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PERIODIC OSCILLATION IN THE DELAYED CF-SYSTEM

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Abstract. This paper deals with the stability analysis of an autonomous system of differential equations and a nonlinear system of reaction diffusion equations with discrete time delay which models the behavior of a predator population whose dynamics depends on the past history of the prey population on which it is acting. This delay is regarded as the lag due to gestation of the predator. Basic mathematical properties of the model are discussed. The most important observation is that as the delay is increased, the originally asymptotic stable interior equilibrium loses its stability, furthermore at a certain critical value a Hopf bifurcation takes place: a small amplitude periodic solution arises. The possibility of a Turing–Hopf, i. e., the occurrence of time-periodic pattern is also studied.

1991 *Mathematics Subject Classification:* 92D25 (34K18, 35K57, 92D40)

Keywords: predator-prey system, discrete delay, Hopf bifurcation, diffusion driven instability, periodic oscillation

1. INTRODUCTION

The system of equations constructed by M. Cavani and M. Farkas (CF-system), which describes the predator-prey interaction with Holling's type functional response of the predator is governed by

$$\left.\begin{aligned}\dot{N} &= \varepsilon N\,(1-N/K)-\beta NP/(\beta+N),\\ \dot{P} &= -P(\gamma+\delta P)/(1+P)+\beta NP/(\beta+N),\end{aligned}\right\}\tag{1.1}$$

where dot means differentiation with respect to time t; $N(t)$ and $P(t)$ are the prey and predator densities at time t, $\varepsilon > 0$, $\beta > 0$, $K > 0$ and $\kappa > 0$ are the specific growth rate of prey, the conversion rate and the carrying capacity with respect to the prey, $\gamma > 0$ and $\delta > 0$ are the minimal mortality and the limiting mortality of the predator, respectively (see [5]). This system has the advantage over the other Gause-type predator-prey systems (cf. [11]) that here predator mortality is neither a constant nor an unbounded function (as it is, e. g., in [19] and, respectively, in [16]), still, it is increasing with quantity. To have more realism the authors of the above system have introduced an infinite delay into the second equation of the system for prey density and have shown that under some conditions the increase of the delay destabilizes the originally stable equilibrium by Hopf bifurcation. Delays play an important role in the dynamics of populations. In many processes of the real word, especially, in a great many biological phenomena, the present dynamics, the present rate of change of the state variables depends not only on the present state of the processes but also on the history of the phenomenon, on past values of the state variables. As in physical sciences, in biology there are two traditions on which one can call for insight into delay problems (see [15]). In population biology one finds many systems in which the emphasis is on the distribute lag (as in [5]) but there is also a long tradition of using discrete delays to account for individual development (see [17] and the references therein).

In this paper we incorporate a discrete lag into the CF-system and into its reaction diffusion version and study the existence of periodic solutions. This delay will be considered as the lag due to the gestation of the predator.

The organization of the paper is as follows: the Section 2 is about the basic mathematical properties of the delayed CF-system such as steady states, nonnegativity and existence of solutions, respectively. In Section 3 we will discuss the stability of the trivial solution and the existence of Hopf bifurcation. In Section 4 the CF-system will be modified by assuming that the prey and predator are diffusing according to Ficks law in a spatial habitat with hexagonal boundary and the effect of the delay on the stability of the positive equilibrium will be studied.

2. THE MODEL

Let us consider the delayed version of (1.1)

$$\left.\begin{aligned}\dot{N} &= \varepsilon N\,(1-N/K)-\beta NP/(\beta+N),\\ \dot{P} &= -P(\gamma+\delta P)/(1+P)+\beta N(\cdot-\tau)P/(\beta+N(\cdot-\tau))\end{aligned}\right\}\tag{2.1}$$

with the initial conditions $\varphi = (\phi_1, P)$ in the Banach space

$$\left\{\varphi\in C\left([-\tau,0],\mathbb{R}^2_+\right)\;\middle|\;\phi_1(\theta)=N(\theta)\right\}$$

where $\varphi_1(\theta)\geq 0$ $(\theta\in[-\tau,0))$.

In [5] the authors have shown that the following conditions are reasonable and natural:

$$\gamma<\beta\leq\delta,\tag{2.2}$$

$$\beta<K,\tag{2.3}$$

$$\gamma<\beta K/(\beta+K)\,;\tag{2.4}$$

and under these conditions (1.1) has at least three equilibria: $(0,0)$ and $(K,0)$ which are unstable and at least one equilibrium with positive coordinates $(\overline{N},\overline{P})$ as intersection of the prey null-cline

$$P = H_1(N) := (K-N)(\beta+N)\varepsilon/(\beta K)$$

and the predator null-cline

$$P = H_2(N) := ((\beta-\gamma)N - \beta\gamma)\,/\,((\delta-\beta)N + \beta\delta)$$

which is asymptotically stable if

$$0 < (K-\beta)/2 \le \overline{N} \tag{2.5}$$

holds. If $0 < \overline{N} < (K-\beta)/2$, i. e., $\overline{N}$ lies in the Allée-effec zone (in the zone where the increase of the prey density is favorable to its growth rate), then it may or may not be stable.

Example 1.

(1) For $\beta := 0.5000$, $\gamma := 0.1000$, $\delta := 0.5000$, $\varepsilon := 0.1000$ and $K := 5.0000$ the equilibrium $(\overline{N}, \overline{P}) = (0.2100, 0.1360)$ lies in the Allée-effect zone $(0.2100 < 4.5000/2)$ and is asymptotically stable (see Figure 1).

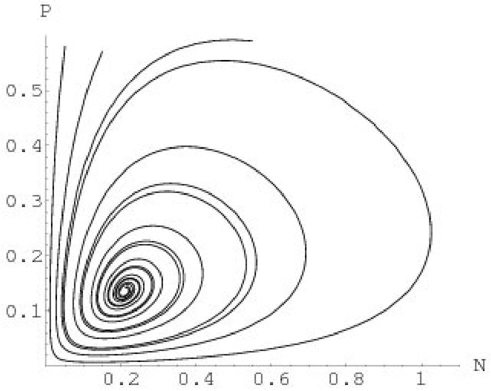

FIGURE 1. The interior equilibrium of the system (1.1) showing its asymptotic stability (MATHEMATICA®)

(2) For $\beta := 0.1065$, $\gamma := 0.0085$, $\delta := 0.1065$, $\varepsilon := 1.6000$, and $K := 35.3500$, the equilibrium $(\overline{N}, \overline{P}) = (15.1736, 131.0240)$ lies in the Allée-effect zone $(15.1736 < 35.2435/2)$ and is unstable.

In what follows we assume that inequalities (2.2)–(2.4) hold.

System (2.1) describes an animal population, therefore it is very important to prove that there are positive initial data for which both predator and prey quantities remain positive, we will even prove that all positive initial data have this property.

Clearly, system (2.1) is of the form

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x}) + \boldsymbol{g}(\boldsymbol{x}(\cdot - \tau)),$$

with Lipschitz continuous $\boldsymbol{f}$, continuous $\boldsymbol{g}$ and $\boldsymbol{g}(\boldsymbol{s}) \ge 0$ for $\boldsymbol{s} \in (\mathbb{R}^+)^2$. Thus, applying Theorem 1.2 from [1] and the majorant method described, e. g., in [10, p. 101], we see the validity of the following

Theorem 1. *Solutions of* (2.1) *with nonnegative initial conditions are defined on* $[0,+\infty)$ *and remain nonnegative for all* $t \geq 0$.

3. STABILITY OF THE EQUILIBRIA

Clearly the equilibria of (1.1) are steady states of (2.1), also. Now, we are going to determine the stability of equilibria for system (2.1). The variational system of (2.1) with respect to the solution $(\widetilde{N},\widetilde{P})$ (see [9, p. 478]) takes the form

$$\begin{pmatrix}\dot{V}_N\\ \dot{V}_P\end{pmatrix}=\begin{pmatrix}\varepsilon-\frac{2\varepsilon\widetilde{N}}{K}-\frac{\beta^2\widetilde{P}}{(\beta+\widetilde{N})^2} & -\frac{\beta\widetilde{N}}{\beta+\widetilde{N}}\\ 0 & \frac{\beta\widetilde{N}}{\beta+\widetilde{N}}-\frac{\gamma(1+\widetilde{P})-\delta\widetilde{P}(2+\widetilde{P})}{(1+\widetilde{P})^2}\end{pmatrix}$$
$$\times\begin{pmatrix}V_N\\ V_P\end{pmatrix}+\begin{pmatrix}0 & 0\\ \frac{\beta^2\widetilde{P}}{(\beta+\widetilde{N})^2} & 0\end{pmatrix}\begin{pmatrix}V_N(\cdot-\tau)\\ V_P(\cdot-\tau)\end{pmatrix}.$$

Thus, the linearized system: 1. At $(0,0)$ has the form

$$\begin{pmatrix}\dot{V}_N\\ \dot{V}_P\end{pmatrix}=\begin{pmatrix}\varepsilon & 0\\ 0 & -\gamma\end{pmatrix}\begin{pmatrix}V_N\\ V_P\end{pmatrix}+\begin{pmatrix}0 & 0\\ 0 & 0\end{pmatrix}\begin{pmatrix}V_N(\cdot-\tau)\\ V_P(\cdot-\tau)\end{pmatrix}$$

which leads one to the characteristic equation

$$\Delta_{(0,0)}(z,\tau):=(\varepsilon-z)(-\gamma-z)=0;$$

2. At $(K,0)$ is

$$\begin{pmatrix}\dot{V}_N\\ \dot{V}_P\end{pmatrix}=\begin{pmatrix}-\varepsilon & -\frac{\beta K}{\beta+K}\\ 0 & \frac{\beta K}{\beta+K}-\gamma\end{pmatrix}\begin{pmatrix}V_N\\ V_P\end{pmatrix}+\begin{pmatrix}0 & 0\\ 0 & 0\end{pmatrix}\begin{pmatrix}V_N(\cdot-\tau)\\ V_P(\cdot-\tau)\end{pmatrix}$$

whose (asymptotical) stability is determined by the real part of the roots of the characteristic equation

$$\Delta_{(K,0)}(z,\tau):=(-\varepsilon-z)\left(\frac{\beta K}{\beta+K}-\gamma-z\right)=0;$$

3. At $(\bar{N},\bar{P})$ has the form

$$\begin{pmatrix}\dot{V}_N\\ \dot{V}_P\end{pmatrix}=\begin{pmatrix}\eta\Theta_1\Theta_2 & -\Theta_1\\ 0 & -\eta\Theta_3\Theta_4\end{pmatrix}\begin{pmatrix}V_N\\ V_P\end{pmatrix}+\begin{pmatrix}0 & 0\\ \beta^2\eta\Theta_3 & 0\end{pmatrix}\begin{pmatrix}V_N(\cdot-\tau)\\ V_P(\cdot-\tau)\end{pmatrix},$$

where $\eta:=\varepsilon(K\beta)^{-1}$ and

$$\left.\begin{aligned}\Theta_1&:=\frac{\beta\bar{N}}{\beta+\bar{N}}, & \Theta_2&:=K-\beta-2\bar{N},\\ \Theta_3&:=\frac{K-\bar{N}}{\beta+\bar{N}}, & \Theta_4&:=\frac{\left((\delta-\beta)\bar{N}+\beta\delta\right)^2}{\delta-\gamma}\end{aligned}\right\}$$

(see [6]). The corresponding characteristic equation is

$$\begin{aligned}\Delta_{(\bar{N},\bar{P})}(z,\tau) &:= \det\begin{pmatrix}\eta\Theta_1\Theta_2 - z & -\Theta_1\\ \beta^2\eta\Theta_3\exp(-z\tau) & -\eta\Theta_3\Theta_4 - z\end{pmatrix}\\ &= z^2 + \eta(\Theta_3\Theta_4 - \Theta_1\Theta_2)z - \eta^2\Theta_1\Theta_2\Theta_3\Theta_4 +\\ &\quad + \beta^2\eta\Theta_1\Theta_3\exp(-z\tau) = 0.\end{aligned}$$

Since ε is a positive root of $\Delta_{(0,0)}$, it follows that $(0,0)$ is an unstable equilibrium of (2.1) for all $\tau \geq 0$. Because of (2.4), $\beta K/(\beta+K) - \gamma$ is a positive root of $\Delta_{(K,0)}$, and, therefore, $(K,0)$ is an unstable equilibrium of (2.1) for all $\tau \geq 0$.

Clearly, $\Delta_{(\bar{N},\bar{P})}$ has the form

$$\Delta_{(\bar{N},\bar{P})}(z,\tau) \equiv p(z) + q(z)\exp(-z\tau)$$

where $p(z) := z^2 + \eta(\Theta_3\Theta_4 - \Theta_1\Theta_2)z - \eta^2\Theta_1\Theta_2\Theta_3\Theta_4$ and $q(z) := \beta^2\eta\Theta_1\Theta_3$ are trivially analytic functions in a right half-plane $\operatorname{Re} z > -c$ $(c > 0)$ that satisfy the following conditions:

(1) p and q have no common imaginary root;
(2) $\overline{p(-iy)} = p(iy)$, $\overline{q(-iy)} = q(iy)$ $(y \in \mathbb{R})$;
(3) $p(0) + q(0) \neq 0$;
(4) $\limsup_{|z|\to\infty, \operatorname{Re} z \geq 0} \left|\dfrac{q(z)}{p(z)}\right| < 1$.

To obtain stability switch one needs to have an imaginary root of $\Delta_{(\bar{N},\bar{P})}$. Let $z = iy$. Then $\Delta_{(\bar{N},\bar{P})}(z,\tau) = 0 \Leftrightarrow |p(z)| = |q(z)|$ and

$$\begin{aligned}\sin(y\tau) &= \frac{p^I(y)q^R(y) - p^R(y)q^I(y)}{|q(iy)|^2},\\ \cos(y\tau) &= -\frac{p^R(y)q^R(y) + p^I(y)q^I(y)}{|q(iy)|^2},\end{aligned}$$

where $p(iy) =: p^R(y) + p^I(y)i$ and $q(iy) =: q^R(y) + q^I(y)i$. In this case, one has $|q(iy)|^2 = \beta^4\eta^2\Theta_1^2\Theta_3^2 > 0$.

Let us define the auxiliary function $F(y) := |p(iy)|^2 - |q(iy)|^2$ $(y \in \mathbb{R})$. Hence

$$F(y) = y^4 + \eta^2\left[\Theta_1^2\Theta_2^2 + \Theta_3^2\Theta_4^2\right]y^2 + \eta^2\Theta_1^2\Theta_3^2\left[\eta^2\Theta_2^2\Theta_4^2 - \beta^4\right] \quad (y \in \mathbb{R}).$$

The necessary condition for the change in stability is the existence of $\psi_0 > 0$ such that $F(\psi_0) = 0$. Thus, applying the theorem of [2,7] (see also [14]) we can prove the following

Theorem 2. *If*

(1) $\beta^2 < |\eta\Theta_2\Theta_4|$, *then the equilibrium* $(\bar{N},\bar{P})$ *of* (2.1) *remains stable for all* $\tau \geq 0$*;*

(2) $\beta^2 > |\eta\Theta_2\Theta_4|$, *then as* τ *increases and passes through* τ_0,

$$\tau_0 := \frac{1}{\psi_0}\sin^{-1}\left(\frac{(\Theta_3\Theta_4 - \Theta_1\Theta_2)\psi_0}{\beta^2\Theta_1\Theta_3}\right),$$

where

$$\psi_0 := \Bigg\{\Big(-\eta^2\left[\Theta_1^2\Theta_2^2 + \Theta_3^2\Theta_4^2\right] + \sqrt{\eta^2\left[\Theta_1^2\Theta_2^2 - \Theta_3^2\Theta_4^2\right]^2 + 4\beta^4\eta^2\Theta_1^2\Theta_3^2}\Big)/2\Bigg\}^{1/2},$$

the equilibrium $(\bar{N}, \bar{P})$ *undergoes a Poincaré–Andronov–Hopf bifurcation, i. e., there occurs a small amplitude periodic solution with a period approximately equal to* $2\pi/\psi_0$.

Proof. Step 1. If $\beta^2 < |\eta\Theta_2\Theta_4|$, then F has no positive root, therefore no stability switch may occur, i. e., the stability of $(\bar{N}, \bar{P})$ does not change as τ is increased from zero to infinity.

Step 2. If $\beta^2 > |\eta\Theta_2\Theta_4|$, then as F has one positive root ψ_0, and there may be only the critical value τ_0 for which

$$\sin\psi_0\tau_0 = \frac{\eta\,(\Theta_3\Theta_4 - \Theta_1\Theta_2)\,\psi_0}{\beta^2\eta\Theta_1\Theta_3}$$

holds and the the equilibrium $(\bar{N}, \bar{P})$ loses its stability. Therefore we only need to check the sign of $\varphi'(\tau_0)$ where $z = \varphi + \psi i$ and $\varphi(\tau_0) = 0$. Using the implicit function theorem we are going to determine the derivative of the implicit function z_0 at τ_0 (where z_0 denotes the root of (3.3) that assumes the value $i\psi_0$ at τ_0)

$$\begin{aligned} z_0'(\tau_0) &= -\frac{\partial_\tau \Delta_{(\bar{N},\bar{P})}(i\psi_0, \tau_0)}{\partial_z \Delta_{(\overline{N},\bar{P})}(i\psi_0, \tau_0)} \\ &= \frac{i\psi_0\beta^2\eta\Theta_1\Theta_3}{[2i\psi_0 + \eta(\Theta_3\Theta_4 - \Theta_1\Theta_2)]\exp(i\psi_0\tau_0) - \tau_0\beta^2\eta\Theta_1\Theta_3}. \end{aligned}$$

Hence we have

$$\begin{aligned} \varphi'(\tau_0) &= \frac{d}{d\tau}\operatorname{Re} z_0(\tau)|_{\tau=\tau_0} = \operatorname{Re}\left.\frac{dz_0(\tau)}{d\tau}\right|_{\tau=\tau_0} \\ &= \psi_0^2\beta^4\eta^2\Theta_1^2\Theta_3^2\left[2\psi_0^2 + \eta^2\left(\Theta_1^2\Theta_2^2 + \Theta_3^2\Theta_4^2\right)\right] \\ &\quad\times \Big\{\big[\eta(\Theta_3\Theta_4 - \Theta_1\Theta_2)\psi_0^2 - \eta^3(\Theta_3\Theta_4 - \Theta_1\Theta_2) \\ &\quad\times \Theta_1\Theta_2\Theta_3\Theta_4 + \tau_0\beta^4\eta^2\Theta_1^2\Theta_3^2\big]^2 \\ &\quad+ \left[2\psi_0^3 + \eta^2\psi_0\left(\Theta_1^2\Theta_2^2 + \Theta_3^2\Theta_4^2\right)\right]^2\Big\}^{-1} > 0. \end{aligned}$$

Thus, by the Hopf bifurcation theorem [8, 12] the theorem is proved. ☐

Example 2. In the case where $\beta := 0.1000$, $\gamma := 0.0100$, $\delta := 0.1055$, $\varepsilon := 1.0000$, and $K := 1.0000$m the equilibrium $(\overline{N}, \overline{P}) = (0.4486, 3.0250)$ lies in the Allée-effect zone $(0.4486 < 0.9000/2)$ and is asymptotically stable for $\tau = 0$ and for $\tau_0 := 1.9090$ there is a switching in stability (see Figure 2).

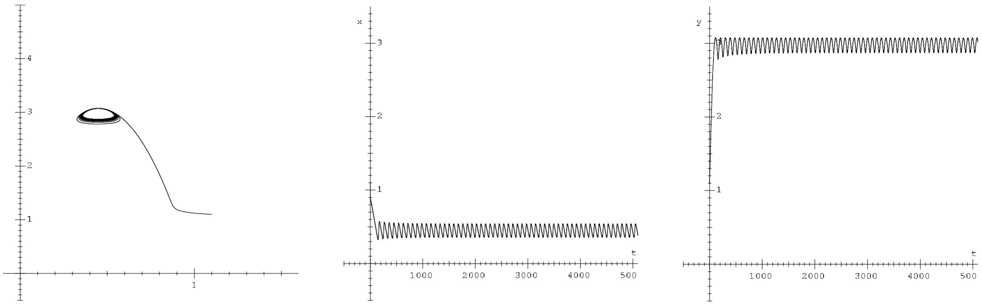

FIGURE 2. Time evolution of system (2.1) for $\beta := 0.1000$, $\gamma := 0.0100$, $\delta := 0.1055$, $\varepsilon := 1.1000$, the delay $\tau_0 := 2.2$ and time $t = 5100.0000$ with the notation $x := N$ and $y := P$ (DifEqu®).

4. THE MODEL WITH DIFFUSION

Let us modify system (2.1) assuming that the prey and predator are diffusing to Fick's law in the spatial habitat

$$\varOmega_H := \left\{ (x,y) \in \mathbb{R}^2 \,\middle|\, |x| < \frac{H\sqrt{3}}{2},\ \left| y + \frac{x}{\sqrt{3}} \right| < H \right\} \qquad (H > 0)$$

i. e., consider the reaction-diffusion system

$$\left.\begin{aligned} \partial_t N &= \varDelta_{\boldsymbol{r}} N + \varepsilon N(1 - N/K) - \beta NP/(\beta + N), \\ \partial_t P &= d\varDelta_{\boldsymbol{r}} P - P(\gamma + \delta P)/(1 + P) + \beta N(\cdot - \tau)P/(\beta + N(\cdot - \tau)), \end{aligned}\right\} \tag{4.1}$$

where d is the diffusion coefficient about which we assume only that it has a positive sign,

$$(\boldsymbol{n} \cdot \nabla_{\boldsymbol{r}})\,\mathrm{col}\,[N, P] = \mathbf{0} \quad \text{in} \quad \partial\varOmega_H \times [-\tau, +\infty) \tag{4.2}$$

and

$$\mathrm{col}\,[N, P] = \boldsymbol{\Phi} \geq \mathbf{0} \quad \text{on} \quad \overline{\varOmega}_H \times [-\tau, 0]. \tag{4.3}$$

Clearly, a spatially constant solution $\mathrm{col}\,[N(\cdot), P(\cdot)]$ of system (4.1) satisfies boundary conditions (4.2) and system (2.1). The equilibria of system (2.1) are constant solutions of (4.1), (4.2) at the same time.

The linearized equation: 1. At $(0,0)$ has the form

$$\left.\begin{aligned}\partial_t V_N &= \Delta_{\boldsymbol{r}} V_N + \varepsilon V_N,\\ \partial_t V_P &= d\Delta_{\boldsymbol{r}} V_P - \gamma V_P,\end{aligned}\right\} \tag{4.4}$$

which is asymptotically stable if for all $n \in \mathbb{N}$ the polynomial

$$\begin{aligned}\widetilde{\Delta}_{(0,0)}(z,\tau) &:= \det\begin{pmatrix}\varepsilon-\lambda_n-z & 0\\ 0 & -\gamma-\lambda_n d-z\end{pmatrix}\\ &= z^2-(\varepsilon-\lambda_n-\gamma-\lambda_n d)z+(\lambda_n-\varepsilon)(\gamma+\lambda_n d)\end{aligned}$$

has roots with negative real part [3,4], where $\lambda_n := 16\pi^2/(9H^2)n^2$ $(n \in \mathbb{N})$ is the nth eigenvalue of the minus Laplacian on Ω_H with no-flux boundary conditions.

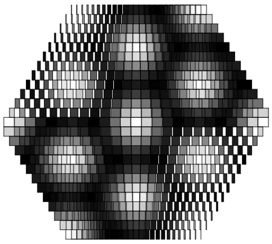

FIGURE 3. Eigenfunction of the minus Laplacian corresponding to the eigenvalue $\lambda_3(H)$ with $H = 5$ (Maple®).

2. At $(K,0)$ is

$$\left.\begin{aligned}\partial_t V_N &= \Delta_{\boldsymbol{r}} V_N - \varepsilon V_N - \frac{\beta K}{\beta+K}V_P,\\ \partial_t V_P &= d\Delta_{\boldsymbol{r}} V_P + \left(\frac{\beta K}{\beta+K}-\gamma\right)V_P,\end{aligned}\right\} \tag{4.5}$$

whose (asymptotical) stability is determined by the real part of the roots of the polynomial

$$\begin{aligned}\widetilde{\Delta}_{(K,0)}(z,\tau) &:= \det\begin{pmatrix}-\varepsilon-\lambda_n-z & -\frac{\beta K}{\beta+K}\\ 0 & \frac{\beta K}{\beta+K}-\gamma-\lambda_n d-z\end{pmatrix}\\ &= z^2+\left(\varepsilon+\lambda_n-\frac{\beta K}{\beta+K}+\gamma+\lambda_n d\right)z+(\varepsilon+\lambda_n)\\ &\quad\times\left(\gamma+\lambda_n d-\frac{\beta K}{\beta+K}\right).\end{aligned}$$

3. At $(\bar{N}, \bar{P})$ is

$$\left.\begin{aligned} \partial_t V_N &= \Delta_{\boldsymbol{r}} V_N + \eta \Theta_1 \Theta_2 V_N - \Theta_1 V_P \\ \partial_t V_P &= d \Delta_{\boldsymbol{r}} V_P - \eta \Theta_3 \Theta_4 V_P + \beta^2 \eta \Theta_3 V_N(\cdot - \tau) \end{aligned}\right\} \tag{4.6}$$

which is asymptotically stable if for all $n \in \mathbb{N}$ the quasi-polynomial

$$\begin{aligned} \widetilde{\Delta}_{(\bar{N},\bar{P})}(z,\tau) := \det & \begin{pmatrix} \eta \Theta_1 \Theta_2 - \lambda_n - z & -\Theta_1 \\ \beta^2 \eta \Theta_3 \exp(-z\tau) & -\eta \Theta_3 \Theta_4 - \lambda_n d - z \end{pmatrix} \\ = z^2 & - [\eta (\Theta_1 \Theta_2 - \Theta_3 \Theta_4) - \lambda_n (d+1)] z \\ & - [\eta \Theta_1 \Theta_2 - \lambda_n][\eta \Theta_3 \Theta_4 + \lambda_n d] + + \beta^2 \eta \Theta_1 \Theta_3 \exp(-z\tau) \end{aligned}$$

has roots with negative real part (see [18]).

Since for $n = 0$ the constant term of $p_{(0,0)}$ is negative, therefore $(0,0)$ remains an unstable equilibrium of (4.1)–(4.3) for all $\tau > 0$.

Because of (2.4) there exist $n \in \mathbb{N}$ such that the constant term $p_{(K,0)}$ is negative, therefore $(K,0)$ remains an unstable equilibrium of (4.1)–(4.3) for all $\tau > 0$.

The stability of $p_{(\bar{N},\bar{P})}$ depends on several parameters. In the remainder of this section we assume that $d > 1$. In the case without delay,

$$\begin{aligned} \widetilde{\Delta}_{(\bar{N},\bar{P})}(z,0) \equiv z^2 & - [\eta (\Theta_1 \Theta_2 - \Theta_3 \Theta_4) - \lambda_n (d+1)] z \\ & - [\eta \Theta_1 \Theta_2 - \lambda_n][\eta \Theta_3 \Theta_4 + \lambda_n d] + \beta^2 \eta \Theta_1 \Theta_3, \end{aligned}$$

which is stable (see [6, 13]) if

(1) $\Theta_2 \le 0$, i. e., the equilibrium $(\bar{N}, \bar{P})$ lies outside the Allée-effect zone (on the descending branch of the prey null-cline) or

(2) the parameters ε, β, K, γ, δ are Turing admissible which implies $\Theta_2 > 0$, and

$$\frac{\eta \Theta_1 \Theta_2}{\lambda_1} \le 1 \quad \text{or} \quad \Theta_2 \le \frac{16\pi^2}{9H^2 \eta \Theta_1}. \tag{4.7}$$

With respect to the parameter τ, the quasi-polynomial for $p_{(\bar{N},\bar{P})}$ has a similar structure as $\Delta_{(\bar{N},\bar{P})}$:

$$\widetilde{\Delta}_{(\bar{N},\bar{P})}(z,\tau) \equiv \widetilde{p}(z) + \widetilde{q}(z) \exp(-z\tau) \tag{4.8}$$

where

$$\widetilde{p}(z) := z^2 - [\eta (\Theta_1 \Theta_2 - \Theta_3 \Theta_4) - \lambda_n (d+1)] z - (\eta \Theta_1 \Theta_2 - \lambda_n)(\eta \Theta_3 \Theta_4 + \lambda_n d)$$

and $\widetilde{q}(z) := \beta^2 \eta \Theta_1 \Theta_3$ are trivially analytic functions in the right half-plane $\operatorname{Re} z > -c$ $(c > 0)$ and satisfy the following conditions:

(1) $\widetilde{p}$ and $\widetilde{q}$ have no common imaginary root;

(2) $\overline{\widetilde{p}(-iy)} = \widetilde{p}(iy)$, $\overline{\widetilde{q}(-iy)} = \widetilde{q}(iy)$ $(y \in \mathbb{R})$;

(3) $\widetilde{p}(0) + \widetilde{q}(0) \neq 0$;

(4) $\limsup_{|z|\to\infty,\,\mathrm{Re}\,z\geq 0}\left|\dfrac{\widetilde{q}(z)}{\widetilde{p}(z)}\right| < 1.$

To obtain stability switch one has to examine the existence of real roots of the function (see [2,7])

$$\begin{aligned}\widetilde{F}(y) &:= |\widetilde{p}(iy)|^2 - |\widetilde{q}(iy)|^2 = \left|-y^2 + Aiy + B\right|^2 - |C|^2\\ &= \left(B - y^2\right)^2 + A^2y^2 + C^2 = y^4 + (A^2 - 2B)y^2 + B^2 - C^2 \quad (y \in \mathbb{R}),\end{aligned}$$

where

$$\begin{aligned}A &:= \lambda_n(d+1) - \eta\,(\Theta_1\Theta_2 - \Theta_3\Theta_4)\,,\\ B &:= -(\eta\Theta_1\Theta_2 - \lambda_n)\,(\eta\Theta_3\Theta_4 + \lambda_n d)\,,\end{aligned}$$

and $C := \beta^2\eta\Theta_1\Theta_3$. A stability switch may occur only if $\widetilde{F}$ has a positive root $\widetilde{\psi}_0$. Viéte's formula implies that it may happen in the following three cases:

$$B^2 - C^2 > 0, \qquad A^2 - 2B < 0, \qquad (A^2 - 2B)^2 = 4(B^2 - C^2); \tag{4.9a}$$

$$B^2 - C^2 \in \mathbb{R}, \qquad A^2 - 2B < 0, \qquad (A^2 - 2B)^2 > 4(B^2 - C^2); \tag{4.9b}$$

$$B^2 - C^2 < 0, \qquad A^2 - 2B \in \mathbb{R}, \qquad (A^2 - 2B)^2 > 4(B^2 - C^2), \tag{4.9c}$$

where case (4.9c) reduces to $B^2 - C^2 < 0$ because this inequality implies the condition $(A^2 - 2B)^2 > 4(B^2 - C^2)$. Because $(A^2 - 2B)^2 - 4(B^2 - C^2) = A^2(A^2 - 4B) + 4C^2$ and $A^2 - 4B = [\lambda_n(d-1) + \eta(\Theta_1\Theta_2 + \Theta_3\Theta_4)]^2 > 0$ we deal with one of the last two cases. If $B^2 - C^2 < 0$, then we have one positive solution

$$\widetilde{\psi}_0 := \frac{1}{\sqrt{2}}\sqrt{2B - A^2 + \sqrt{A^2(A^2 - 4B) + 4C^2}}$$

at which switching can occur. The condition $B^2 - C^2 < 0$ is equivalent to

$$\begin{aligned}&[\eta\Theta_1\Theta_2 - \lambda_n]^2\,[\eta\Theta_3\Theta_4 + \lambda_n d]^2 - \beta^4\eta^2\Theta_1^2\Theta_3^2\\ &\qquad = \left[\eta^2\Theta_1\Theta_2\Theta_3\Theta_4 + \eta\Theta_1\Theta_2\lambda_n d - \eta\Theta_3\Theta_4\lambda_n - \lambda_n^2 d\right]^2 - \left[\beta^2\eta\Theta_1\Theta_3\right]^2\\ &\qquad = \left[\Theta_1\Theta_3\eta\left(\eta\Theta_2\Theta_4 + \beta^2\right) + \lambda_n(\eta\Theta_1\Theta_2 d - \eta\Theta_3\Theta_4 - \lambda_n d)\right]\\ &\qquad\qquad \times\left[\Theta_1\Theta_3\eta\left(\eta\Theta_2\Theta_4 - \beta^2\right) + \lambda_n(\eta\Theta_1\Theta_2 d - \eta\Theta_3\Theta_4 - \lambda_n d)\right] < 0.\end{aligned}$$

Thus, we conclude that if $\beta^2 > |\eta\Theta_1\Theta_2|$ and

1. $\Theta_2 < 0$, i. e., the equilibrium $(\overline{N}, \overline{P})$ lies outside the Allée-effect zone, or
2. $\Theta_2 > 0$ and $\frac{\eta\Theta_1\Theta_2}{\lambda_1} \leq 1$, i. e., the equilibrium $(\overline{N}, \overline{P})$ lies in Allée-effect zone and is asymptotically stable if the diffusive system is a system without delay,

then for every integer n such that

$$d\lambda_n^2 + \eta(\Theta_3\Theta_4 - \Theta_1\Theta_2 d)\lambda_n < \Theta_1\Theta_3\eta\left(\eta\Theta_2\Theta_4 + \beta^2\right) \tag{4.10}$$

there may be a switching in stability at the point

$$\tau_0(n) = \frac{1}{\widetilde{\psi}_0}\sin^{-1}\left(\frac{[\lambda_n(d+1)-\eta(\Theta_1\Theta_2-\Theta_3\Theta_4)]\,\widetilde{\psi}_0}{\beta^2\eta\Theta_1\Theta_3}\right).$$

Numerical calculations show that in the following cases there is a switch of stability indeed.

Example 3. For $\beta := 0.1000$, $\gamma := 0.0100$, $\delta := 0.1055$, $\varepsilon := 1.0000$ and $K := 1.0000$ the asymptotically stable equilibrium $(\bar{N}, \bar{P}) = (0.4486, 3.0250)$ of (1.1) lies inside the Allée-effect zone $(0.4486 < 0.9000/2)$, for $d = 1.1$, $H = 55$ it is diffusionally stable and (4.9) assumes the form

$$0.0030 \cdot n^4 + 0.0008 \cdot n^2 < 0.0083$$

which is fulfilled for $n \in \{0; 1\}$ and

(1) for $n = 0$ there is a switching in stability at $\tau_0(0) = 18.9969$ because for a root $z = \varphi + \psi i$ of (4.8) at which $\varphi(\tau_0(0)) = 0$ holds $\operatorname{sign}\varphi'(\tau_0(0)) = 1$;
(2) for $n = 1$ there is a switching in stability at $\tau_0(1) = 1508.1225$ because for a root $z = \varphi + \psi i$ of (4.8) at which $\varphi(\tau_0(0)) = 0$ holds $\operatorname{sign}\varphi'(\tau_0(0)) = 1$.

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