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Review on the behaviour of a many predator–one prey system

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Abstract. We consider a known predator-prey system, where more than one predator compete for the same prey. Mainly the case with two predators is considered. A review of general results is given, among them conditions for the extinction of one predator and an investigation of the different types of coexistence of predators. In non-degenerate cases the predators in this model cannot coexist at an equilibrium, but there can be a cyclic or more complicated coexistence. Many numerical results are presented. A model map for a Poincaré map is given under some conditions. But the most interesting case where there can arise "spiral-like" attractors is not well known here, and we pose open questions. We discuss some bifurcations and the existence of systems with several attractors.

Keywords: bifurcation, chaos, predator-prey.

1. Introduction

In this work we make a review of the behaviour of a system of two predators and one prey. We discuss extinction and possible types of coexistence. The coexistence can be cyclic or chaotic of different types. In some cases the chaos is well described by a model map, in other cases it seems to be a spiral-like attractor. We conjecture that at least some of the spiral chaos comes from bifurcations from a contour described here. There is an open question whether there are even more types of chaos. We also give examples, where the system has more than one attractor. Some of the results are more general for the case of more predators, like dissipativity and extinction.

The general system of n competing predators feeding on the same prey is considered to be of the type

$$\begin{aligned} X_i' &= p_i\varphi_i(S)X_i - d_iX_i, \qquad i = 1, \dots, n, \\ S' &= H(S) - \sum_{i=1}^{n} q_i\varphi_i(S)X_i, \end{aligned} \tag{1.1}$$

where the variable S represents the prey populations and the variables X_i represent the predator populations. They are, of course, non-negative. The function φ_i is assumed non-decreasing. The function H describes the behaviour of the prey without predators and is usually of logistic type. An exception is the Lotka-Volterra system, the behaviour of which is simple in this case. These systems were introduced by Hsu and Waltman [6, 7, 8]. We mainly consider the case where

$$H(S) = rS\left(1 - \frac{S}{K}\right), \quad \varphi_i(S) = \frac{S}{S + A_i}, \quad i = 1, \ldots, n. \tag{1.2}$$

A. V. Osipov [12] introduced a family defined by some conditions on the functions of system (1.1) given below.

We assume $H(0) = H(K) = 0$ for some $K > 0$, $H'(K) < 0$, $H''(s) < 0$ and $\varphi_i(0) = 0, \varphi_i'(s) > 0$. The functions φ_i and H are of the class $C^2[0, \infty)$ and the variables x_i and s are non-negative: $x_i \geq 0, s \geq 0$. The change of variables $s = \dfrac{S}{K}$ and $x_i = \dfrac{q_i}{K}X_i$ gives the system

$$\begin{aligned} x_i' &= \phi_i(s)x_i, \quad i = 1, \ldots, n, \\ s' &= h(s) - \sum_{i=1}^{n} \psi_i(s)x_i, \end{aligned} \tag{1.3}$$

where

$$h(s) = \frac{1}{K}H(sK), \quad \psi_i(s) = \varphi_i(sK), \quad \phi_i(s) = p_i\psi_i(s) - d_i.$$

The following conditions $A_1 - A_5$ are the main conditions introduced by Osipov [12]. Here and further we will assume that i takes values from the set $\{1, 2, \ldots, n\}$.

- A_1. All the considered functions are of the class $C^2[0, \infty)$ and the variables x_i and s are non-negative: $x_i \geq 0, s \geq 0$.
- A_2. $\psi_i(0) = 0$, $\psi_i'(s) > 0$ for $s > 0$.
- A_3. $\phi_i'(s) > 0$ for $s > 0$ and there exists a $\lambda_i > 0$ such that $\phi_i(\lambda_i) = 0$.
- A_4. $h(0) = h(1) = 0$, $h'(1) < 0$ and $h''(s) < 0$ for $s > 0$.
- A_5. $0 < \lambda_n < \cdots < \lambda_2 < \lambda_1 < 1$.

If λ_i in (A_3) are all different we can always reorder the equations so that (A_5) is satisfied. We observe that if $\lambda_i \geq 1$ for some i, then the corresponding predator cannot survive.

The most standard example of system (1.3), which we will consider now, is obtained from the functions in (1.2). We assume $p_i > d_i$. If not, the corresponding predator will not survive. Using the time change $\tau = rt$, where τ is the new time, and the variable changes $s = \dfrac{S}{K}, x_i = \dfrac{q_i}{rK}X_i$, we get the simplified equations

$$\begin{aligned} x_i' &= m_i\frac{s - \lambda_i}{s + a_i}x_i, \\ s' &= \left(1 - s - \sum_{i=1}^{n} \frac{x_i}{s + a_i}\right)s, \end{aligned} \tag{1.4}$$

where

$$a_i = \frac{A_i}{K}, \quad m_i = \frac{p_i - d_i}{r}, \quad \lambda_i = \frac{d_i A_i}{K(p_i - d_i)}.$$

In earlier works [4, 5, 13, 14], for $n = 2$, we have discussed the behaviour of the system, boundaries for extinction, different types of coexistence of the predators, cyclic and chaotic. In some cases we have conjectured the existence of spiral chaos [15, 16, 17, 11]. In this work we present an overview of earlier results and some new results from numerical experiments of this system. It is a serious update of the review in [14], but without elementary introduction. Before we consider the properties of this systems, we shortly look at the Lotka-Volterra system, where in (1.1) the functions are

$$H(S) = rS, \quad \varphi_i(S) = S,$$

and thus the system becomes

$$\begin{aligned} X_i' &= (p_i S - d_i) X_i, \quad i = 1, \ldots, n, \\ S' &= \left(r - \sum_{i=1}^{n} q_i X_i \right) S, \end{aligned}$$

A change of the time $\tau = rt$ and the variables $x_i = \dfrac{q_i X_i}{r}$ gives the system

$$\begin{aligned} x_i' &= m_i (s - \lambda_i) x_i, \quad i = 1, \ldots, n, \\ s' &= \left(1 - \sum_{i=1}^{n} x_i \right) s, \end{aligned}$$

where $m_i = \dfrac{p_i}{r}, \lambda_i = \dfrac{d_i}{p_i}$. Further, suppose that $\lambda_n < \cdots < \lambda_2 < \lambda_1$. Then all predators except the population x_n go extinct. To see that, use the Lyapunov function $\ln \left(\dfrac{x_i^{m_n}}{x_n^{m_i}} \right)$.

The main system we consider is anyhow rich in the behaviour of coexistence of the predators and it is one of the first systems, where the known Ecological Principle of Exclusion does not hold in general.

The outline of our work is the following. We start with discussing the dissipativity and extinction problem for any number of predators. Then we restrict ourselves to two predators and after shortly mentioning the chaos got from a model map (details can be found in earlier works) we give some typical results from numerical examination of the system. We look for extinction boundaries and for boundaries between different cyclic and chaotic behaviour. We continue with discussing a contour from which the spiral-like chaos might bifurcate. Then we show a bifurcation diagram from which we immediately conclude the existence of, at least, two attractors. At the end we give an example of the dynamics of a Poincaré map and mention about modifications in order to get more realistic systems from a biological point of view.

2. Dissipativity

We consider system (1.3). We find a positively invariant set for the system. More results on dissipativity are found in [12]. Let

$$w_i = \sup_{0<s<1} \tilde{w}_i(s), \tilde{w}_i(s) = \frac{\phi_i(s) + \frac{h(s)}{1-s}}{\psi_i(s)}, V = \frac{x_1}{w_1} + \frac{x_2}{w_2} + \dots + \frac{x_n}{w_n} + s.$$

The value of w_i is finite and positive, because $\tilde{w}_i(s) \to -\infty$ for $s \to 0+0$ and $\tilde{w}_i(s) \to \frac{\phi_i(1)-h'(1)}{\psi_i(1)} = Q_i > 0$ for $s \to 1-0$. We now claim the following:

Statement 1. *The set formed by the inequalities $s, x_i \geq 0$ and $V \leq 1$ is positively invariant for system 1.3 satisfying conditions $A_1 - A_5$ and all trajectories of the system with positive initial values enter the set in finite time.*

Proof. It can be checked directly, that if $s = 1$ then $V' < 0$ except at $(0, \dots, 0, 1)$ where $V' = 0$. In other points we get

$$\begin{aligned} V' &= h(s) + \sum_{i=1}^{n} \left[\frac{\phi_i(s)}{w_i} - \psi_i(s) \right] x_i = \\ &= \frac{h(s)}{1-s}(1-V) + \frac{h(s)}{1-s}(V-s) + \sum_{i=1}^{n} \frac{x_i}{w_i} \left[\phi_i(s) - w_i \psi_i(s) \right] = \\ &= \frac{h(s)}{1-s}(1-V) + \sum_{i=1}^{n} \frac{x_i}{w_i} \left[\frac{h(s)}{1-s} + \phi_i(s) - w_i \psi_i(s) \right] < 0. \end{aligned}$$

From here the statment follows. □

Let us examine the case where

$$h(s) = (1-s)s, \phi_i(s) = \frac{s^{b_i} - \lambda_i}{s^{b_i} + a_i}, \psi_i(s) = \frac{s^{b_i}}{s^{b_i} + a_i}. \tag{2.1}$$

If $0 < b_i \leq 1$ then $\tilde{w}_i(s)$ increases and $w_i = Q_i$. If $b_i > 1$ then it is possible that $w_i > Q_i$. For example, $b_i = 2a_i = 1, \lambda_i = 0.1$ gives $\tilde{w}_i(0.5) = 3.1$ and $Q_i = 2.9$.

3. Extinction

We here look for the competition between predators i and j for system (1.4). We find sufficient conditions for the extinction of one of them. More general results on extinction are found in [12]. We assume there is some j such that $\lambda_j < \lambda_i$, that is $i > j$.

Statement 2. *Let $L = \dfrac{\lambda_i(1-\lambda_j)}{\lambda_j(1-\lambda_i)}$ and $\lambda_i > \lambda_j$. If $a_j > \dfrac{a_i}{L + a_i(L-1)}$ then the predator i goes extinct.*

Because $L > 1$ the predator i always goes extinct when $a_j > \dfrac{1}{L-1}$. We observe that condition

$$a_j > \frac{a_i}{L + a_i(L-1)} \tag{3.1}$$

follows from $a_j > \dfrac{a_i}{L}$ and $a_j > a_i$.

Proof. We look at the function η defined by

$$\eta(s) = \frac{\phi_j(s)}{\phi_i(s)} = \eta_1(s)\eta_2(s),$$

where

$$\eta_1(s) = \frac{m_j(s-\lambda_j)}{m_i(s-\lambda_i)}, \eta_2(s) = \frac{s+a_i}{s+a_j}.$$

We use notations $\gamma = \eta(0), \alpha = \eta(1)$. We notice that $\gamma < \alpha$ is equivalent to $a_j > \dfrac{a_i}{L + a_i(L-1)}$. We introduce two numbers

$$\kappa_0 = \max_{s \in [0,\lambda_j]} \eta(s), \kappa_1 = \min_{s \in [\lambda_i, 1]} \eta(s).$$

They exist and are positive. We prove $\kappa_0 < \kappa_1$. We start with the case where $a_i \le a_j$. From $\lambda_j < \lambda_i$ follows $\eta_1(s) < 1$ for $0 < s < \lambda_j$ and $\eta_1(s) > 1$ for $s > \lambda_i$. Thus we get $\eta(s) < \eta_2(s)$ for $0 < s < \lambda_j$ and $\eta(s) > \eta_2(s)$ for $s > \lambda_i$. Because η_2 is increasing or constant for $a_1 \le a_2$ we conclude that $\eta(s_1) > \eta_2(s_1) \ge \eta_2(s_0) > \eta(s_0)$ for $s_0 < \lambda_j$ and $s_1 > \lambda_i$ from which follows $\kappa_0 < \kappa_1$ and (3.2).

We now consider the case where $a_j \le a_i$. We observe that in this case both η_1 and η_2 are decreasing and thus also η. Then $\kappa_0 = \eta(0) = \gamma$ and $\kappa_1 = \eta(1) = \alpha$. We observe that if κ is a number such that $\kappa_0 < \kappa < \kappa_1$ then

$$\kappa\phi_i(s) - \phi_j(s) < 0 \tag{3.2}$$

for all $s \in (0, 1)$.

Really, for $s \in (0, \lambda_j]$, $\phi_i(s)$ is negative and $\phi_j(s)$ is non-positive and from $\eta(s) < \kappa_0$ we get $\phi_j(s) > \kappa_0\phi_i(s) > \kappa\phi_i(s)$ implying (3.2). For $s \in (\lambda_j\lambda_i]$, $\phi_i(s) \le 0 < \phi_j(s)$ implying (3.2). Finally for $s \in (\lambda_i, 1)$ both $\phi_i(s)$ and $\phi_j(s)$ are positive and from $\eta(s) > \kappa_1$ we get $\phi_j(s) > \kappa_1\phi_i(s) > \kappa\phi_i(s)$ implying (3.2).

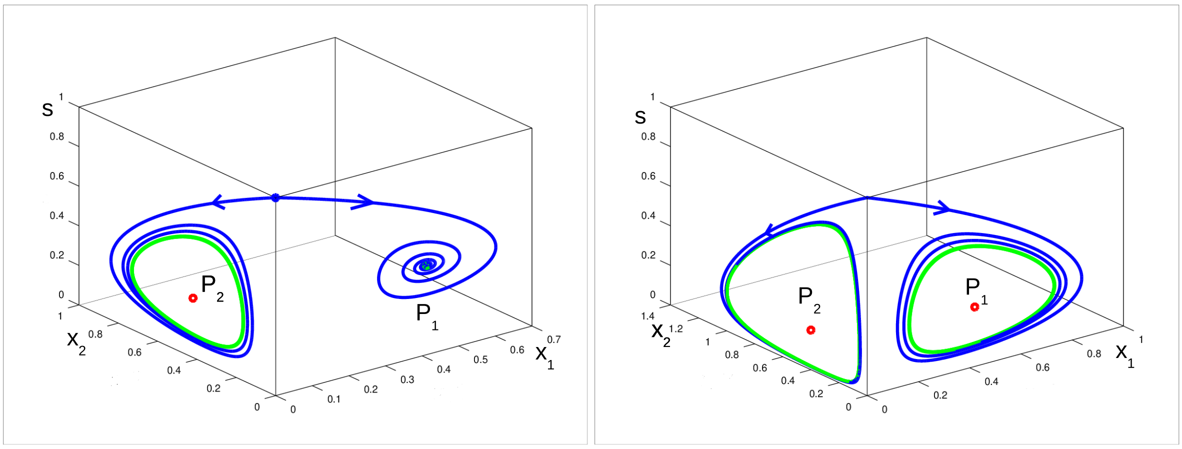
Consider now the function U defined by $U(x, y) = \ln\left(\dfrac{x_i^\kappa}{x_j}\right)$. For the time derivative we get $U' = \kappa\phi_i(s) - \phi_j(s) < 0$ and predator x_i goes extinct. □

Remark. We notice that the proof can easily be modified for the functions in (2.1), so that the statement holds also if these functions are chosen for system (1.3).

It is well known [3] that when the number of predators increases, the probability for coexistence of all of them tends to zero. This is quite natural also from our estimates showing that for coexistence we must have $a_i > La_{i-1}$, where $L > 1$ is defined as in statement 2 for $j = i - 1$.

4. General behaviour

We shortly decribe the main local behaviour of the three-dimensional system. According to assumption (A_5) we suppose $\lambda_1 > \lambda_2$. The system always has two equilibria: (0,0,0), which always is a saddle with two-dimensional stable manifold in the plane $s = 0$, and (0,0,1), which is a saddle with one-dimensional stable manifold on the axis $x_1 = x_2 = 0$ if $\lambda_1, \lambda_2 < 1$ (in other cases at least one predator goes extinct and the system reduces to smaller dimension). When $\lambda_1, \lambda_2 < 1$ there are two more equilibria:



a) $\lambda_1 = 0.45, \lambda_2 = 0.3, a_1 = a_2 = 0.3, m_1 = m_2 = 1$ b) $\lambda_1 = 0.3, \lambda_2 = 0.2, a_1 = a_2 = 0.3, m_1 = m_2 = 1$

Fig. 1. (a) In plane $x_2 = 0$ the equilibrium P_1 is a global attractor, in the whole space a saddle with one-dimensional unstable manifold, in plane $x_1 = 0$ there is a limit cycle, the equilibrium in this plane is a saddle with one-dimensional stable manifold. (b) Plane $x_1 = 0$ there is a limit cycle, the equilibrium in this plane is a saddle with one-dimensional stable manifold. In plane $x_2 = 0$ there is a limit cycle, the equilibrium in this plane is a sink.

- $P_1 = ((1 - \lambda_1)(1 + a_1)), 0, \lambda_1)$ *which is a saddle with one-dimensional unstable manifold for* $\lambda_1 > \dfrac{1 - a_1}{2}$ *and a source if* $\lambda_1 < \dfrac{1 - a_1}{2}$. *In the case* $\lambda_1 > \dfrac{1 - a_1}{2}$, P_1 *is a global attractor in the plane* $x_2 = 0$.
- $P_2 = (0, (1 - \lambda_2)(1 + a_2)), \lambda_2)$ *which is a saddle with one-dimensional stable manifold for* $\lambda_2 < \dfrac{1 - a_2}{2}$ *and a sink if* $\lambda_2 > \dfrac{1 - a_2}{2}$. *In the case* $\lambda_2 > \dfrac{1 - a_2}{2}$, P_2 *is a global attractor in the plane* $x_1 = 0$.

There is a unique globally attracting limit cycle in the plane $x_2 = 0$ if $\lambda_1 < \dfrac{1 - a_1}{2}$ and a unique globally attracting stable limit cycle in the plane $x_1 = 0$ if $\lambda_2 < \dfrac{1 - a_2}{2}$.

This was first proved by Cheng [2]. The uniqueness of limit cycles for this and similar systems can also be proved using the known Zhang Zhi-fen theorems [18]. Estimates for the size of the cycles for critically small a_i and λ_i are given in [9, 10]. The size of the cycle we determine by the maximal and minimal populations on the cycle. The cycle is called big if at least one population sometimes gets small. The behaviour around the coordinate planes is shown in figure 1.

There is no equilibrium for $\lambda_1 \neq \lambda_2$ or $a_1 \neq a_2$, where the predators coexist, anyhow they can coexist in a cyclic or chaotic way. Conditions for construction of some well-defined Poincaré maps on $s = const, s' < 0$ are obtained in [13].

In the case where the Poincaré map is well-defined, very often there is a strong contraction in the $(x_1 + x_2)$-direction and it is shown by numerical experiments and theoretical estimating arguments that the one dimensional model map given by

$$f(v) = \beta + v - \frac{k_1 + k_2 e^v}{1 + e^v} u,$$

where β, u and k_i are constants and $v = \ln(x_2/x_1)$ gives a good approximation. This map is derived and analyzed for simple behaviour in [4, 5].

4.1. Charts of dynamical regimes

We now present some result of numerical two-parametric analysis.

In figures 2 – 4 we see the results of numerical investigations of the behaviour of the system for fixed λ_i and m_i where $i = 1, 2$. We have examined the behaviour for five different random initial conditions for a grid of parameter values of a_1 and a_2. A predator is considered to go extinct if the populations becomes less than e^{-100}. We call the attractor n-cyclic if the intersection with $s = \lambda_2, s' < 0$ is n-periodic under the Poincaré map defined on this surface. We have denoted regions with `x` if the first predator x_1 goes extinct and with `y` if the second predator x_2 goes extinct. Regions, where there is observed only simple one-periodic cycles, are coloured cyan. Regions, where there is observed a 2-cyclic attractor, are coloured magenta. Regions, where there is observed a 3-cyclic attractor, are coloured dark yellow. Sometimes also regions where the second predator x_2 goes extinct can be seen in green. Regions, where there is observed chaos, but no 3-cyclic attractor, are coloured blue. We observe, that for some parameter values two different types of attractors have been detected.

In figures 2 – 3 we have added a figure calculating the boundaries for extinction of the predator x_1 for different values of m_i and compared with the theoretical estimate (the curve to the left).

We make the observation that the behaviour depends on m_1 and m_2 and strongly on the difference of λ_1 and λ_2. When $\lambda_1 \to \lambda_2$ we roughly have the following situation for a_1 increasing: for a_1 small, the predator x_1 goes extinct, for a little bigger, the predator x_2 goes extinct and for even bigger a_1 there is a simple cyclic coexistence. The predator x_2 can go extinct only if $a_1 < 1 - 2\lambda_1$, because if $a_1 > 1 - 2\lambda_1$ then there is saddle equilibrium in the coordinate plane $x_2 = 0$ and there is more likely to

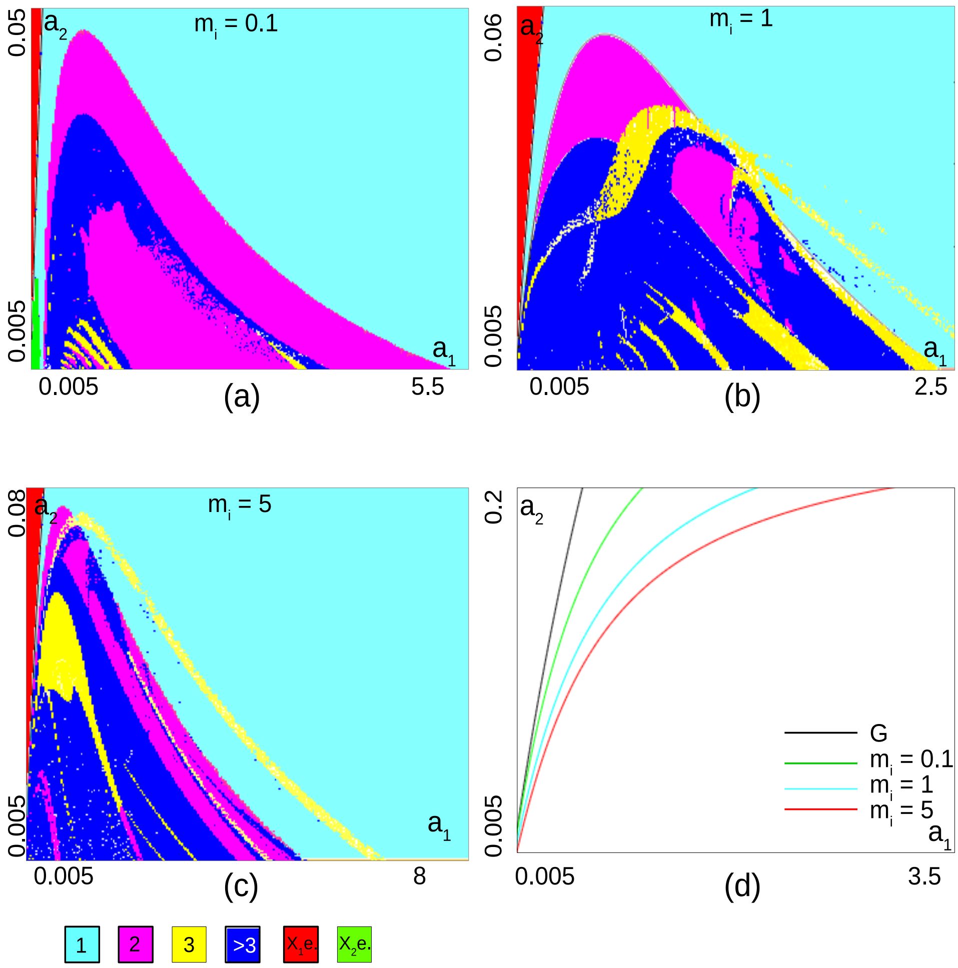


Fig. 2. (a),(b),(c) Charts of dynamical regimes for the system 1.4 on the parameter plane (a1, a2) for $m_i = 0.1$, $m_i = 1$, and $m_i = 5$, respectively ($\lambda_1 = 0.35, \lambda_1 = 0.2$). Cyan color (1) corresponds to simple periodic regimes; magenta color (2) — 2-periodic regimes; dark yellow (3) — 3-periodic regimes; blue (> 3) — periodic regimes with period > 3 and a chaotic regimes; red color (x_{1e}) — regime corresponding to the extinction of the first predator x_1; and green color (x_{2e}) — the extinction of the second predator x_2. (d) Curves of the extinction of the predator x_1: G theoretical estimate (3.1), green, blue, and red curves are given by compared (3.1) for $m_i = 0.1$, $m_i = 1$, and $m_i = 5$, respectively.

be some kind of spiral chaos if it is not cyclic. Of this reason there is no extinction of the second predator in figure 3.

We have not included pictures for small λ_1 and λ_2. In this case there is a hope to obtain theoretical estimates for the stability of the limit cycles in the coordinate planes. If both are unstable the predators coexist.

Open problem. Find out good reasons for the different behaviour observed in the

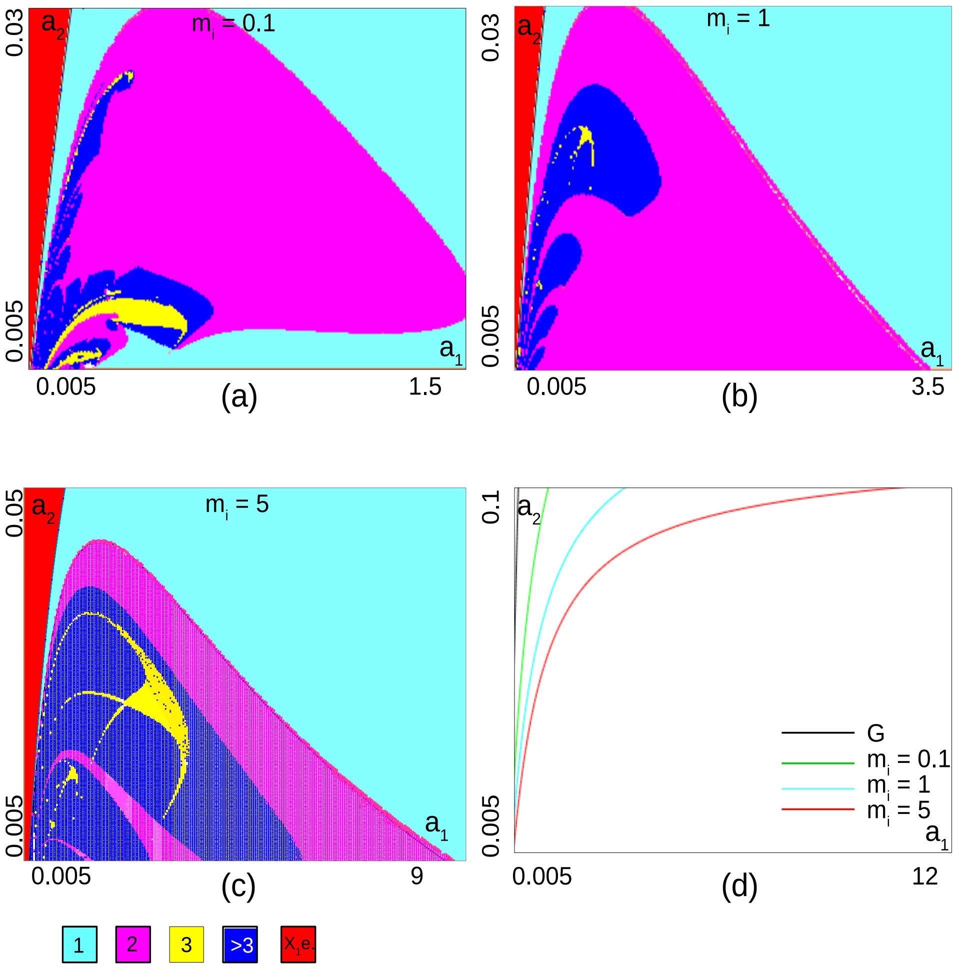


Fig. 3. (a),(b),(c) Charts of dynamical regimes for the system 1.4 on the parameter plane (a1, a2) for $m_i = 0.1$, $m_i = 1$, and $m_i = 5$, respectively ($\lambda_1 = 0.5, \lambda_1 = 0.2$). Cyan color (1) corresponds to simple periodic regimes; magenta color (2) — 2-periodic regimes; dark yellow (3) — 3-periodic regimes;blue ($>$ 3) — periodic regimes with period $>$ 3 and a chaotic regimes; red color (x_{1e}) — regime corresponding to the extinction of the first predator x_1. (d) Curves of the extinction of the predator x_1: G theoretical estimate (3.1), green, blue, and red curves are given by compared (3.1) for $m_i = 0.1$, $m_i = 1$, and $m_i = 5$, respectively.

figures and find approximate expressions for different bifurcation lines. Find bifurcation curves for attractors by numerical methods. How many attractors can we have in the same system for different parameters?

The cases where $\lambda_1 = 0.3$ and $\lambda_1 = 0.2$ and $m_i > 0.2$ are very interesting even if we do not include a figure here. But the existence of three different attractors is frequent in these cases.

In figure 5 we can see a case with three attractors.

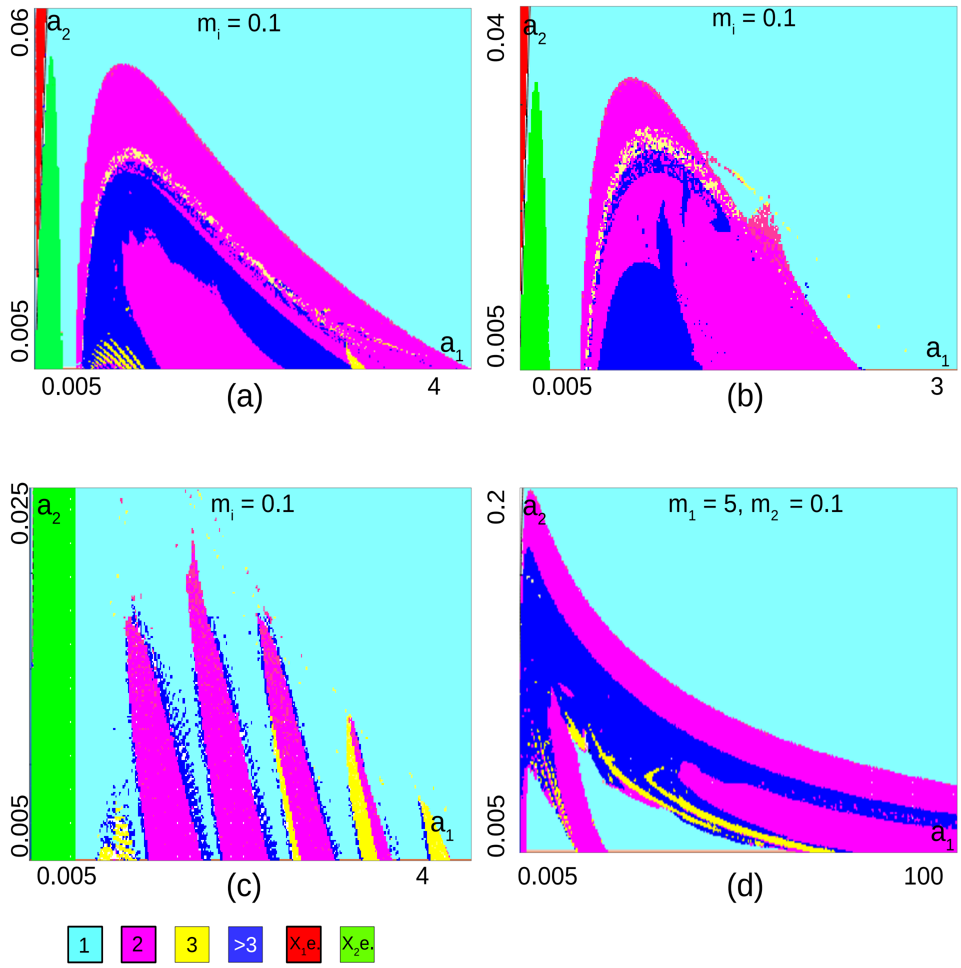


Fig. 4. (a), (b), (c), (d) Charts of dynamical regimes for the system 1.4 on the parameter plane (a1, a2) for (a),(b) $\lambda_1 = 0.3$ and $\lambda_1 = 0.2$ and $m_i = 0.1$, (c) $\lambda_1 = 0.25$ and $\lambda_1 = 0.2$ and $m_i = 0.1$, (d) $\lambda_1 = 0.35$ and $\lambda_1 = 0.2$ and $m_1 = 5$ and $m_2 = 0.1$. Cyan color (1) corresponds to simple periodic regimes; magenta color (2) — 2-periodic regimes; dark yellow (3) — 3-periodic regimes; blue (> 3) — periodic regimes with period > 3 and a chaotic regimes; red color (x_{1e}) — regime corresponding to the extinction of the first predator x_1; and green color (x_{2e}) — the extinction of the second predator x_2.

We now analyze the bifurcation diagram in [14]. This was produced for $a_2 = 0.02, \lambda_1 = 0.35, \lambda_2 = 0.2, m_1 = m_2 = 1$ and for a_1 as bifurcation parameter. New versions of this bifurcation diagram are produced in figure 6.

In figure 6 (a) we produce a bifurcation diagram looking at the value of $\ln\left(\dfrac{x_2}{x_1}\right)$ on the intersection of the attractor with $s = \lambda_2, s' < 0$. The initial values for $a_1 = 0.1$ were taken as $x_1 = x_2 = s = 0.5$ and increasing a_1 for the next value of a_1 we take the

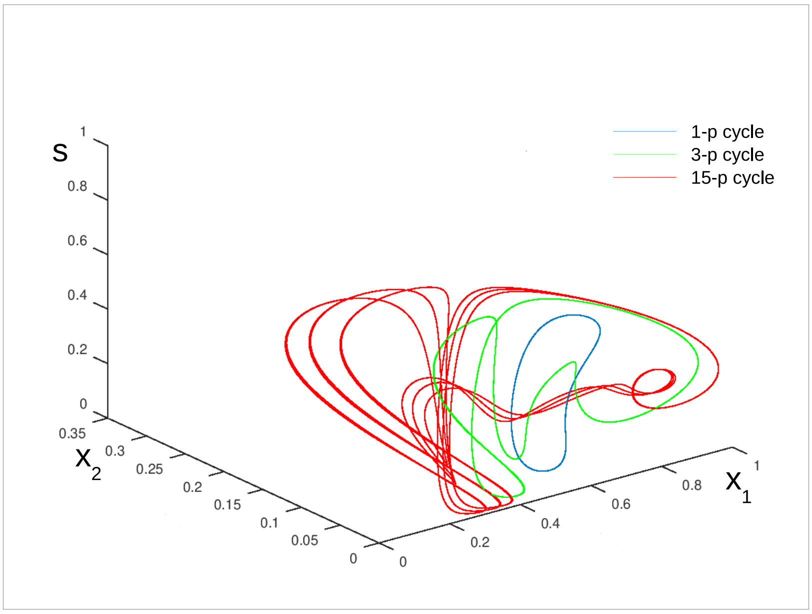


Fig. 5. Attractors for parameters $a_1 = 0.855, \lambda_1 = 0.3, a_2 = 0.0154, \lambda_2 = 0.2, m_1 = m_2 = 0.5$. There is a simple cycle (cyan) a 3-cyclic (green) and a 15-cyclic (red) attractor.

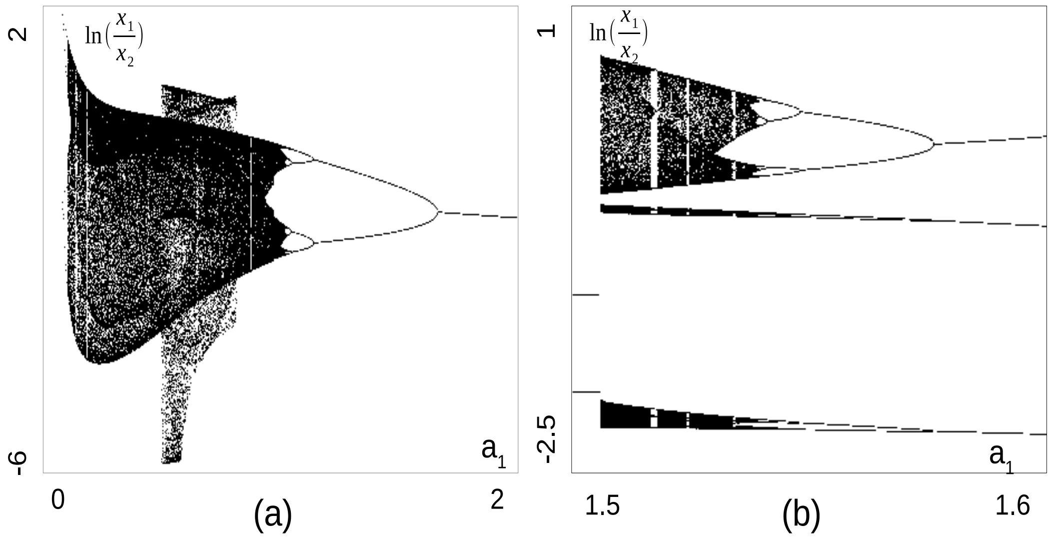


Fig. 6. (a) bifurcation diagram for $a_2 = 0.02, \lambda_1 = 0.35, \lambda_2 = 0.2, m_1 = m_2 = 1$. The range of bifurcation parameter a_1 goes from 0.1 to 2. (b) bifurcation diagram for $a_2 = 0.02, \lambda_1 = 0.35, \lambda_2 = 0.2, m_1 = m_2 = 1$. The range of bifurcation parameter a_1 goes from 1.5 to 1.6.

initial values to be the last point on the attractor calculated for the previous value of a_1. In figure 6(b) the bifurcation diagram is produced for the same fixed parameters as in the previous bifurcation diagram, but the value of a_1 goes from 1.6 to 1.5. The initial values for $a_1 = 1.6$ are chosen as $x_1 = 0.34, x_2 = 0.22, s = 0.35$ and decreasing a_1 for the next value of a_1 we take the initial values to be the last point on the attractor calculated for the previous value of a_1.

Comparing the bifurcation diagrams we easily see two attractors for values of a_1 around 1.6.

5. Spiral chaos from a contour?

Finally, we discuss the nature of "spiral" attractors observed in the system for parameters $a_1 = 0.5, \lambda_1 = 0.33, a_2 = 0.001\nu, \lambda_2 = 0.01\nu, m_1 = 1, m_2 = 0.2$, see figure 7. Usually, such attractors appear due to a Shilnikov homoclinic orbit to the saddle-focus equilibrium [15, 16, 17, 11]. In the problem under consideration all equilibria are located in the invariant planes and, thus, we cannot have a homoclinic orbit. We suppose that in our problem another scenario is possible, when spiral chaos appears from a heteroclinic cycle.

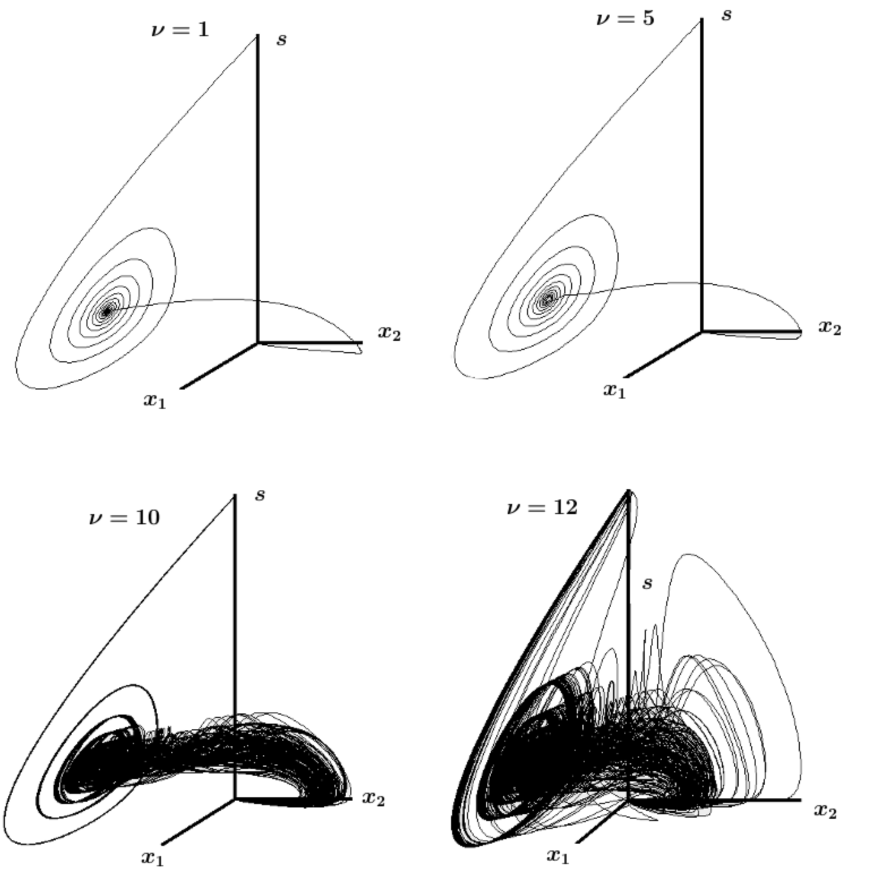


Fig. 7. Attractors for parameters $a_1 = 0.5, \lambda_1 = 0.33, a_2 = 0.001\nu, \lambda_2 = 0.01\nu, m_1 = 1, m_2 = 0.2$, in the cases $\nu = 1, 4, 10, 12$.

1. The unstable separatrix of the equilibrium at $((1-\lambda_1)(\lambda_1+a_1), 0, \lambda_1)$ until it hits $s = 0$ at $P^* = (x_1^*, x_2^*, 0)$ in the case $a_2 = \lambda_2 = 0$.
2. The curve along $x_2 = Cx_1^\gamma$, where $\gamma = \dfrac{m_2\lambda_2 a_1}{m_1\lambda_1 a_2}$ and $C = x_2^*(x_1^*)^{-\gamma}$ from P^* to $(0,0,0)$.
3. The line segment $x_1 = x_2 = 0, 0 < s < 1$.
4. The unstable separatrix of the equilibrium $(0,0,1)$ in the plane $x_2 = 0$ reaching the equilibrium, where part 1 starts.

We suppose that the spiral chaos arises from this contour. We support the conjecture by showing some attractors developing from the contour changing a parameter. We look at some attractors for $a_1 = 0.5, \lambda_1 = 0.33, a_2 = 0.001\nu, \lambda_2 = 0.01\nu, m_1 = 1, m_2 = 0.2$. We can see them in figures 7-8. The attractor for $\nu \leq 1$ is so near to the contour that we can not see the differences. Increase in ν shows us a series of attractors, where we can observe some spiral-like chaos development.

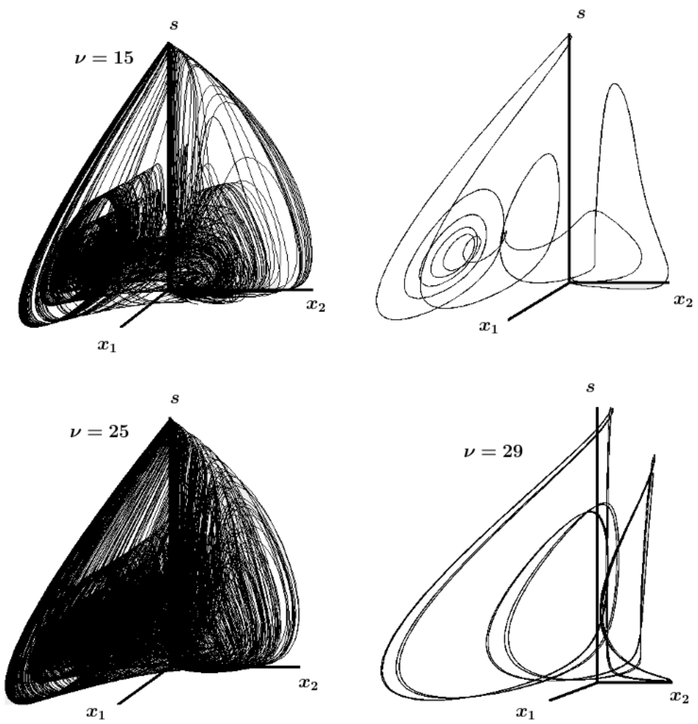


Fig. 8. Attractors for parameters $a_1 = 0.5, \lambda_1 = 0.33, a_2 = 0.001\nu, \lambda_2 = 0.01\nu, m_1 = 1, m_2 = 0.2$, in the cases $\nu = 15, 22, 25, 29$.

We also find out how the intersection of an attractor with a Poincaré section looks like. In figure 9 we see the attractor and intersection with $s' = 0$ in the part, where s' is increasing. It is an open problem to find some kinds of model maps in such cases.

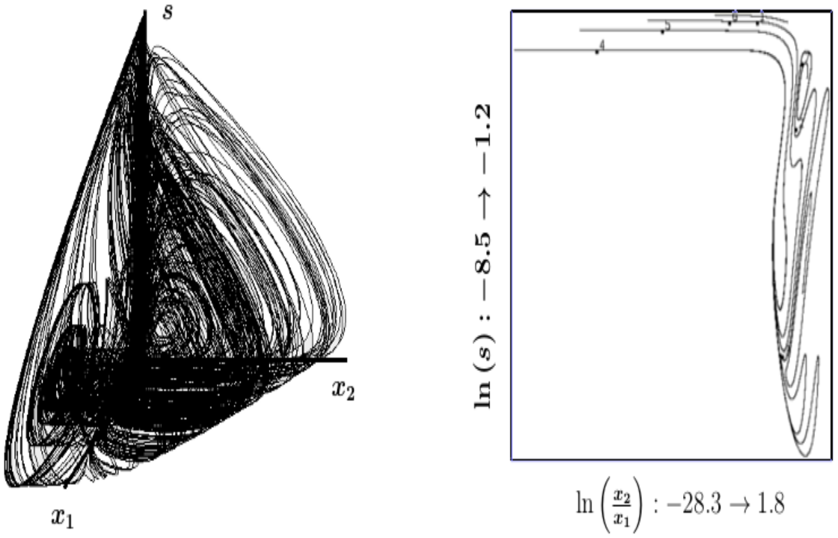


Fig. 9. Attractor and intersection with a Poincaré section for parameters $a_1 = 0.5, \lambda_1 = 0.33, a_2 = 0.015, \lambda_2 = 0.15, m_1 = 1, m_2 = 1$. The sequence of numbered points are iterates of the corresponding Poincaré map.

6. Conclusion.

We have given an overview of results of system (1.1) starting from dissipativity and extinction. The results of dissipativity could be improved to get a smaller positively invariant set using non-linear upper boundary like it was done for the system with only one predator in [10]. The results of extinction use only the equations for the predators, they can be improved by also using the equation for the prey. Our numerical results try to include the general picture of the behaviour of the system when we assume λ_i and m_i constant and change the parameters a_i. We have discussed the open problem of how many attractors can be found. We give numerical results which argument for the bifurcation leading to chaos starting from a contour got for some parameters tending to zero. A typical behaviour of the dynamics on an attractor on a Poincaré section is shown in figure 9.

In most of the chaotic behaviour studied here one population can get very low, and there is the question whether this can be realistic. Some modifications were suggested in [14]. Anyhow, there is also complicated behaviour in systems, where the populations are not getting too low. Such an example was also given in [14]. Another realistic case is the example we gave with three attractors. Yet another such interesting example we get for $a_1 = 1.5, \lambda_1 = 0.3, a_2 = 0.01, \lambda_2 = 0.2, m_1 = m_2 = 1$, where easily three attractors can be observed. One simple cyclic, another 3-periodic and a 4-periodic one. Studying the bifurcations of these attractors changing parameter $0.5 < a_1 < 2$ we see that the simple periodic one always exists, while the branches from the 3- and 4-periodic attractors exist for intervals which overlap on a smaller interval.

The standard system has cycles with very low populations for small a and λ. In nature this does not occur because the predator changes behaviour to feeding on other preys, where however it cannot survive for ever. Because this change is sudden in Arctic regions (stochastic in Middle Europe) we there get a system with switches.

Such a system is given in [14].

References

1. *Afraimovich V. S., Gonchenko S. V., Lerman L. M., Shilnikov A. L., Turaev D. V.* Scientific Heritage of L.P. Shilnikov, Regular and Chaotic Dynamics 19, No.4, 435-460 (2014).
2. *Cheng K. S.* Uniqueness of limit cycle for a predator-prey system, SIAM J. Appl. Anal. 12, No.4, 541-548 (1981).
3. *Coste J.* Dynamical regression in many species ecosystems: The case of many predators competing for several preys, SIAM J. Appl. Math. 45, 555-564 (1985).
4. *Eirola T., Osipov A. V., Söderbacka G.* Chaotic regimes in a dynamical system of the type many predators one prey. Research reports A 386, Helsinki University of Technology, (1996).
5. *Eirola T., Osipov A. V., Söderbacka G.* On the appearance of chaotic regimes in one dynamical system of type two perdators — one prey, Actual Problems of Modern Mathematics, Boxitogorsk, 1, 39-70 (1996).
6. *Hsu B., Hubell S. P., Waltman P.* Competing predators, SIAM J. Appl. Math. 35, No.4, 617-625 (1978).
7. *Hsu S. B.* Limiting behaviour for competing species, SIAM J. Appl. Math. 34, No.4, 760-763 (1978).
8. *Hsu B., Hubell S. P., Waltman P.* A contribution to the theory of competing predators, Ecological Monographs 48, No.3, 337-349 (1978).
9. *Hsu S.-B., Shi J.* Relaxation oscillation profile of limit cycle in predator-prey system, Discrete and Continuous Dynamical Systems Series B 11, No.4, 893-911 (2009).
10. *Lundström N. L. P., Söderbacka G.* Estimates of size of cycle in a predator-prey system, Differential Equations and Dynamical Systems, DOI: 10.1007/s12591-018-0422-x (2018).
11. *Ovsyannikov I. M., Shilnikov L. P.* On systems with a saddle-focus homoclinic curve. Matematicheskii Sbornik 172, No.4, 552–570 (1986).
12. *Osipov A. V., Söderbacka G.* Extinction and coexistence of predators, Dinamicheskie Sistemy 6(34), No.1, 61-70 (2016).
13. *Osipov A. V., Söderbacka G.* Poincaré map construction for some classic two predators-one prey systems. Int. J. Bifurcation Chaos Appl. Sci. Eng. 27, No.8, Article ID 1750116, 9 p. (2017).
14. *Osipov A. V., Söderbacka G.* Review of results on a system of the type many predators – one prey, Nonlinear Systems and Their Remarkable Mathematical Structures, CRC, Vol.1, 520-540 (2018).
15. *Shil'nikov L. P.* A case of the existence of a countable number of periodic motions. Sov. Math., Dokl. 6, 163-166 (1965).

16. *Shilnikov L. P.* The existence of a countable set of periodic motions in the neighborhood of a homoclinic curve. Sov. Math., Dokl. 8, 102-106 (1967).
17. *Shilnikov L. P.* On the question of the structure of an extended neighborhood of a structurally stable state of equilibrium of saddle-focus type. Mat. Sb., N. Ser. 81(123), 92-103 (1970).
18. *Zhang Z-f., Ding T-r., Huang W-z., Dong Z-x.* Qualitative Theory of Differential Equations, AMS, Providence, Rhode Island, (1991).

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