilde{P}_3(\mathrm{i}\omega,\tau)|^2 - |\tilde{Q}_2(\mathrm{i}\omega,\tau)|^2 \\ &= \omega^6 + \left(\bar{D}_k^2 - 2\bar{E}_k - \frac{\gamma^2\lambda^2}{K^2}\right)\omega^4 + \left[\bar{E}_k + 2\delta_1\delta_2\mu_k\frac{\gamma^2\lambda^2}{K^2} - (\delta_1+\delta_2)^2\right]\omega^2 \\ &\quad + \bar{G}_k^2 - \frac{\gamma^2\lambda^2}{K^2}\delta_1^2\delta_2^2\mu_k^2 \\ &= \omega^6 + A\omega^4 + B\omega^2 + C, \end{aligned}\right\} \tag{4.17}$$

where

$$\begin{aligned} A &= \bar{D}_k^2 - 2\bar{E}_k - \frac{\gamma^2\lambda^2}{K^2}, \\ B &= \bar{E}_k + 2\delta_1\delta_2\mu_k\frac{\gamma^2\lambda^2}{K^2} - (\delta_1+\delta_2)^2, \\ C &= \bar{G}_k^2 - \frac{\gamma^2\lambda^2}{K^2}\delta_1^2\delta_2^2\mu_k^2. \end{aligned}$$

Applying the change of variable $z = \omega^2$, we can write (4.17) in the form

$$\tilde{F}(z,\tau) = z^3 + Az^2 + Bz + C. \tag{4.18}$$

Then, to obtain a stability switch one has to examine the existence of positive real roots of the equation $F(z,\tau) = 0$. A stability switch may occur only if $\tilde{F}(z,\tau)$ has a positive real root.

Proceeding again as in § 2 and defining the coefficients for $F(z)$ as

$$A_1 = A, \qquad A_2 = B, \qquad A_3 = C,$$

we have the following.

Theorem 4.4.

(i) *Assume that the conditions in* ($\bar{\mathrm{H}}$1) *hold. If the equilibrium* E *is stable (unstable) at* $\tau = 0$*, then* E *remains stable (unstable) for all* $\tau \geqslant 0$.

(ii) *Assume that the conditions in* ($\bar{\mathrm{H}}$2) *hold. Then* E *is unstable for all* $\tau \geqslant 0$.

(iii) *Assume that the conditions in either* ($\bar{\mathrm{H}}$3) *or* ($\bar{\mathrm{H}}$4) *hold. As* τ *increases, stability switches may occur.*

REMARK 4.5. Note that if theorem 4.4(i) holds, then the zip bifurcation phenomenon sustains. On the other hand, if (iii) holds, the phenomenon may not sustain.

5. Discussion

We have studied a three-dimensional predator–prey model in which two predator species compete for a single prey. In the absence of predation the prey species population follows logistic growth dynamics with carrying capacity K. A discrete delay is considered for the predator population. The functional responses of the predators are of Holling II type, that is, the increase in the prey population leads to an increase in the predator efficiency for relatively low prey abundance.

It is observed that, in the absence of time delay, the trivial equilibrium is unstable, whereas the non-trivial isolated equilibrium is stable for a certain range of values of the carrying capacity, and for other values it is unstable. Furthermore, there exists a continuum of equilibria in the interior of the positive octant that exhibit the phenomenon of zip bifurcation. Now, for the time-delay model, the trivial equilibrium is unstable, and the non-trivial isolated equilibrium may change its stability depending on the value of the delay parameter and the carrying capacity. There also exists a continuum of equilibria in the interior of the positive octant, and it is observed that though these equilibria undergo a zip bifurcation, surprisingly, the zip bifurcation is unsustainable. More interestingly, even the introduction of diffusion in the time-delay model does not change the unsustainability of this kind of zip bifurcation. The numerical studies of the delay model reveal that the non-isolated interior equilibria, for certain specific values of the parameters of the model, undergo a Hopf-like bifurcation. However, this fact remains to be established from a mathematical point of view. This is an interesting phenomenon and needs more intensive scrutiny. Our assumptions create an abstract ideal situation in which two predators of equal prey thresholds compete, one achieving this threshold by being an r-strategist and the other by being a K-strategist. Also, bifurcation of a stable periodic solution representing coexistence can be established using our assumptions. The situation with regard to the presence of non-isolated equilibria may be viewed as a consequence of overfeeding of the species (not necessarily due to competition), leading to the suspension of all biological activities, which, of course, is justifiable in reality.

In the real world a number of factors will confound understanding of the interactions among the competing species; simplified models such as the one presented in this paper may seem like a toy model. However, the present study shows that even simplified models exhibit rich and complicated dynamics. From this point of view, the present study provides scope for the development of increasingly realistic models.

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