Dynamical Systems: Ecological Modeling

G Söderbacka

Abstract

Ecological modeling is becoming increasingly more important for modern engineers. The mathematical language of dynamical systems has been applied by engineering since ancient times. In this seminar we introduce and discuss some main methods for studying dynamical systems, in particular for the analysis of nonlinear systems of predators and preys. We show how important results can be obtained by simple methods that are based on elementary mathematics. Most models of predators and preys indicate cycles where populations are becomming unrealisticly small. We point out that Deterministic Models are heavily criticised, e.g. amongst Swedish specialists in stochastics. On the other hand, subarctic biologists confirm that predators are not behaving stochasticly, but rather switching feeding between species. This leads to dynamical systems with switches, also well known in other engineering applications. To conclude, we will also mention some challenging open problems in this subject.

Outline

1. Lotka-Volterra equations
2. Rosenzweig equations
3. Two predators - one prey
4. More predators - one prey
5. Modifications for realistic behaviour

Lotka-Volterra equations

$$s' = as - bxs, \; x' = -cx + dxs$$

s - prey, x - predator, derivative with resp to time

Assumptions

1. The prey population finds ample food at all times.
2. The food supply of the predator population depends entirely on the size of the prey population.
3. The rate of change of population is proportional to its size.
4. During the process, the environment does not change in favour of one species and genetic adaptation is inconsequential.
5. Predators have limitless appetite.

Math

Integral

$$V(s,x) = ds - c \ln s + bx - a \ln x$$

Solutions closed curves $V(s,x) = const.$
Equilibrium $\left(\frac{c}{d}, \frac{a}{b}\right)$ - center

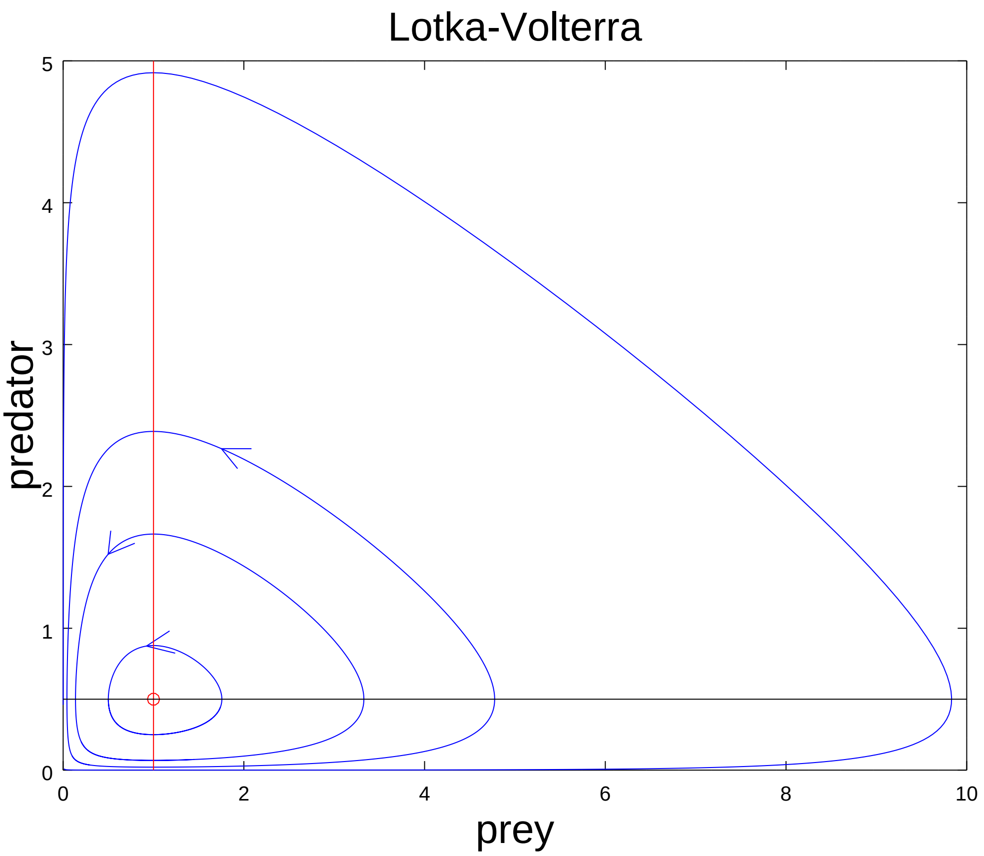

Figure 1: a=1, b=2, c=1, d=1

Trajectories of Lotka-Volterra equations

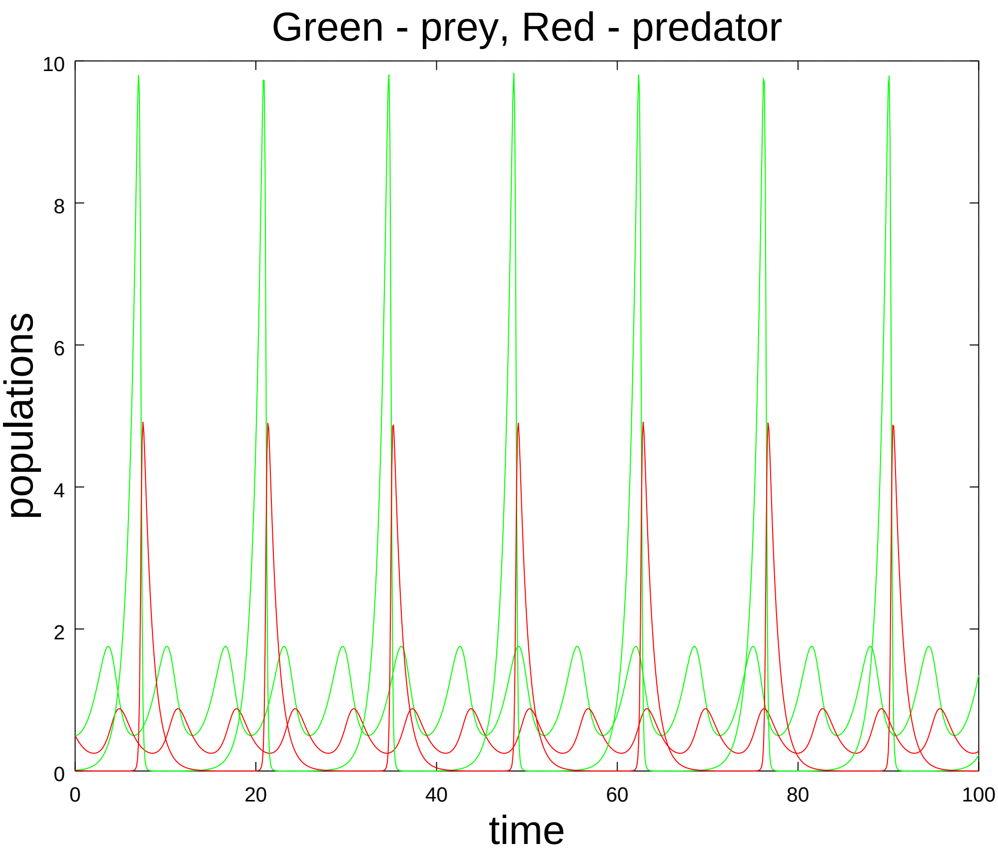

Figure 2: a=1, b=2, c=1, d=1

Solutions of Lotka-Volterra equations

Rosenzweig-McArthur equations

$$s' = as\left(1 - \frac{s}{K}\right) - \frac{bxs}{1 + As}$$

$$x' = -cx + \frac{dxs}{1 + As}$$

Notation: $\alpha = \frac{Ac}{d}$, $\epsilon = \frac{c}{Kd}$.

1. Predator cannot survive if either condition $\alpha > 1$ is satisfied or both conditions $\alpha < 1$ and $\epsilon > 1 - \alpha$ are satisfied
2. If $\alpha < 1$ and $\frac{\alpha - \alpha^2}{1+\alpha} < \epsilon < 1 - \alpha$ the system has a stable equilibrium as global attractor where the species coexist.
3. If $\alpha < 1$ and $\epsilon < \frac{\alpha - \alpha^2}{1+\alpha}$ the system has a stable unique cycle as global attractor.

Time change $t = \frac{\tau}{A}$ and special choice of parameters

$$K = b = 1,\ A = \frac{1}{a},\ c = \lambda, d = 1 + \frac{\lambda}{a}$$

give equations (we call it standard system)

$$\dot{s} = s\left(1 - s - \frac{x}{s + a}\right)$$

$$\dot{x} = \frac{s - \lambda}{s + a}x$$

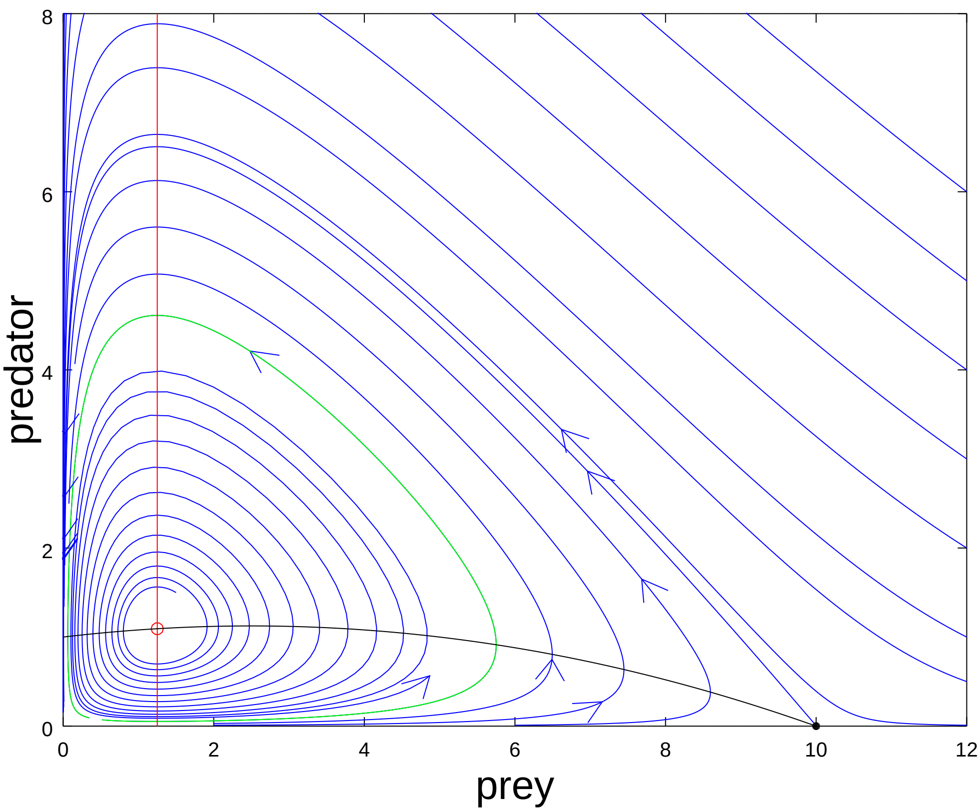

Figure 3: a=1, b=1, c=1, d=1, K=10, A=0.2

Globally attracting limit cycle

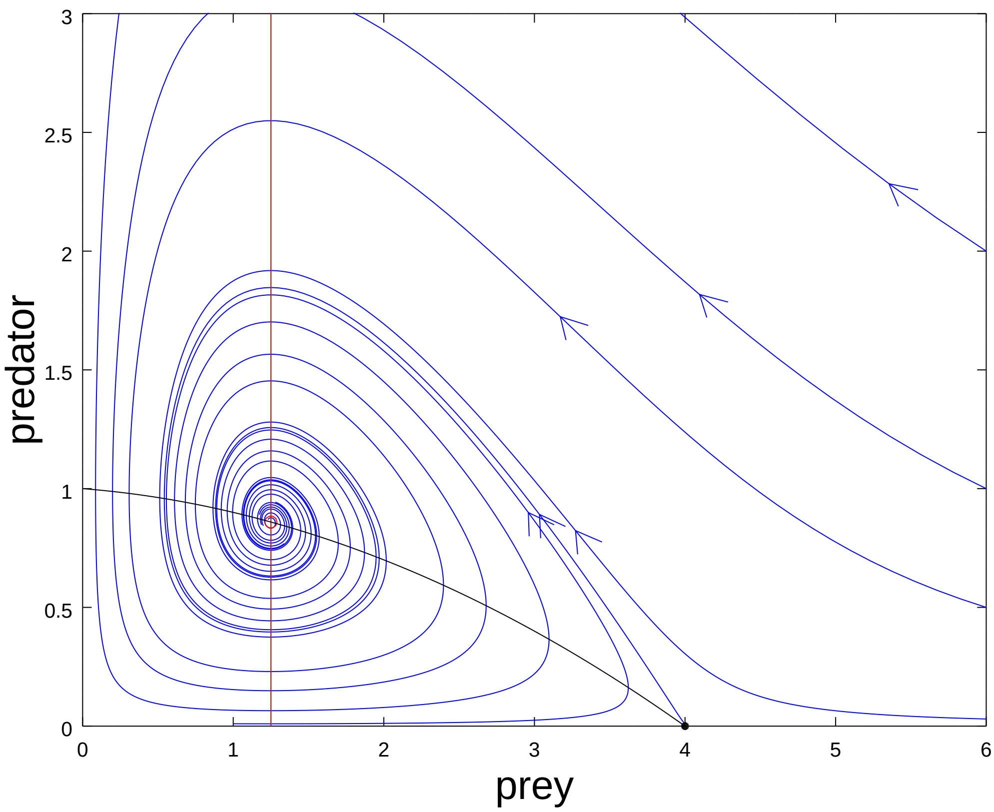

Figure 4: a=1, b=1, c=1, d=1, K=4, A=0.2

Globally attracting equilibrium

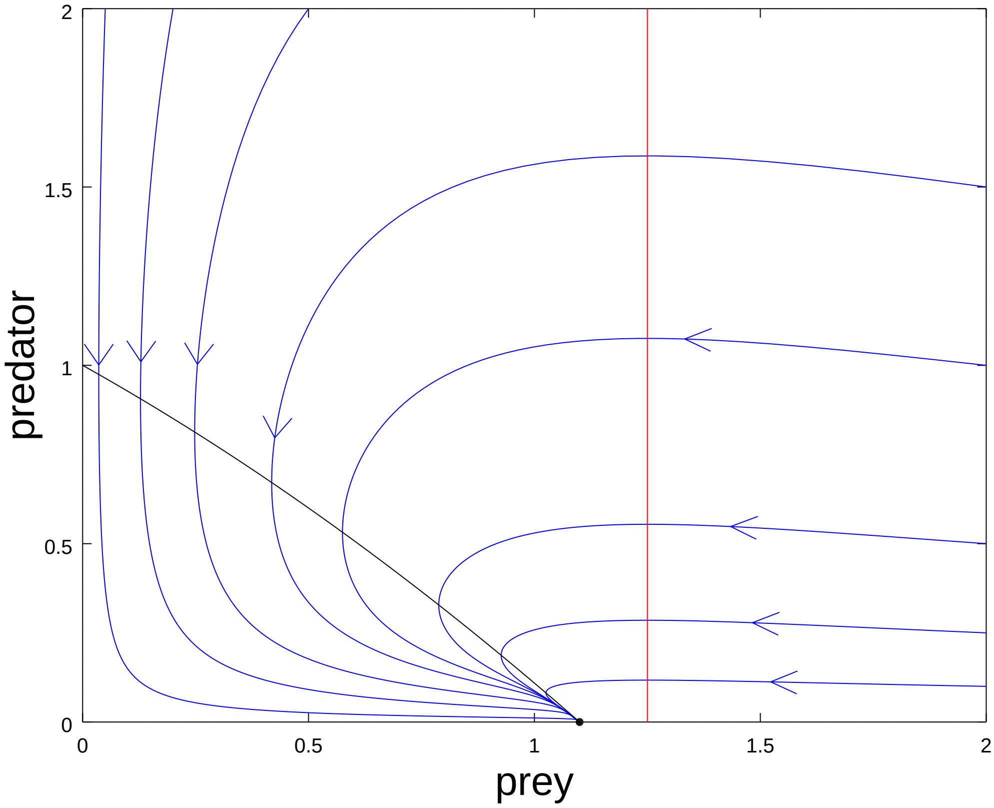

Figure 5: a=1, b=1, c=1, d=1, K=1.1, A=0.2

Extinction of predator

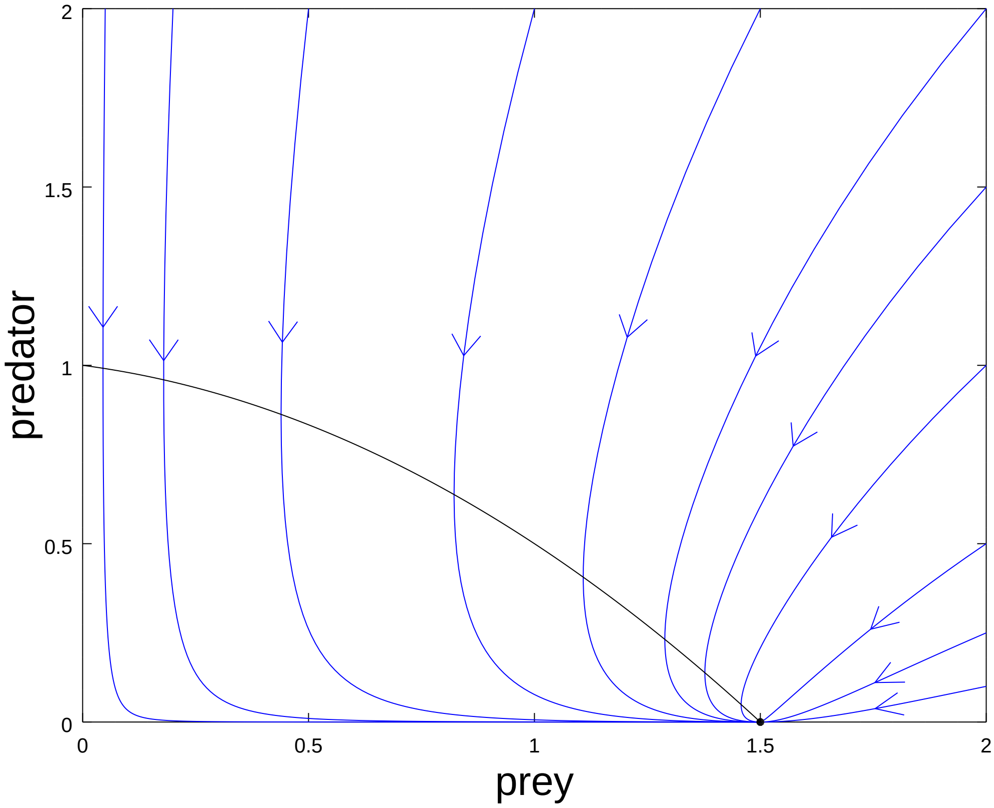

Figure 6: a=1, b=1, c=3, d=1, K=1.5, A=0.5

Strong extinction of predator

Mathematical tools

Topological equivalence

Two dynamical systems are topologically equivalent, if there is a homeomorphism h mapping orbits of system 1 to orbits of system 2 homeomorphically, and preserving orientation of the orbits.

Grobman-Hartman Theorem

If J is the Jacobian matrix at an equilibrium and the real parts of the eigenvalues of J are non-zero, then there is a neighbourhood of the equilibrium in which the system is topologically equivalent to the linear system $x' = Jx$ given by the Jacobian matrix.

We differ between three types of equilibria:

- *sinks* (stable), eigenvalues are real less than zero (nodes), or complex with negative real parts (focus)
- *sources*, eigenvalues are real greater than zero (nodes), or complex with positive real parts (focus)
- *saddles*, real parts of eigenvalues have different signs, attracts in some directions and repelling in some directions

Standard system after a change in time takes form

$$x' = (s-\lambda)x,\ s' = (h(s)-x)s,\ h(s) = (1-s)(s+a)$$

Possible equilibria: $(0,0)$, $(0,1)$, $(h(\lambda),\lambda)$
General Jacobian matrix is

$$J = \begin{pmatrix} s-\lambda & -x \\ -s & h'(s)s + h(s) - x \end{pmatrix}$$

$$J(0,0) = \begin{pmatrix} -\lambda & 0 \\ -0 & a \end{pmatrix}$$

$(0,0)$ - always saddle

$$J(0,1) = \begin{pmatrix} 1-\lambda & 0 \\ -1 & -a \end{pmatrix}$$

$(0,1)$ - stable for $\lambda > 1$, saddle for $\lambda < 1$

$$J(h(\lambda),\lambda) = \begin{pmatrix} 0 & -h(\lambda) \\ -\lambda & 1-a-2\lambda \end{pmatrix}$$

$(h(\lambda),\lambda)$ - stable for $\frac{1-a}{2} < \lambda < 1$, source for $\lambda < \frac{1-a}{2}$

The *basin of attraction of* a stable equilibrium is the set of initial conditions for which the trajectory tends to the equilibrium. To estimate basins of attractions we use *Lyapunov functions*.

Theorem. Let V be a function defined in a neighbourhood N of the equilibrium. Suppose in the neighbourhood N

- $V(x) \geq 0$
- $V'(x) < 0$
- $V(x) < c$

Then the region M defined by $V(x) < c$ is in the basin of attraction of the equilibrium.

For standard system:

Using Lotka-Volterra integral as Lyapunov function it is possible to prove $(h(\lambda), \lambda)$ - globally stable for $\frac{1-a}{2} < \lambda < 1$

In case $\lambda < \frac{1-a}{2}$ there is a unique globally attracting limit cycle. Can be proved using Zhang Zhi-fen theorems.

Estimates for the size of the cycle for critical small a and λ are given in

N L P Lundström, G Söderbacka. Estimates of size of cycle in a predator-prey system (Manuscript)

Two predators - one prey

$$\begin{aligned} x' &= \frac{s-\lambda_1}{s+a_1}x, \\ y' &= \frac{s-\lambda_2}{s+a_2}y, \\ s' &= \left(1 - s - \frac{x}{s+a_1} - \frac{y}{s+a_2}\right)s, \end{aligned}$$

x, y predators, s -prey
a_i, λ_i, $i = 1, 2$ - positive parameters

Possible equilibria: $(0, 0, 0)$, $(0, 0, 1)$,
$((1-\lambda_1)(\lambda_1 + a_1), 0, \lambda_1)$, $((1-\lambda_2)(\lambda_2 + a_2), 0, \lambda_2)$

Dissipativity.

Theorem. Let $V = x/q_1 + y/q_2 + s$, where $q_i = a_i - \lambda_i + 2, \quad i = 1, 2$. All solutions of the system starting in $x, y \geq 0$ enter the region $\{(x, y, s) | \, V \leq 1, \;\; x, y, s \geq 0\}$ and remain there.

Extinction of one predator

The predator x goes extinct if

$$\lambda_1 > \frac{a_1\lambda_2(a_2+1)}{a_1a_2+\lambda_2(a_1-a_2)+a_2}$$

and the predator y goes extinct in the case $\lambda_1 < \lambda_2$.

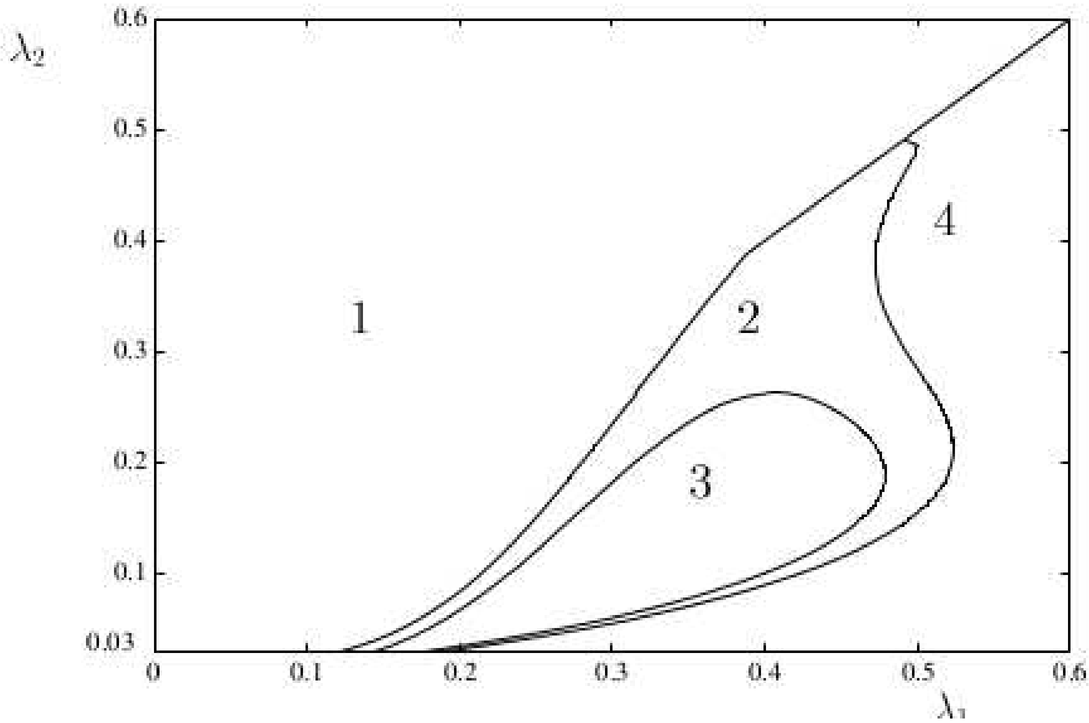

Figure 7: In region 1 predator y goes extinct and x in region 4. An inner solution exists in regions 2 and 3 and on the boundary between them there is a period doubling bifurcation.

A V Osipov, G Söderbacka. Extinction and coexistence of predators. To appear in Dynamical Systems.

Periodic coexistence

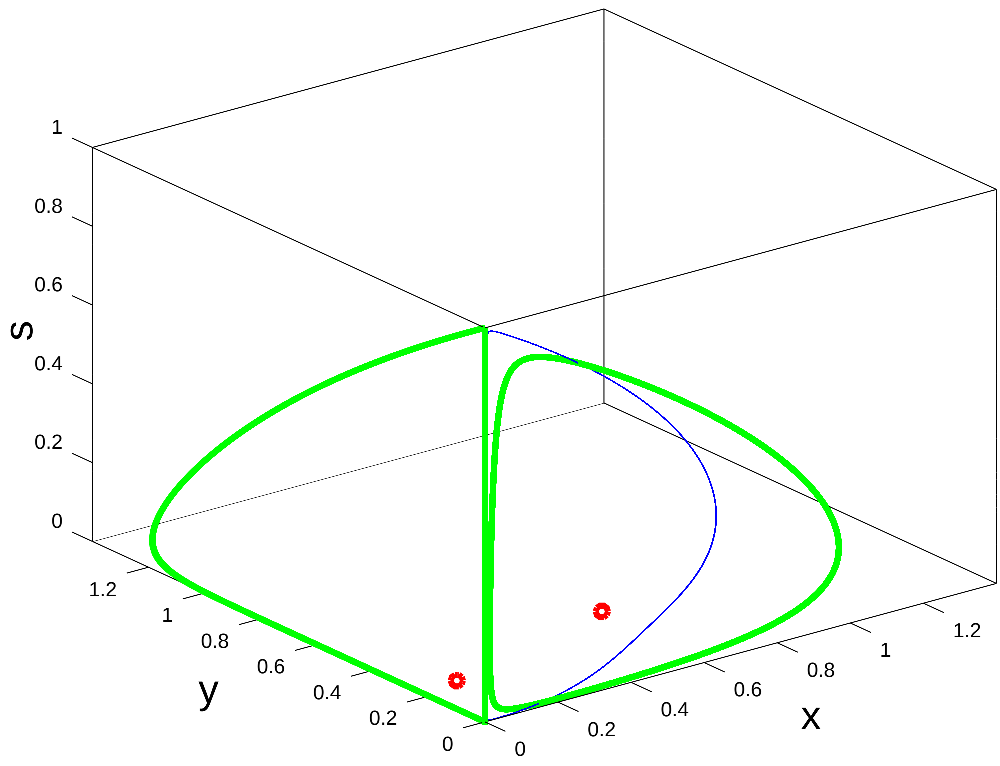

Figure 8: $a_1 = 0.2$, $\lambda_1 = 0.2$, $a_2 = 0.036$, $\lambda_2 = 0.072$

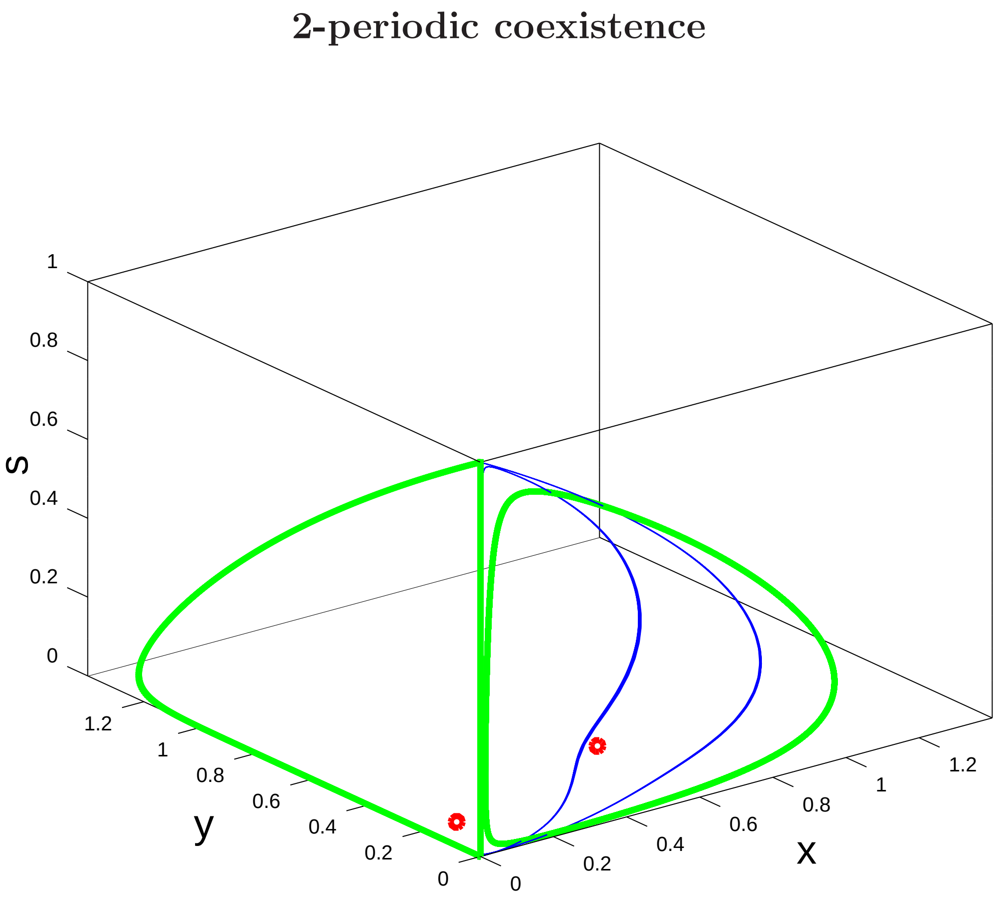

Figure 9: $a_1 = 0.2$, $\lambda_1 = 0.2$, $a_2 = 0.03$, $\lambda_2 = 0.06$

Chaotic coexistence

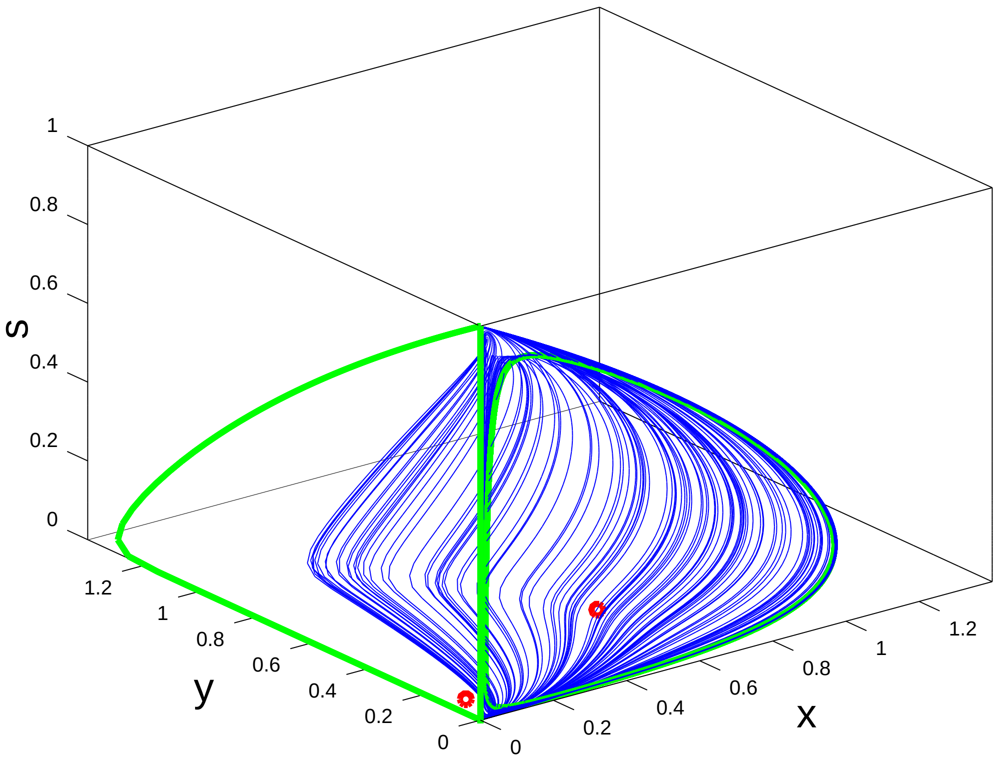

Figure 10: $a_1 = 0.2$, $\lambda_1 = 0.2$, $a_2 = 0.018$, $\lambda_2 = 0.036$

Poincaré map in R^n. The Poincaré map P is defined on a transversal $(n+1)$-dimensional hypersurface Q (without tangency with trajectories). The image $P(x)$ is defined as the next intersection with Q of a trajectory with intial condition x.

Gives possibilities to study the iterates of points under a map instead of whole trajectories.

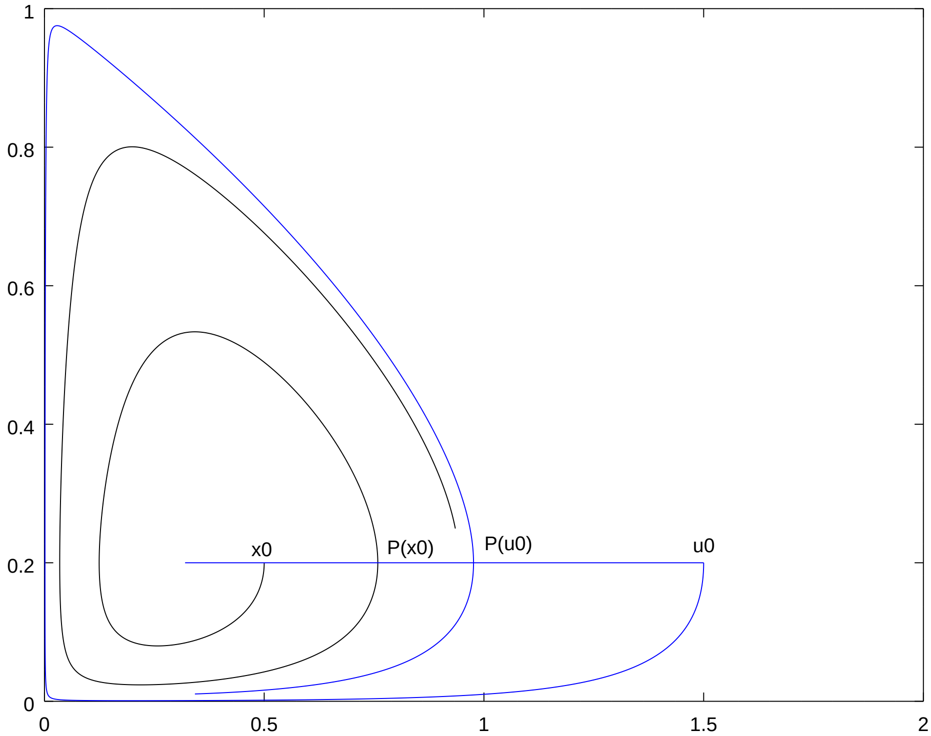

Figure 11: $x0$ and $u0$ with images

Conditions for construction of well defined Poincaré map on $s = 0.1$, $s' < 0$ are obtained in

A V Osipov, G Söderbacka. Poincaré map construction for some classical two predators - one prey systems. Submitted to Internat J of Bifurcation and Chaos.

Model map

In the case when the Poincaré map is correctly defined, very often there is a strong contraction in the $x+y$-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 $v = \ln(y/x)$ gives a good approximation.

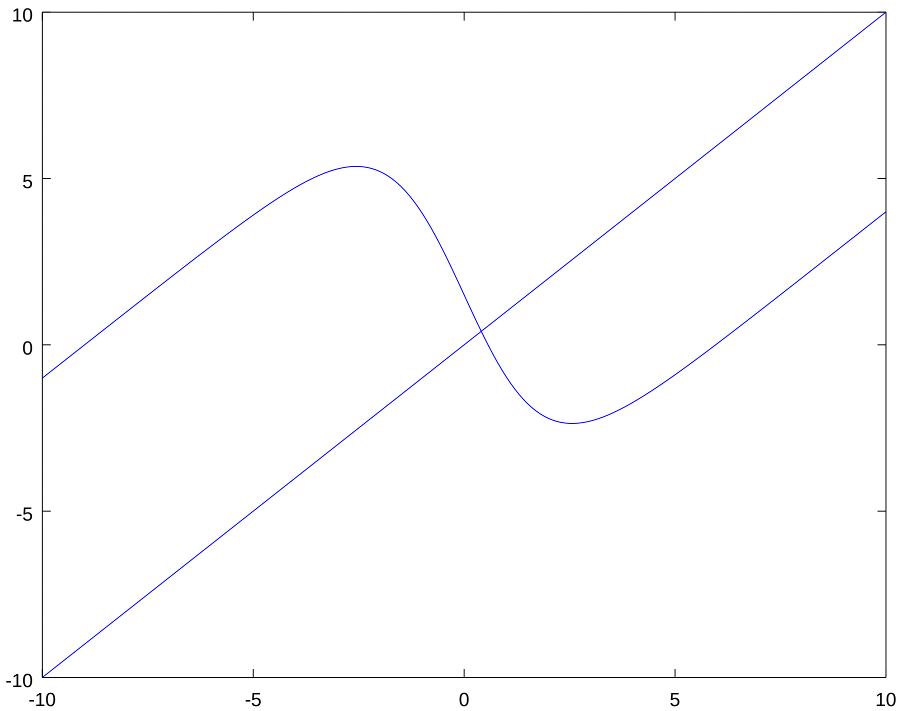

Figure 12: Model map, $b = 10$, $k_1 = 1$, $k_2 = 16$, $u = 1$

Bifurcation diagram. The horisontal axis represents the value of a bifurcation parameter. The vertical axis represents one coordinate of points on an attractor for the given value of the bifurcation parameter.

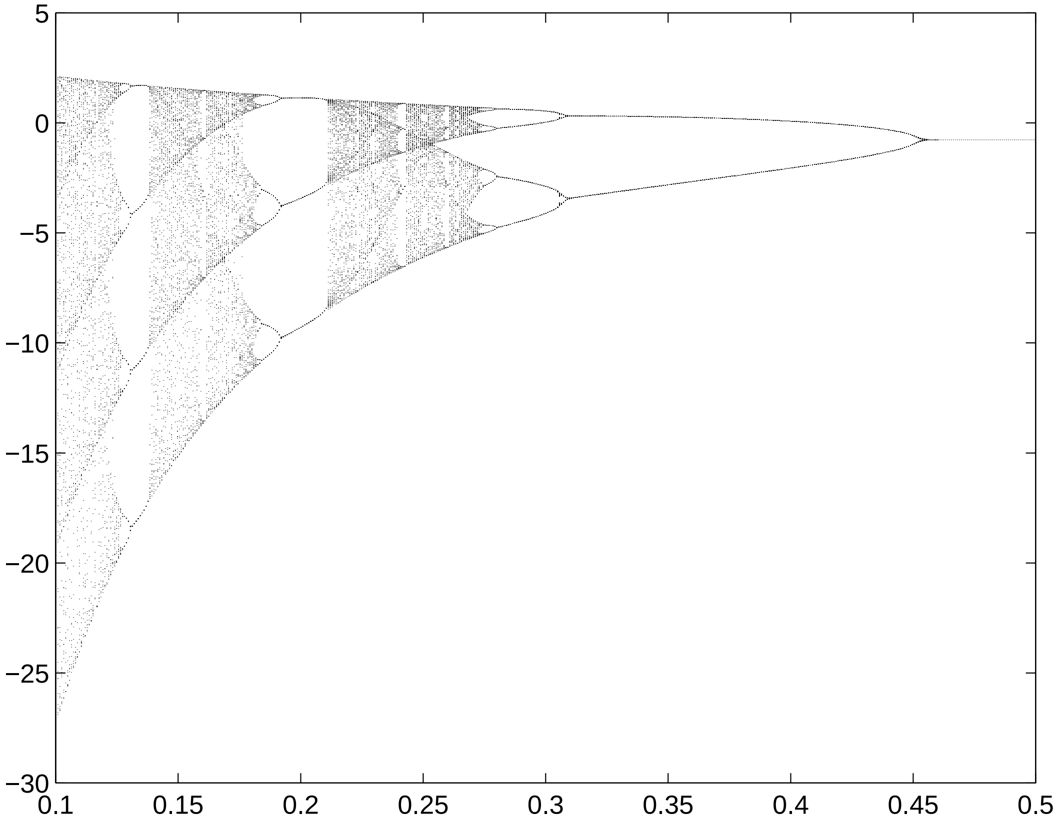

Figure 13: Bifurcation diagram for $a_1 = \lambda_1 = 0.1, \quad a_2 = 0.03\,\nu, \lambda_2 = 0.04\,\nu$. The vertical axis corresponds to the $\ln(y/x)$-coordinates of intersections of trajectories with $s = 0.1$, $s' < 0$. The horisontal axis corresponds to values of parameter ν.

Complicated chaotic coexistence

When construction of Poincaré map does not work the chaotic attractor can be more complicated.

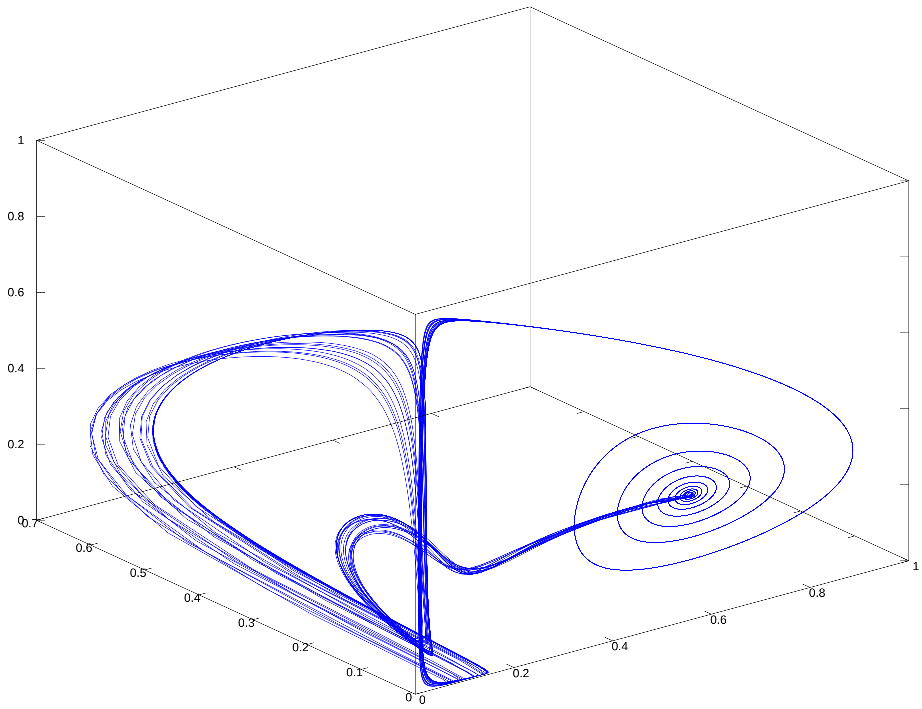

Figure 14: Inner attractor for $a_2 = 0.002$, $\lambda_2 = 0.2$, $a_1 = 0.5$, $\lambda_1 = 0.33$

Open problem. Can we have more than one attractor where all species coexist?

Many predators - one prey

Consider the $(n+1)$-dimensional Osipov system

$$\dot{x}_i = \phi_i(s)x_i\,, \qquad \dot{s} = h(s) - \sum_{i=1}^{n} \psi_i(s)x_i\,, \qquad i = 1, 2, ..., n.$$

Assume:

$A_1:$ 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 $s > 0$.

Here and further we will suppose, that i takes values from the set $\{1, 2, \ldots, n\}$.
$A_3:$ $\phi_i'(s) > 0$ for $s > 0$ and there exists $\lambda_i > 0$ such that $\phi_i(\lambda_i) = 0$.

$A_4:$ $h(0) = h(1) = 0$, $h'(1) < 0$ and $h''(s) < 0$ for $s > 0$.

$A_5:$ $0 < \lambda_n < \cdots < \lambda_2 < \lambda_1 < 1$.

Results for coexistence obtained in four dimensional case and for extinction in general case by
A Gunnare, A V Osipov and G Söderbacka

Open problem. It there a possibility for coexistence even if there is no coexistence in some hyperplanes of lower dimension.

Modified standard system

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

We consider two 3-dimensional systems

$$\begin{aligned} s' &= \left(1 - s - \frac{x}{s+a_1}\right) s \\ z' &= (1-z)z \\ x' &= \frac{s-\lambda_1}{s+a_1} x \end{aligned}$$

$$\begin{aligned} s' &= (1-s)s \\ z' &= \left(1 - z - \frac{x}{z+a_2}\right) z \\ x' &= \frac{z-\lambda_2}{z+a_2} x \end{aligned}$$

Suppose $\lambda_1 < \frac{1-a_1}{2}$ (implies cycle) and $\lambda_2 > 1$ (implies extinction). The main prey is s, the secondary is z. The predator feeds on the main prey until density becomes lower than a limit $\epsilon_- < \lambda_1$ and then feeds on z until the main prey reaches a density of ϵ_+, $\epsilon_- < \epsilon_+ \leq \lambda_1$.

Results: Cycle becomes smaller or chaos arises.

Open problem. Examine the dynamics of systems of many predators - one prey with this behaviour of the prey.