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BIFURCATIONS IN A PREDATOR-PREY MODEL WITH MEMORY AND DIFFUSION. I: ANDRONOV–HOPF BIFURCATION

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1. Introduction

We start off with the model

$$(1.1)\qquad \begin{cases} \dot N = \varepsilon N(1 - N/K) - \beta NP/(\beta + N), \\ \dot P = -P(\gamma + \delta P)/(1 + P) + \beta NP/(\beta + N) \end{cases}$$

where dot means differentiation with respect to time t; $N(t)$ and $P(t)$ are the quantities of prey and predator, respectively; $\varepsilon > 0$ is the specific growth rate of prey in the absence of predation and without environmental limitation; in the absence of predators the prey population grows logistically to carrying capacity $K > 0$; the functional response of the predator is of Holling's type (see [11, 12]) with satiation coefficient or conversion rate $\beta > 0$; the specific mortality of predators in absence of prey

$$(1.2)\qquad E(P) = (\gamma + \delta P)/(1 + P)$$

depends on the quantity of predators, $\gamma > 0$ is the mortality at low density and $\delta > 0$ is the limiting, maximal mortality (the natural assumption is $\gamma < \delta$).

This system seems to us a fairly realistic one if neither hereditary effects nor spatial distribution are taken into account. The Holling type functional response is widely used and has a vast literature, and if $\gamma = \delta$ then the mortality of predator reduces to a constant (see e.g. [9]). The advantage of the present model over the more often used models is that here the predator mortality is neither a constant nor an unbounded function, still, it is increasing with quantity.

First we study the stability of equilibria of this system and possible bifurcations.

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It is reasonable to assume that the present level of predator quantity effects instantaneously the growth of prey, on the other hand, the growth of predator is influenced by past values of prey quantity. Therefore, secondly, we replace N in the second equation of (1.1) by its time average over the past. We shall be concerned, primarily, in the destabilising effect of the influence of the past and in the character of the possible bifurcations.

Finally, we shall assume that predator and prey undergo Fickian diffusion in space.

Accordingly, in Section 2 conditions for stable equilibria of system (1.1) will be established. In Section 3 an Andronov–Hopf bifurcation will be calculated at a special constellation of the parameters. In Section 4 the delay will be introduced, and conditions for stability will be established. In Section 5 the Andronov–Hopf bifurcation will be calculated when the delay is increased. The study of the reaction-diffusion equation built upon (1.1) will be accomplished in a subsequent paper.

2. Stability of equilibrium points

Clearly, the positive quadrant of the N, P plane is invariant for system (1.1), and one may prove, similarly as it was done in [9], that all solutions with non-negative initial conditions stay bounded in $t \in [0, \infty)$.

On the boundary of the positive quadrant the system has two equilibrium points: (0,0) and $(K, 0)$. A simple linear stability analysis shows that (0,0) is always unstable, and that $(K, 0)$ is asymptotically stable if

$$\gamma > \beta K/(\beta + K), \tag{2.1}$$

and unstable if

$$\gamma < \beta K/(\beta + K). \tag{2.2}$$

Note that (2.2) is equivalent to $0 < \beta\gamma/(\beta - \gamma) < K$ and implies $\gamma < \beta$ and $\gamma < K$.

However, for reasonable parameter configurations we may establish the global stability of $(K, 0)$.

THEOREM 2.1. *If*

$$\gamma \geqq \beta \quad \text{and} \quad \delta \geqq \beta \tag{2.3}$$

then $(K, 0)$ is globally asymptotically stable with respect to the positive quadrant of the N, P plane.

PROOF. Decreasing the first term on the right hand side of the second equation of (1.1) by writing β for γ and δ we get that

$$\dot{P} \leqq -\beta P(1 - N/(\beta + N)) < -cP$$

for some $c > 0$, since $N(t)$ is bounded in $t \in [0, \infty)$. As a consequence, any solution $P(t)$ corresponding to non-negative initial conditions tends to zero as t tends to infinity. Thus, the omega limit set Ω of every solution with positive initial conditions is contained in $\{(N, 0) : N \geqq 0\}$. But for $N > K$ we have $\dot{N} < 0$, so, $\Omega \subset \{(N, 0) : 0 \leqq N \leqq K\}$. Taking into account that $(0, 0) \notin \Omega$ and that Ω is a nonempty, closed, invariant set we get that $\Omega = \{(K, 0)\}$. □

Note that since the right hand side of (2.1) is less than β, the first inequality of (2.3) implies (2.1), i.e. it implies the asymptotic stability of $(K, 0)$. The intuitive meaning of $\gamma \geqq \beta$ is clear: the minimal mortality of the predator is high compared to the conversion rate; this leads to the extinction of the predator. If we assume that the mortality of the predator grows with its quantity, i.e. $\delta > \gamma$ then the first inequality of (2.3) implies the second.

THEOREM 2.2. *If*

$$\gamma < \beta \leqq \delta \tag{2.4}$$

and

$$K \leqq \beta\gamma/(\beta - \gamma) \tag{2.5}$$

then $(K, 0)$ is globally asymptotically stable with respect to the positive quadrant of the N, P plane.

Note that if $\beta > \gamma$ then (2.5) with a strict inequality is equivalent to (2.1), so if (2.5) is strict we know that the equilibrium is *locally* asymptotically stable.

PROOF. First, consider the case when (2.5) is strict, i.e. (2.1) holds. This implies that an $\eta > 0$ exists such that $\gamma > \beta(K + \eta)/(\beta + K + \eta)$, and so if $N(t) \leqq K + \eta$ then applying (2.4)

$$\dot{P}(t) < -\left(\gamma - \frac{\beta N(t)}{\beta + N(t)}\right) P(t) \leqq -\left(\gamma - \frac{\beta(K + \eta)}{\beta + K + \eta}\right) P(t).$$

But the set $\{(N, P) : 0 < N \leqq K + \eta,\ P > 0\}$ is positively invariant since $\dot{N} < 0$ if $N = K + \eta$, $P \geqq 0$. So if the initial values satisfy $N(0) \leqq K + \eta$, $P(0) > 0$ then $P(t) \to 0$ exponentially as $t \to \infty$. If $N(0) > K + \eta$ then

$$\dot{N}(t) < -\varepsilon\eta N(t) \quad \text{while} \quad N(t) > K + \eta.$$

So N will be equal to $K+\eta$ in finite time, and then $P(t)\to 0$ as before. From here on one may repeat the proof of the previous theorem to complete the proof for this case.

Secondly, assume that (2.5) is an equality, i.e. $\gamma=\beta K/(\beta+K)$. We substitute this value into system (1.1) and move the origin into $(K,0)$ by the coordinate transformation $n=N-K$, $p=P$. We get the system in the form

$$(2.6)\quad \begin{cases} \dot{n}=-\varepsilon(n+K)n/K-\beta(n+K)p/(\beta+K+n),\\ \dot{p}=-p(\beta K/(\beta+K)+\delta p)/(1+p)+\beta(n+K)p/(\beta+K+n). \end{cases}$$

Now, we use the positive definite Liapunov function

$$V(n,p)=(\beta/K)n^2+(\beta+K)p^2.$$

If we denote the derivative of V with respect to the system (2.6) by $\dot{V}$ we have

$$\begin{aligned}-(1/2)\dot{V}(n,p)(\beta+K+n)(1+p)&=n^2(n+K)(\beta+K+n)(p+1)\beta\varepsilon/K^2+\\ &+np(n+K)(p+1)\beta^2/K+p^2(\delta(\beta+K)p+\beta K)(\beta+K+n)-\\ &-\beta(\beta+K)p^2(n+K)(p+1),\end{aligned}$$

and applying (2.4) a simple calculation shows that $\dot{V}(n,p)<0$ for $n\geqq 0$, $p>0$. This means that all solutions with positive initial conditions either tend (in principle) to $(n,p)=(0,0)$ or leave the $n\geqq 0$, $p>0$ quadrant through the line $n=0$ in finite time. Now, the strip $\{(n,p):-K<<n<0,\ p>0\}$ is positively invariant and if $-K<n(t)<0$ then applying (2.4)

$$\begin{aligned}\dot{p}(t)&\leqq -p(t)(\beta K/(\beta+K)+\beta p(t))/(1+p(t))+\\ &+\beta(n(t)+K)p(t)/(\beta+K+n(t))=\\ &=-p(t)\left(\frac{\beta K}{\beta+K}-\frac{\beta(K+n(t))}{\beta+K+n(t)}+\frac{\beta^2p(t)}{(1+p(t))(\beta+K)}\right)<0.\end{aligned}$$

Thus, once, in the strip, $p(t)$ is monotone decreasing and $p(t)\to\alpha\geqq 0$, $t\to\infty$. If $\alpha>0$ were the case then

$$\dot{p}(t)<-p(t)\frac{\alpha\beta^2}{\left(1+p(t_0)\right)(\beta+K)},\quad t>t_0$$

would hold for some $t_0>0$, and this would imply that p tends to zero exponentially contradicting the assumption $\alpha>0$. So $p(t)$ tends to zero, and the proof of the previous theorem can be repeated again. □

Note that, as a corollary, conditions (2.4), (2.5) imply that system (1.1) has no equilibrium point in the positive quadrant $N > 0$, $P > 0$.

We now turn to the case when an equilibrium point exists with positive coordinates. Making the right hand sides of system (1.1) equal to zero we get that the prey null-cline is the parabola

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

and the predator null-cline is the hyperbola

$$P = H_2(N) := \frac{(\beta - \gamma)N - \beta\gamma}{(\delta - \beta)N + \beta\delta}.$$

To have a reasonable concave down predator curve we have to assume $\delta \geqq \beta$, so since the case when also $\gamma \geqq \beta$ has been treated in Theorem 2.1 we shall assume in the sequel that (2.4) holds. In the special case when $\delta = \beta$ the predator curve is the straight line

$$P = H_3(N) := (\beta - \gamma)N/\beta^2 - \gamma/\beta.$$

Since $H_1(N) > 0$ if and only if $-\beta < N < K$ and $H_2(N) > 0$ ($H_3(N) > 0$) if and only if $N > \beta\gamma/(\beta - \gamma)$ the system has an equilibrium point (at least) with positive coordinates $(\overline{N}, \overline{P})$ if and only if

$$\beta\gamma/(\beta - \gamma) < \overline{N} < K \tag{2.7}$$

(cf. condition (2.5); this shows again that if (2.4) and (2.5) hold then there is no equilibrium in the interior of the positive quadrant). The stability of the positive equilibrium can partly be settled by linear stability analysis.

THEOREM 2.3. *Assume that*

$$\gamma < \beta \leqq \delta, \tag{2.4}$$

$$\beta\gamma/(\beta - \gamma) < K, \tag{2.8}$$

and denote a positive equilibrium of system (1.1) *by* $(\overline{N}, \overline{P})$, $\overline{N} > 0$, $\overline{P} > 0$. *If* $K \leqq \beta$ *then system* (1.1) *has a single positive equilibrium and it is asymptotically stable; if* $0 < (K - \beta)/2 \leqq \overline{N}$ *then* $(\overline{N}, \overline{P})$ *(which may not be the only positive equilibrium) is asymptotically stable.*

PROOF. If $K \leqq \beta$ then H_1 is monotone decreasing in the interval $(0, K)$. Since H_2 is monotone increasing in $(\beta\gamma/(\beta - \gamma), \infty)$ this yields the uniqueness of the positive equilibrium.

The Jacobian of the right hand sides of system (1.1) evaluated at $(\overline{N},\overline{P})$ is

$$J(\overline{N},\overline{P}) = \begin{bmatrix} \frac{\varepsilon\overline{N}(K-\beta-2\overline{N})}{K(\beta+\overline{N})} & -\frac{\beta\overline{N}}{\beta+\overline{N}} \\ \frac{\beta^2\overline{P}}{(\beta+\overline{N})^2} & -\frac{(\delta-\gamma)\overline{P}}{(1+\overline{P})^2} \end{bmatrix}.$$

$$\operatorname{Tr} J(\overline{N},\overline{P}) = \frac{\varepsilon\overline{N}(K-\beta-2\overline{N})}{K(\beta+\overline{N})} - \frac{(\delta-\gamma)\overline{P}}{(1+\overline{P})^2},$$

$$\det J(\overline{N},\overline{P}) = \frac{\beta\overline{N}\,\overline{P}}{\beta+\overline{N}}\left[-\frac{\varepsilon(\delta-\gamma)(K-\beta-2\overline{N})}{K\beta(1+\overline{P})^2} + \frac{\beta^2}{(\beta+\overline{N})^2}\right].$$

If $K < \beta$ then, in view of (2.4), clearly, Tr < 0 and det > 0, i.e. $(\overline{N},\overline{P})$ is asymptotically stable indeed. If $(K-\beta)/2 \leqq \overline{N}$ the same applies. □

Note that in case $\beta < K$ we have an interval $N \in (0,(K-\beta)/2)$ where the Allée effect holds, i.e. the increase of the prey quantity is beneficial to its growth rate. In this case the sufficient condition of stability $\overline{N} \geqq (K-\beta)/2$ is, in fact, the "Rosenzweig–MacArthur graphical criterion", cf. [6,7]. In our case when $0 < \overline{N} < (K-\beta)/2$ then the equilibrium may still be stable.

3. The case $\delta = \beta$

In this section we assume that (2.4) and (2.8) hold with the equality valid in the former. This, as we have seen, ensures the existence of a positive equilibrium. In this special case the coordinates of the positive equilibrium can be determined explicitly and an Andronov–Hopf bifurcation can be calculated by hand. Now the equilibrium point $(\overline{N},\overline{P})$ is the intersection of the parabola $P = H_1(N)$ with the straight line $P = H_3(N)$. We get that

$$\text{(3.1)}\qquad \overline{N} = (1/2)\Big(K-\beta-(1-\gamma/\beta)K/\varepsilon+ \\ +\left((K-\beta-(1-\gamma/\beta)K/\varepsilon)^2 + 4K(\beta+\gamma/\varepsilon)\right)^{1/2}\Big).$$

Assuming that $K > \beta$, the sufficient condition of asymptotic stability proved in Theorem 2.3 is $(K-\beta)/2 \leqq \overline{N}$. Substituting (3.1) into this condition we get that $(\overline{N},\overline{P})$ is asymptotically stable if

$$\text{(3.2)}\quad g(K,\beta,\gamma,\varepsilon) := (1-(1-\gamma/\beta)2/\varepsilon)K^2 + 2(\beta+\beta/\varepsilon+\gamma/\varepsilon)K + \beta^2 \geqq 0.$$

This, obviously, means that *if* $\varepsilon \geqq 2(1-\gamma/\beta)$ *then* $\left(\overline{N},\overline{P}\right)$ *is asymptotically stable (for arbitrary* $K>0$*).* On the other hand if

$$\varepsilon < 2(1-\gamma/\beta) \tag{3.3}$$

then $g(K,\beta,\gamma,\varepsilon) \geqq 0$ for $0<K\leqq K^*$, and $g(K,\beta,\gamma,\varepsilon)<0$ for $K>K^*$ where

$$K^* = \left(\beta(\varepsilon+1)+\gamma+\left(4\varepsilon\beta^2+(\beta+\gamma)^2\right)^{1/2}\right)/(2(1-\gamma/\beta)-\varepsilon). \tag{3.4}$$

Thus, we have arrived at a corollary of Theorem 2.3.

COROLLARY 3.1. *If* $\gamma<\beta=\delta$, (2.8) *and* (3.3) *hold, and* $0<K\leqq K^*$ *then* $\left(\overline{N},\overline{P}\right)$ *is asymptotically stable.*

Now, let us turn to the most interesting case when (3.3) holds and $K>K^*$. Then g is negative and $\left(\overline{N},\overline{P}\right)$ lies on the up-going branch of the prey isocline, i.e. to the left from the maximum, in the Allée effect zone. An easy calculation shows that in this case $\det J\left(\overline{N},\overline{P}\right)>0$ always. On the other hand

$$\begin{aligned} &\operatorname{Tr} J\left(\overline{N},\overline{P}\right) = \\ &= \varepsilon\left(1-2\overline{N}/K\right)-\varepsilon\beta\left(\beta^2+\beta-\gamma\right)\left(1-\overline{N}/K\right)/\left(\left(\beta-\gamma\right)\left(\beta+\overline{N}\right)\right), \end{aligned} \tag{3.5}$$

hence

$$\begin{aligned} &\operatorname{sgnTr} J\left(\overline{N},\overline{P}\right) = \\ &= \operatorname{sgn}\left(1-\overline{N}/\left(K-\overline{N}\right)-\beta\left(\beta^2+\beta-\gamma\right)/\left(\left(\beta-\gamma\right)\left(\beta+\overline{N}\right)\right)\right). \end{aligned}$$

Thus, $\left(\overline{N},\overline{P}\right)$ is asymptotically stable, resp. unstable if

$$\beta\left(\beta^2+\beta-\gamma\right)/\left(\left(\beta-\gamma\right)\left(\beta+\overline{N}\right)\right)+\overline{N}/\left(K-\overline{N}\right)>1, \quad \text{resp.} \quad <1.$$

Substituting $\overline{N}$ from (3.1) and introducing the notations

$$\begin{aligned} &A = 2(\beta-\gamma)/\left(\varepsilon\beta^2\right)-1/\beta,\ B = 1+\left(\beta^2+\beta-\gamma\right)/(\beta-\gamma)+2\gamma/(\varepsilon\beta), \\ &C = \left(\beta^2+\beta-\gamma\right)/(\beta-\gamma),\ D = (\beta\varepsilon+\gamma)/\varepsilon,\ E = (\varepsilon\beta-(\beta-\gamma))/(2\varepsilon\beta) \end{aligned}$$

we get that the condition of asymptotic stability can be written in the form

$$\left((EK-\beta/2)^2+DK\right)^{1/2} < BK/(AK+C)-EK+\beta/2 \tag{3.6}$$

(and we have instability if the inequality sign is reversed). Because of (3.3), clearly, $A, B, C, D > 0$. The last condition of stability makes sense only if the right hand side is positive. In this case it can be brought to the equivalent form

$$a_2K^2 + a_1K + a_o < 0$$

where

$$a_2 = A(AD+2BE),\ a_1 = 2ACD+2BCE-\beta AB-B^2,\ a_0 = C(CD-\beta B).$$

Now, an easy calculation shows that the right hand side of (3.6) is positive if

$$EAK^2 + (CE - B - A\beta/2)K - C\beta/2 < 0$$

and this holds if $K \in [0, \widetilde{K})$ where $\widetilde{K} = \infty$ if $E \leqq 0$, and

$$0 < \widetilde{K} = \frac{1}{2EA}\Big[B + A\beta/2 - CE +$$
$$+(B^2 + (A\beta/2 + CE)^2 + 2B(A\beta/2 - CE))^{1/2}\Big]$$

if $E > 0$. If we assume that $\beta \leqq \varepsilon/2$ (which is a fairly reasonable assumption taking into account that ε is the maximum growth rate of prey, and β is the predation rate) then it is easy to see that $a_2 > 0$, $a_0 < 0$, i.e. the equation

$$a_2K^2 + a_1K + a_0 = 0 \tag{3.7}$$

has two real roots of different signs. Let us denote the positive root by K_b. Clearly, if $0 < K < K_b$ then $(\overline{N}, \overline{P})$ is asymptotically stable; if $K_b < K$ then it is unstable. Since the determinant of the Jacobian stays positive, and the trace is changing its sign, the loss of stability happens by some kind of an Andronov–Hopf bifurcation. The parameters $\varepsilon, \beta, \gamma$ will be considered fixed, $K > 0$ will play the role of the bifurcation parameter. According to what has been established above we nay expect stability for some $K > K^*$ only if $K^* < \widetilde{K}$. If $K^* \geqq \widetilde{K}$ then the equilibrium point is unstable for all $K > K^*$.

THEOREM 3.2. *If $\gamma < \beta = \delta$, (2.8) holds,*

$$\beta \leqq \varepsilon/2 < 1 - \gamma/\beta, \tag{3.8}$$

$K^* < \widetilde{K}$, and $K_b \in \left(K^*, \widetilde{K}\right)$ then the equilibrium point $\left(\overline{N}(K), \overline{P}(K)\right)$ of system (1.1) undergoes an Andronov–Hopf bifurcation at $K = K_b$; the bifurcation is supercritical, resp. subcritical according as the number

$$\rho = (1/\omega)\big[\left(-\left(1 + r^2\right)\left(s\omega C/\left(\beta + \overline{N}\right) + \varepsilon/K_b\right) + \right. \tag{3.9}$$

$$+rs\beta^2\left(\beta^4/\left((\beta-\gamma)^2(\beta+\overline{N})^2\right)-C\right)/(\beta+\overline{N})^2)\cdot$$
$$\cdot\left(\left(1-r^2+2rsC\right)\omega/\left(\beta+\overline{N}\right)-\right.$$
$$-\beta^2\left(r\beta\left(1-\beta^2/\left((\beta-\gamma)\left(\beta+\overline{N}\right)\right)\right)/(\beta-\gamma)-sC\right)/\left(\beta+\overline{N}\right)^2+$$
$$+2r\varepsilon/K_b)+\left(\left(1+r^2\right)\omega/\left(\beta+\overline{N}\right)+\right.$$
$$+r\beta^3\left(1-\beta^2/\left((\beta-\gamma)\left(\beta+\overline{N}\right)\right)\right)/\left((\beta-\gamma)\left(\beta+\overline{N}^2\right)^2\right)\right)\cdot$$
$$\cdot\left(\left(\left(r^2-1\right)sC-2r\right)\omega/\left(\beta+\overline{N}\right)+\right.$$
$$+\beta^2\left(1-rs\left(\beta^4/\left((\beta-\gamma)^2(\beta+\overline{N})^2\right)-C\right)\right)/\left(\beta+\overline{N}\right)^2+$$
$$+\left(r^2-1\right)\varepsilon/K_b)\big]+s\left(1+r^2\right)3\omega/\left(\beta+\overline{N}\right)^2+$$
$$+\beta^2\left(2rsC-1-3r^2\left(1-\beta^4/\left((\beta-\gamma)\left(\beta+\overline{N}\right)\right)\right)\right)/\left(\beta+\overline{N}\right)^3$$

where $\overline{N}=\overline{N}(K_b)$, $\omega=\left(\det J\left(\overline{N}(K_b),\overline{P}(K_b)\right)\right)^{1/2}$,

$$r=-\varepsilon\beta^3\left(1-\overline{N}/K_b\right)/(\omega(\beta-\gamma)\left(\beta+\overline{N}\right),$$

$$s=\varepsilon\beta\left(1-\overline{N}/K_b\right)/\left(\omega\left(\beta+\overline{N}\right)\right),$$

is negative, resp. positive.

PROOF. Denote the characteristic polynomial of system (1.1) at $(\overline{N}(K),\overline{P}(K))$ by

$$p(\lambda)=\lambda^2-\mathrm{Tr}\,(K)\lambda+\det(K)$$

where $\mathrm{Tr}\,(K)=\mathrm{Tr}\,J\left(\overline{N}(K),\overline{P}(K)\right)$, $\det(K)=\det J\left(\overline{N}(K),\overline{P}(K)\right)$ are given at the end of Section 2 (to be read with $\delta=\beta$). We have seen that $\det(K)>0$ for $K>0$, and that $\mathrm{Tr}\,(K)<0$ for $K\in(0,K_b)$, $\mathrm{Tr}\,(K)>$ >0 for $K\in\left(K_b,\widetilde{K}\right)$. $\mathrm{Tr}\,(K_b)=0$ (this is actually equation (3.7) with the positive root substituted into it). Denote the roots of p by $\lambda_1(K)$, $\lambda_2(K)$. Clearly $\mathrm{Re}\,\lambda_i(K)\gtrless 0$ according as $K\gtrless K_b$. At $K=K_b$, $\mathrm{Re}\,\lambda_i(K_b)=$ $=0$ and $\mathrm{Im}\,\lambda_i(K_b)=\pm i\omega$ where $\omega=(\det(K_b))^{1/2}$. To establish the statement about the occurrence of the bifurcation we have to show that the transversality condition

$$d\mathrm{Re}\,\lambda_1(K_b)/dK=(1/2)\,d\mathrm{Tr}\,(K_b)/dK>0$$

holds. Introducing the notation $f(K)=\overline{N}(K)/K$ we get from (3.5) that

$$\mathrm{Tr}\,(K)=-\varepsilon+\varepsilon(1-f(K))(2-\beta C/\left(\beta+\overline{N}(K)\right),$$

hence

$$d\mathrm{Tr}\,(K)/dK = -\varepsilon f'(K)\left(2 - \beta C/\left(\beta + \overline{N}(K)\right)\right) + \\ + \varepsilon(1 - f(K))\beta C\overline{N}'(K)/\left(\beta + \overline{N}(K)\right)^2.$$

From (3.1) we have

$$f^2(K) - (2E - \beta/K)f(K) - D/K = 0.$$

Differentiating

$$f'(K) = \beta(f(K) - D/\beta)/(K^2(2f(K) - 2E + \beta/K)) < 0$$

since $2f(K) - 2E + \beta/K > 0$ because of (3.1), and $f(K) - D/\beta < 0$ because, clearly, $f(K) < 1$, and $D/\beta = (\varepsilon\beta + \gamma)/(\varepsilon\beta) > 1$. From (3.8) we get $C < 2$, thus $2 - \beta C/\left(\beta + \overline{N}(K)\right) > 0$. We are going to show that $\overline{N}'(K) > 0$. We know that $\overline{N}(K)$ is the solution of $H_1(N) = H_3(N)$ (see Fig. 1), i.e.

(3.10) $$\varepsilon\left(K - \overline{N}(K)\right)\left(\beta + \overline{N}(K)\right) \equiv \beta K\left((\beta - \gamma)\overline{N}(K)/\beta^2 - \gamma/\beta\right).$$

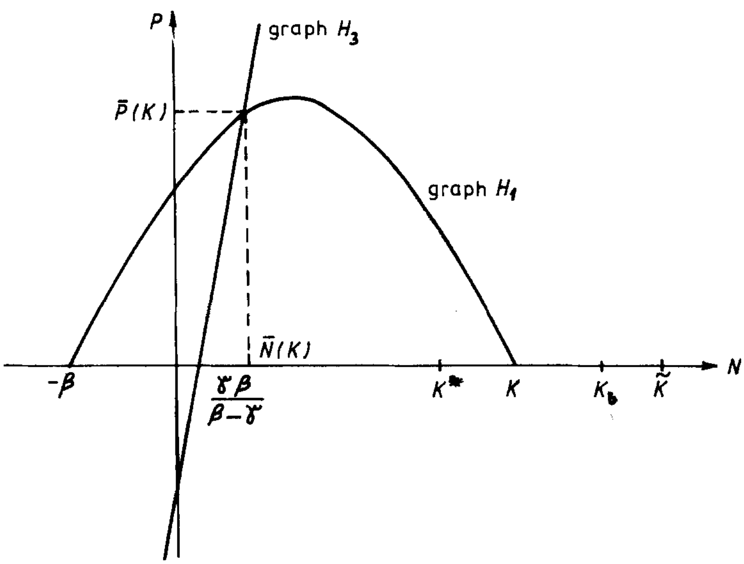

Fig. 1

Differentiating the last identity we get

$$\left(\beta + \overline{N}(K)\right)\overline{N}(K)\varepsilon/(\beta K^2) = \\ = \overline{N}'(K)\left(K(\beta - \gamma) + \varepsilon\beta^2 - \varepsilon\beta K + \varepsilon\beta 2\overline{N}(K)\right)/(\beta^2 K).$$

Thus, $\overline{N}'(K) > 0$ iff

$$K(\beta-\gamma)+\varepsilon\beta^2-\varepsilon\beta K+2\varepsilon\beta\overline{N}(K)>0. \tag{3.11}$$

Expressing K from (3.10) in terms of $\overline{N}$ we get

$$K=\varepsilon\beta\left(\beta+\overline{N}\right)\overline{N}/\left(\varepsilon\beta\left(\beta+\overline{N}\right)+\beta\gamma-(\beta-\gamma)\overline{N}\right).$$

Note that since $K>0$, we have

$$\varepsilon\beta\left(\beta+\overline{N}\right)+\beta\gamma-(\beta-\gamma)\overline{N}>0. \tag{3.12}$$

Substituting the expression for K into (3.11) yields the condition

$$\beta\left(1+\overline{N}\varepsilon\right)+\overline{N}\varepsilon\beta^3/\left(\varepsilon\beta\left(\beta+\overline{N}\right)+\beta\gamma-(\beta-\gamma)\overline{N}\right)>0$$

which holds true, indeed, in view of (3.12). Thus, $d\mathrm{Tr}\,(K)/dK>0$, i.e. all the conditions of the Hopf bifurcation theorem hold (see e.g. [8]). Transforming system (1.1) into normal form and applying Bautin's formula (see [1]) we get (3.9) and this completes the proof of the theorem. □

EXAMPLE. Set $\beta=\delta=0.106$, $\gamma=0.008$, $\varepsilon=1.8000$. These values satisfy the conditions of Theorem 3.2. $\left(K^*,\widetilde{K}\right)=(12.46,\ 31.07)$, and $K_b=$ $=12.92$. Note that for $K\in(K^*,K_b)=(12.46,\ 12.92)$ the asymptotically stable equilibrium $\left(\overline{N}(K),\overline{P}(K)\right)$ is in the Allée effect zone (like the case shown on Fig. 1).

$$\left(\overline{N}(K),\overline{P}(K)\right)=(6.40,\ 55.77),\quad \text{and}\quad \rho=-1.62\cdot10^{-4}.$$

Thus, at $K=K_b$ the equilibrium undergoes a supercritical Andronov–Hopf bifurcation, i.e. for $K>12.92$ (not too large) the system has a small amplitude orbitally asymptotically stable periodic solution.

4. The model with memory

We get a more realistic model if in the second equation of (1.1) we replace the present value of prey by the time average of prey quantity over the past. We follow Cushing [3], MacDonald [10] and Farkas [5] (see also Szabó [13]) in assuming that the influence of the past is fading away exponentially. Accordingly, instead of $N(t)$ the function

$$Q(t):=\int_{-\infty}^{t}N(\tau)a\exp\left(-a(t-\tau)\right)d\tau,\quad a>0 \tag{4.1}$$

will be introduced. Here the exponential weight function satisfies

$$\int_{-\infty}^{t} a \exp\left(-a(t-\tau)\right) d\tau = \int_{0}^{\infty} a \exp\left(-as\right) ds = 1.$$

The smaller $a > 0$ is the longer is the time interval in the past in which the values of N are taken into account, i.e. $1/a$ is the "measure of the influence of the past".

Thus, (1.1) will be replaced by the integro-differential equation

$$\text{(4.2)} \qquad \begin{cases} \dot{N} = \varepsilon N(1 - N/K) - \beta NP/(\beta + N), \\ \dot{P} = -P(\gamma + \delta P)/(1 + P) + \beta PQ/(\beta + Q) \end{cases}$$

where Q is in given by (4.1). It can be easily shown that on the interval $t \in [0, \infty)$ (4.2) is equivalent to the ordinary differential system

$$\text{(4.3)} \qquad \begin{cases} \dot{N} = \varepsilon N(1 - N/K) - \beta NP/(\beta + N) \\ \dot{P} = -P(\gamma + \delta P)/(1 + P) + \beta PQ/(\beta + Q) \\ \dot{Q} = a(N - Q) \end{cases}$$

(see [4]). This system has the following equilibrium points. The origin $(0, 0, 0)$ which is unstable and of no interest, the point $(K, 0, K)$ which is asymptotically stable if $\beta K/(\beta + K) < \gamma$ and unstable if $\beta K/(\beta + K) > \gamma$, and one or more equilibria with positive coordinates if and only if $\beta K/(\beta + + K) > \gamma$, or equivalent iff

$$\text{(4.4)} \qquad 0 < \beta\gamma/(\beta - \gamma) < K$$

(cf. (2.7)). The coordinates $\left(\overline{N}, \overline{P}, \overline{Q}\right)$ of an equilibrium are determined by the conditions $\overline{Q} = \overline{N}$, $\overline{P} = H_1\left(\overline{N}\right) = H_2\left(\overline{N}\right)$ where H_1 and H_2 are the functions introduced in Section 2 describing the prey and the predator null--clines, respectively. From the equality of H_1 and H_2 we get that $\overline{N}$ must be a positive root of the cubic polynomial

$$\text{(4.5)} \qquad q(N) = N^3 + q_2 N^2 + q_1 N + q_0$$

where

$$q_0 = -\beta^2 K(\varepsilon\delta + \gamma)/(\varepsilon(\delta - \beta)),$$

$$q_1 = \beta K(\beta - \gamma)/(\varepsilon(\delta - \beta)) - \beta\delta(K - \beta)/(\delta - \beta) - \beta K,$$

$$q_2 = \beta\delta/(\delta - \beta) - (K - \beta).$$

We assume, as before, that (2.4) holds (this time) with a strict inequality sign, i.e.

$$\gamma < \beta < \delta. \tag{4.6}$$

So the constant term in the cubic polynomial is negative, thus, there is either one or three positive roots. $(\overline{N}, \overline{P}, \overline{N})$ denotes one of these, $\overline{N} > 0$, $\overline{P} > 0$. As in (2.7) we must have

$$\beta\gamma/(\beta-\gamma) < \overline{N} < K. \tag{4.7}$$

In order to check the stability of this equilibrium we linearize the system, introduce the notations

$$\begin{cases} \eta = \varepsilon/(K\beta), \quad \Theta_1 = \beta\overline{N}/\left(\beta+\overline{N}\right), \quad \Theta_2 = K-\beta-2\overline{N}, \\ \Theta_3 = \left(K-\overline{N}\right)/\left(\beta+\overline{N}\right), \quad \Theta_4 = \left((\delta-\beta)\overline{N}+\beta\delta\right)^2/(\delta-\gamma), \end{cases} \tag{4.8}$$

and obtain for the coefficient matrix and for the characteristic equation, respectively,

$$A = \begin{bmatrix} \eta\Theta_1\Theta_2 & -\Theta_1 & 0 \\ 0 & -\eta\Theta_3\Theta_4 & \eta\beta^2\Theta_3 \\ a & 0 & -a \end{bmatrix},$$

$$\lambda^3 + \left(a+\eta\left(\Theta_3\Theta_4-\Theta_1\Theta_2\right)\right)\lambda^2 + \left(a\eta\left(\Theta_3\Theta_4-\Theta_1\Theta_2\right) - \right. \\ \left. -\eta^2\Theta_1\Theta_2\Theta_3\Theta_4\right)\lambda + a\eta\Theta_1\Theta_3\left(\beta^2-\eta\Theta_2\Theta_4\right) = 0. \tag{4.9}$$

Applying the Routh–Hurwitz criterion the eigenvalues have negative real parts if and only if the following inequalities hold:

$$a+\eta\left(\Theta_3\Theta_4-\Theta_1\Theta_2\right) > 0, \tag{4.10}$$

$$a\left(\Theta_3\Theta_4-\Theta_1\Theta_2\right) - \eta\Theta_1\Theta_2\Theta_3\Theta_4 > 0, \tag{4.11}$$

$$a\eta\Theta_1\Theta_3\left(\beta^2-\eta\Theta_2\Theta_4\right) > 0 \tag{4.12}$$

and

$$M(a) := \left(\Theta_3\Theta_4-\Theta_1\Theta_2\right)a^2 + \left(\eta(\Theta_3\Theta_4-\Theta_1\Theta_2)^2 - \beta^2\Theta_1\Theta_3\right)a - \\ -\eta^2\left(\Theta_3\Theta_4-\Theta_1\Theta_2\right)\Theta_1\Theta_2\Theta_3\Theta_4 > 0. \tag{4.13}$$

Clearly, $\eta, \Theta_1, \Theta_3, \Theta_4 > 0$. Three cases can be distinguished.

Case 1: $\Theta_2 < 0$. This means that $(\overline{N}, \overline{P})$ lies on the descending branch of the prey null-cline of system (1.1). In this case the inequalities (4.10)–(4.12) hold true. If

$$\eta(\Theta_3\Theta_4 - \Theta_1\Theta_2)^2 - \beta^2\Theta_1\Theta_3 \geqq 0 \tag{4.14}$$

then (4.13) holds for all $a > 0$ and $(\overline{N}, \overline{P}, \overline{N})$ is asymptotically stable. If (4.14) does not hold then since the constant term of the quadratic polynomial M is positive, this polynomial either has no real root or has two roots of the same sign. If M has no real roots or has two negative roots then (4.13) holds again for all $a > 0$ and the equilibrium is asymptotically stable. If M has two positive roots, $0 < a_1 < a_0$, say, then the equilibrium is asymptotically stable for large values of a, i.e. for small delays. Using a as a bifurcation parameter, the equilibrium is losing its stability by an Andronov–Hopf bifurcation when a is decreased below a_0, i.e. the delay is increased. However, if a is decreased further below a_1 the equilibrium regains its stability.

Case 2: $\Theta_2 = 0$. The point $(\overline{N}, \overline{P})$ is at the maximum point of the prey null-cline of system (1.1). Again (4.10)–(4.12) hold true. Now, (4.13) is equivalent to

$$a > \beta^2\Theta_1/\Theta_4 - \eta\Theta_3\Theta_4.$$

If the right hand side of this inequality is negative or zero (which taking into account that $\eta = \varepsilon/(K\beta)$ roughly means that the specific growth rate of prey is large enough) then $(\overline{N}, \overline{P}, \overline{N})$ is asymptotically stable for all $a > 0$. A more interesting situation arises if

$$a_0 := \beta^2\Theta_1/\Theta_4 - \eta\Theta_3\Theta_4 > 0.$$

In this case the equilibrium is losing its stability if a is decreased below a_0. This loss of stability occurs again by an Andronov–Hopf bifurcation.

Case 3: $\Theta_2 > 0$. This means that $(\overline{N}, \overline{P})$ is in the Allée effect zone, i.e. on the ascending branch of the prey null-cline of system (1.1). In this case (4.10)–(4.12) are not satisfied automatically.

Let us assume that

$$\Theta_3\Theta_4 - \Theta_1\Theta_2 > 0 \tag{4.15}$$

and

$$\beta^2 - \eta\Theta_2\Theta_4 > 0. \tag{4.16}$$

These inequalities imply (4.10) and (4.12). On the other hand (4.13), (4.15) and (4.16) imply (4.11), thus, (4.13), (4.15) and (4.16) together form a sufficient condition of asymptotic stability of the equilibrium.

If (4.15) and (4.16) hold then the polynomial M has a single positive root $a_0 > 0$, $M(a) > 0$ for $a > a_0$, and $M(a) < 0$ for $0 < a < a_0$. If a is decreased below a_0 then the equilibrium $(\overline{N}, \overline{P}, \overline{N})$ undergoes an Andronov–Hopf bifurcation.

EXAMPLE. Set $\beta = 0.1$, $\gamma = 0.01$, $\delta = 0.1055$, $\varepsilon = K = 1$. The polynomial (4.5) is now $q(N) = N^3 + 1.018N^2 - 0.190N - 0.210$. The only positive equilibrium of system (1.1) $(\overline{N}, \overline{P}) = (0.448,\ 3.025)$ is in the Allée effect zone. For these values of the parameters (4.15) and (4.16) hold, $\Theta_2 > 0$, and the positive root of M is $a_0 = 0.51$. At a_0 (4.11) still holds true, i.e. a_0 is the critical point of the bifurcation.

The Andronov–Hopf bifurcation of the equilibrium

We are going to treat the three cases of the last section together under the additional assumptions (4.15) and (4.16). (In the first and second cases these inequalities hold automatically.)

DEFINITION 5.1. The positive parameters $\beta, \gamma, \delta, \varepsilon, K$ are called *admissible* if (4.6), (4.7), (4.15) and (4.16) hold, the polynomial (4.5) has a single positive root, and the polynomial M in (4.13) has a simple positive root a_0 such that $M(a) > 0$ for $a > a_0$.

Note that if the parameters are admissible then for $a > a_0$ system (4.3) has a single asymptotically stable equilibrium $(\overline{N}, \overline{P}, \overline{N})$ in the closed positive octant. Note also that the conditions imposed imply that at $a = a_0$ (4.11) is still valid.

THEOREM 5.1. *Suppose that the parameters of system* (4.3) *are admissible then as the bifurcation parameter a is decreased at a_0 the equilibrium $(\overline{N}, \overline{P}, \overline{N})$ undergoes an Andronov–Hopf bifurcation.*

PROOF. At a_0 the characteristic equation (4.9) assumes the form

$$\left(\lambda^2 + a_0\eta\left(\Theta_3\Theta_4 - \Theta_1\Theta_2\right) - \eta^2\Theta_1\Theta_2\Theta_3\Theta_4\right) \times \\ \times \left(\lambda + a_0 + \eta\left(\Theta_3\Theta_4 - \Theta_1\Theta_2\right)\right) = 0.$$

The eigenvalues are

$$\lambda_0(a_0) = -a_0 - \eta\left(\Theta_3\Theta_4 - \Theta_1\Theta_2\right) < 0, \quad \lambda_{1,2}(a_0) = \pm i\omega$$

where

$$\omega = \left(a_0\eta\left(\Theta_3\Theta_4 - \Theta_1\Theta_2\right) - \eta^2\Theta_1\Theta_2\Theta_3\Theta_4\right)^{1/2} \tag{4.17}$$

(the expression under the root is positive because of (4.11)). A routine calculation shows that

$$\frac{d\mathrm{Re}\,\lambda_1(a_0)}{da} = -\frac{(\Theta_3\Theta_4 - \Theta_1\Theta_2)\left(\omega^2/a_0 + a_0 + \Theta_3\Theta_4 - \Theta_1\Theta_2\right)}{2\left(\omega^2 + (a_0 + \Theta_3\Theta_4 - \Theta_1\Theta_2)^2\right)} < 0.$$

In [2] the Poincaré–Liapunov constant of this bifurcation has been determined whose sign decides about the supercriticality, resp. subcriticality of the bifurcation.

EXAMPLE. Assuming the parameter values of the Example at the end of Section 4: $\beta = 0.100$, $\gamma = 0.010$, $\delta = 0.1055$, $\varepsilon = K = 1$, we have $(\overline{N}, \overline{P}, \overline{N}) = (0.448,\ 3.025,\ 0.448)$, $a_0 = 0.510$. The parameters are admissible and the Poincaré–Liapunov constant is $\rho = -0.207$. This means that a $0 < \alpha < a_0$ exists such that for $a \in (a_0 - \alpha,\ a_0)$ system (4.3) has small amplitude orbitally asymptotically stable periodic solutions with approximate period $2\pi/\omega = 27.8$.

6. Discussion

We have introduced an autonomous (time independent) predator-prey model (1.1) which we consider a fairly realistic one in this category. The growth of prey is restricted by the carrying capacity K of the environment, the functional response of the predator is of Holling's type, i.e. it is growing with increasing prey quantity but is bounded. The mortality of the predator in the absence of prey is a growing but bounded function of the predator quantity. We have shown (Theorem 2.1) that if the mortality of the predator is high compared to the predation rate then the predator dies out. We have also shown (Theorem 2.2) that even in the case when the predation rate is higher than the minimal specific mortality of the predator (but lower than the maximal mortality) the predator dies out provided that the carrying capacity is low. If in this case the carrying capacity is higher but not too high then we have a positive locally stable equilibrium (Theorem 2.3). In a special case it has been shown that the increase of the carrying capacity destabilizes the equilibrium and generates small amplitude periodic oscillations. This happens somewhere in the interior of the Allée effect zone, i.e. when in the neighborhood of the equilibrium the increase of prey quantity is beneficial to its growth rate. A criterion has been given for the stability of these periodic solutions.

We have introduced infinite delay into the model (4.2) assuming that the predator's growth rate depends on past quantities of prey in an exponentially decreasing way. If now the equilibrium lies on the descending branch of the prey null-cline (i.e. in the neighbourhood of the equilibrium point the increase of prey quantity has an adverse effect on its growth rate) then either the equilibrium stays stable for arbitrary large delay or it loses its stability at some value of delay but regains its stability if the delay is increased further. If the equilibrium lies on the ascending branch of the prey null-cline (i.e. in the neighbourhood of the equilibrium the increase of the prey quantity is beneficial to its growth rate), in the Allée effect zone then the increase of delay destabilizes the system and causes the occurrence of periodic oscillations. In the Ph. D. thesis of the first author conditions are given for the stability of the bifurcating periodic solutions. In a second paper we shall introduce spatial distribution into the same model assuming that prey and predator are diffusing according to Fick's law with different diffusion coefficients.

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