n-dimensional ratio-dependent predator-prey systems with memory*

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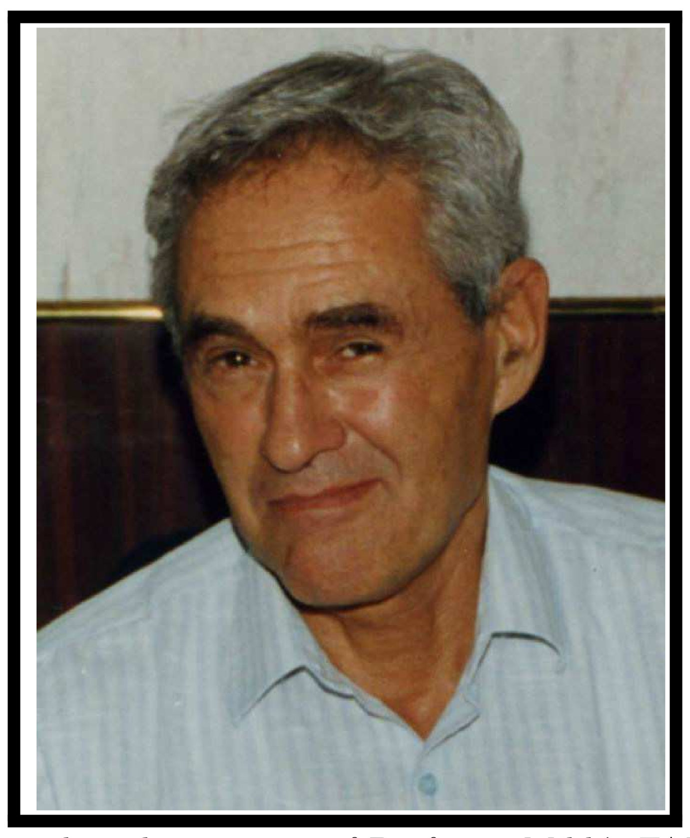
Abstract
The conditions are investigated under which delay in ratio-dependent predator-prey systems cannot cause instability in higher dimension. We give an example when delay causes instability.



Dedicated to the memory of Professor Miklós FARKAS

1 Model without delay

$$\left.\begin{aligned}\dot{x} &= rxg(x,K) - \sum_{i=1}^{n} y_i p_i\left(\frac{y_i}{x}\right)\\ \dot{y}_i &= y_i p_i\left(\frac{y_i}{x}\right) - d_i y_i, \quad i=1,2,\dots,n\end{aligned}\right\}. \tag{1}$$

The per capita growth rate of prey in absence of predators is $rg(x,K)$, $r>0$ is the maximal growth rate of prey, $K>0$ is the carrying capacity of environment with respect to the prey, function g might be e.g. the **logistic** growth rate of prey $g(x,K) = 1-\frac{x}{K}$. The death rate $d_i>0$ of predator i is constant and the per capita birth rate of the same predator is $p_i\left(\frac{y_i}{x}\right)$, see also in [6], where we have already investigated the system with the **Michaelis–Menten** (or **Holling**) type functional response in case of ratio-dependence: $p_i\left(\frac{y_i}{x},a_i\right) = m_i\frac{x}{a_iy_i+x}$ and with the ratio-dependent **Ivlev** functional response: $p_i\left(\frac{y_i}{x},a_i\right) = m_i\left(1-e^{-\frac{x}{a_iy_i}}\right)$, where parameter a_i is the **half saturation constant**, its name coming from the case without ratio-dependence. Details also in [6]. For the survival of predator i it is necessary that $m_i>d_i$.

The presence of predators decreases the growth rate of prey by the amount equal to the birth rate of the respective predator.

Qualitative behaviour of (1) was studied in [6], where it has been supposed that there exists an equilibrium point $E^* = (x^*, y_1^*, \dots, y_n^*)$ in the positive orthant, where x^*, and y_i^* are the solutions of the following equations:

$$rxg(x,K) = \sum_{i=1}^{n} d_i y_i, \quad p_i\left(\frac{y_i}{x}\right) = d_i, \quad i=1,\dots,n. \tag{2}$$

2 Model with delay

The predators' growth rate at present depend on past quantities of prey: a weight (or probability density) function is introduced and $x(t)$ is replaced by its weighted average over the past: $q(t) = \int_{-\infty}^{t} x(\tau)\alpha e^{-\alpha(t-\tau)}d\tau$. This **exponentially fading memory**, see e.g. in [2] means that the smaller $\alpha>0$ is the longer is the time interval in the past in which the values of x are taken into account, i.e. $\frac{1}{\alpha}$ is the **measure of the influence of the past**. With this delay, system (1) is transformed into:

$$\left.\begin{aligned}\dot{x} &= rxg(x,K) - \sum_{i=1}^{n} y_i p_i\left(\frac{y_i}{x}\right)\\ \dot{y}_i &= y_i p_i\left(\frac{y_i}{q}\right) - d_i y_i, \quad i=1,2,\dots,n\\ \dot{q} &= \alpha(x-q)\end{aligned}\right\}. \tag{3}$$

Existence of a positive equilibrium point $E^* = (x^*, y_1^*, \dots, y_n^*)$ of system (1) implies—through the definition $q^* := x^*$—the existence of an equilibrium point $E_d^* = (x^*, y_1^*, \dots, y_n^*, q^*)$ of (3) in the positive orthant. Also, the coefficient matrix A_d of system (3) linearized at E_d^* is can easily be obtained from the coefficient matrix A of the system (1) linearized at E^*.

2.1 One prey two predators with delay

Under natural conditions A_d has the following sign pattern:

$$A_d = \begin{bmatrix} -/0 & - & - & 0\\ 0 & - & 0 & +\\ 0 & 0 & - & +\\ \alpha & 0 & 0 & -\alpha \end{bmatrix}. \tag{4}$$

The characteristic polynomial of A_d is $D(\lambda) = \lambda^4 + a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$. If A_d has the sign pattern as (4), then for all $\alpha>0$ the **necessary condition of stability** $a_i>0$ holds. **Sufficient condition of stability** of matrix A_d in this case is:

$$a_3(a_1a_2 - a_0a_3) - a_1^2 > 0 \tag{5}$$

We have evaluated and investigated this formula using *Mathematica*.

Our starting points are two definitions and and our earlier theorem ([6]). An $n\times n$ matrix $A=[a_{ij}]$ is said to be **stable** if each of its eigenvalues has a negative real part. It is said to be **sign-stable** if each matrix $\tilde{A}$ of the same sign pattern as A is stable.

Theorem 2.1. *If*

$$a_{11} \le 0, \quad p_i'^{*} = p_i'\left(\frac{y_i^*}{x^*}\right) < 0, n, \tag{6}$$

and

$$-d_i - y_i^* p_i'^{*}\frac{1}{x^*} = -d_i - y_i^* p_i'\left(\frac{y_i^*}{x^*}\right)\frac{1}{x^*} < 0, \tag{7}$$

then the coefficient matrix A of the system (1) linearized at E^* is sign-stable, thus, E^* is an asymptotically stable equilibrium point of system (1).

We note that A_d **can not be sign-stable** because its graph have cycles.

The left hand side of condition (5) is of the following form:

$$H(\alpha) = \tilde{A}_3\alpha^3 + \tilde{A}_2\alpha^2 + \tilde{A}_1\alpha + \tilde{A}_0 \tag{8}$$

Lemma 2.1. *If A_d has the same sign pattern as (4) and $a_{11}<0$ then $\tilde{A}_3, \tilde{A}_0 > 0$.*

I.e. the function $H(\alpha)$ given by (8) is positive, and monotone increasing or decreasing depending on $\tilde{A}_1>0$ or $\tilde{A}_1<0$, respectively; and has a convex or concave down shape if $\tilde{A}_2>0$ or $\tilde{A}_2<0$, respectively; at $\alpha=0$.

The form of $H(\alpha)$ under different conditions shows that **there are several cases when delay does not destabilize the system for any** α, for example if $\tilde{A}_2>0$, $\tilde{A}_1>0$, and the cases when $H(\alpha)$ has a single real root only. Furthermore, if α increases through a limit, namely if $\frac{1}{\alpha}$, **measure of the influence of the past** is small, then the system (3) has a locally asymptotically stable equilibrium point E_d^*.

These situations are shown by the following theorem.

Theorem 2.2 (Main result)**.** *If matrix A_d in case of $n=2$ satisfies conditions (6) and (7) (then it also has the same sign pattern as (4)) and the following two conditions also hold*

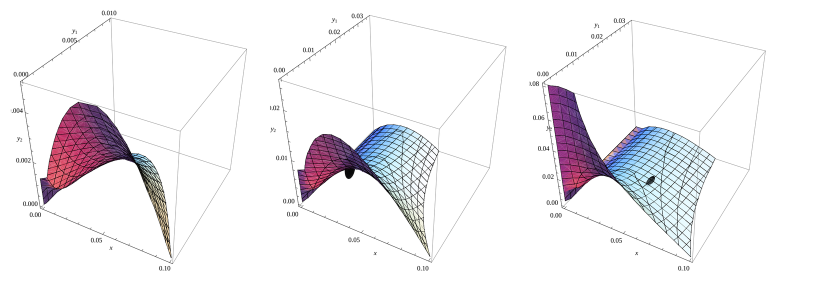
$$a_{11}^2 > a_{33}^2 > -a_{13}a_{34}, \quad a_{11}^2 > a_{22}^2 > -a_{12}a_{24} \tag{9}$$

then A_d is stable and E_d^* is an asymptotically stable equilibrium point of the delayed system (3) for any $\alpha>0$.

This theorem means that the stability behaviour of the system is not too sensitive to the delay, if we are outside the Allée-effect zone. The meaning of **the Allée-effect zone** has been generalized from the two-dimensional case in the sense that we are outside of the Allée-effect zone if in order to keep the prey growth rate zero the increase of prey can be counterbalanced by the decrease of the whole quantities of the different predators.

It can be shown that $a_{11}<0$ holds outside of the Allée-effect zone.

Typical onion-like nullcline surfaces are shown in the following figures.



2.1 Typical zero-clines of prey in case of $r=3,7$ and 10 ($K=0.1$, $m_1=16$, $a_1=4$, $m_2=18$, $a_2=2$)

The big black point in the middle figure shows the equilibrium point in the Allée-effect zone, and in the right figure it is outside of the Allée-effect zone.

Remark 2.1. Conditions $a_{11}^2 > a_{33}^2$, $a_{11}^2 > a_{22}^2$ mean that **intraspecific competition in prey** species is greater than **in predator** species. Conditions $a_{33}^2 > -a_{13}a_{34}$, $a_{22}^2 > -a_{12}a_{24}$ are connected with the phenomenon of their consume strategy: Do they try to ensure their survival by having a relatively high or low growth rate and are able or not to raise their offspring on a scarce supply of food?

These conditions can be ensured by a relative high intrinsic growth rate r of prey, meaning that there is enough food for predators in order to reproduce well, and by not too small values of half saturation constants a_i (e.g. a lower bound of 1 can be proven for these models). In case of ratio-dependent models parameter a_i also has the meaning that the greater a_i is, the more food is needed for predator i.

2.2 One prey, n predators with delay

In this case A_d is a matrix of type $(n+1)\times(n+1)$, and it has a sign pattern similar to (4).

Theorem 2.3. *Suppose A_d satisfies conditions (6) and (7) for all $i=1,2,\dots,n$; furthermore, let $a_{11}<0$. If α is small enough or large enough then A_d is stable, and E_d^* is an asymptotically stable equilibrium state of the delayed system* (3).

2.3 Numerical examples

Consider a three dimensional Holling type ratio-dependent model with delay, and let the constants be given as follows: $m_1=16$, $m_2=18$, $d_1=8$, $d_2=12$, $a_1=4$, $a_2=2$, $K=0.1$. We get

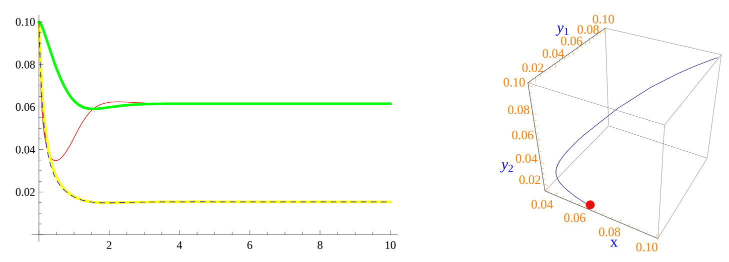
$$E^* = \left(0.1(1-\tfrac{5}{r}), \tfrac{1}{40}(1-\tfrac{5}{r}), \tfrac{1}{40}(1-\tfrac{5}{r})\right),$$

$$E_d^* = \left(0.1(1-\tfrac{5}{r}), \tfrac{1}{40}(1-\tfrac{5}{r}), \tfrac{1}{40}(1-\tfrac{5}{r}), 0.1(1-\tfrac{1}{r})\right),$$

$$A = \begin{bmatrix} 8-r & -4 & -8\\ 1 & -4 & 0\\ 1 & 0 & -4\end{bmatrix}, \quad A_d = \begin{bmatrix} 8-r & -4 & -8 & 0\\ 0 & -4 & 0 & 1\\ 0 & 0 & -4 & 1\\ \alpha & 0 & 0 & -\alpha\end{bmatrix}.$$

The characteristic polynomial of A is easily seen to be a stable polynomial for $r>5$ and A is sign stable for $r\ge 8$.

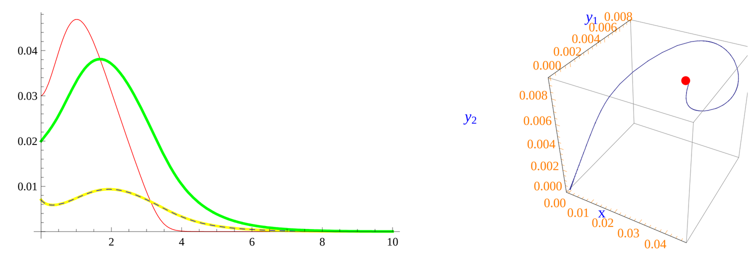
If $r>12$ then conditions (9) hold, E_d^* is asymptotically stable. Time evolutions of the species are shown on the left side of the Figure 2.2, whereas the right side shows the corresponding trajectory together with the equilibrium point.



2.2 Left: Time evolution of the species in case of $r=13$, $\alpha=1$.
Right: The trajectory tends to the asymptotically stable equilibrium point.
(x is red, q is green, y_1 is dashed blue, y_2 is yellow.)

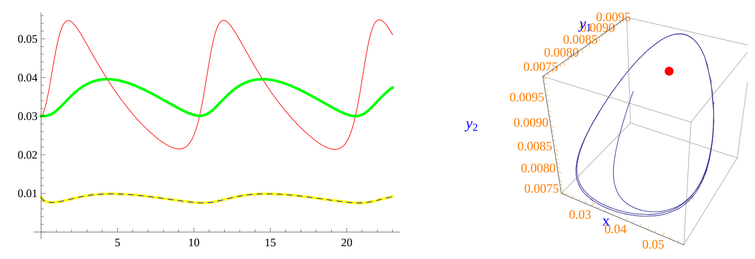
The equilibrium point of the delayed system remains asymptotically stable for any $\alpha>0$. We note that in this case the equilibrium point E^* (of the original system) is outside the Allée-effect zone, see the last figure in Fig. 2.1.

If $12 \ge r > 5$ then conditions (9) are not valid, and there are such cases when E_d^* is stable and there are cases when it is unstable. Time evolution of the species, trajectory together with the equilibrium point are all shown on Figure 2.3.



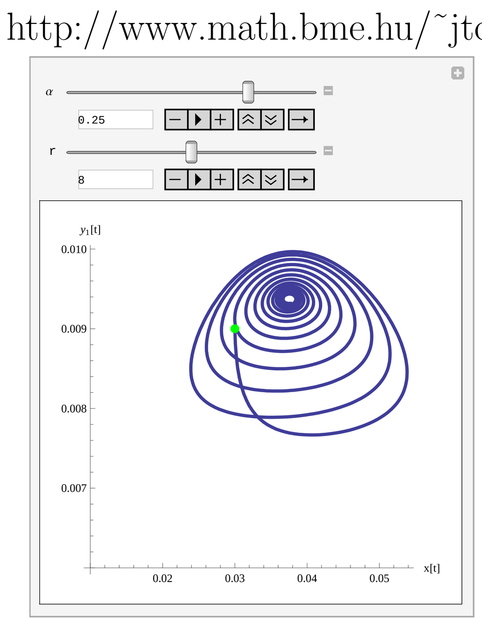
2.3 Left: Time evolution of the species in case of $r=7$, $\alpha=1$.
Right: The trajectory leaves the neighborhood of the unstable equilibrium point.
(x is red, q is green, y_1 is dashed blue, y_2 is yellow.)

We note that in this case the equilibrium point E^* is inside the Allée-effect zone, see the middle figure in Fig. 2.1. Of course this study is not complete. There are many interesting trajectories, periodic orbits, see e. g. figure 2.4.



2.4 Left: Seemingly time periodic evolution of the species in case of $r=8$, $\alpha=0.2$.
Right: The corresponding periodic orbit.
(x is red, q is green, y_1 is dashed blue, y_2 is yellow.)

The interested reader can experiment with the parameters and initial conditions of the model using the *Mathematica* program on the page http://www.math.bme.hu/~jtoth/index.html#kktj.



2.5 The effect of parameter changes can be seen immediately using the `Manipulate` command of *Mathematica*.

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