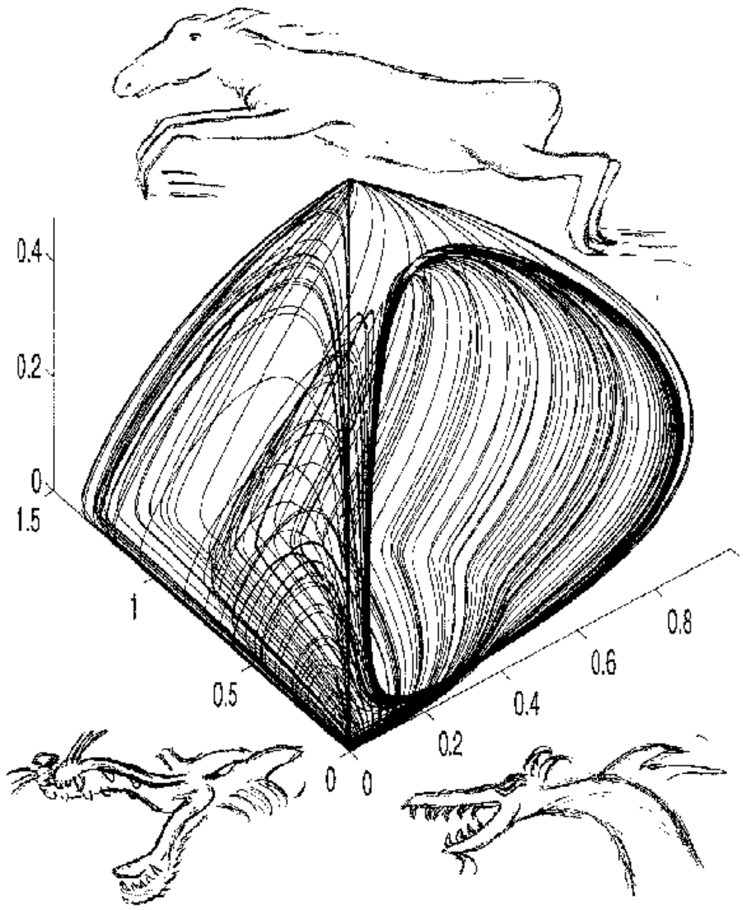
Chaotic Regimes in a Dynamical System of the Type Many Predators One Prey

Timo Eirola, Alexandr V. Osipov, and Gunnar Söderbacka



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Timo Eirola[*], Alexandr V. Osipov[+] and Gunnar Söderbacka[o]:
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Abstract: A multidimensional system of differential equations of the type many predators-one prey is examined. The system has been introduced by S.B. Hsu, S.P. Hubell and P. Waltman and the possibility for coexistence of the predators has been established by different authors. Most of the results here are for the three and four dimensional cases when two or three predators are present. We examine the stability of limit cycles and find parameter regions for different types of coexistence, for example, periodic and chaotic. Bifurcations in the dynamics are also examined. In the three dimensional case a simple one-dimensional map is suggested as model for the dynamics of the Poincaré map on the attractor. This model is supported not only by experiments but mainly as a result of analytical estimates of the trajectories. The model does not work for all parameter values. Examples are given of cases when the model does not work. There the Poincaré maps seem not to be approximated by simple maps and the attractor is more complicated. In the four dimensional case most of the results are experimental.

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[*]Helsinki University of Technology, Institute of Mathematics
Otakaari 1, FIN-2150 Espoo, Finland
E-mail: Timo.Eirolahut.fi

[+]Department of Ordinary Differential Equations
Faculty of Mathematics and Mechanics
St Petersburg State University
Ulianovskaya 1, St Petergof
198904 St Petersburg, Russia

[o]Department of Applied Mathematics
Luleå University of Technology
S-97187 Luleå, Sweden

1 Introduction.

Let us consider a $(n+1)$-dimensional system of differential equations of the form

$$(1.1) \qquad x_i' = f_i(s)x_i, \ \ i = 1,..,n \ \ s' = h(s) - \alpha_1(s)x_1 - ... - \alpha_n(s)x_n,$$

in the region $x_i, s \geq 0$. The system describes the interaction of n predators x_i exploiting the same prey s.

We assume that

$$(1.2) \qquad f_i(s) = \frac{s-\lambda_i}{s+a_i}, \quad \alpha_i(s) = \frac{s}{s+a_i}, \quad h(s) = (1-s)s$$

where $a_i, \lambda_i > 0$ are parameters.

The form of the three dimensional system can be derived from the more standerd form of the system

$$\frac{dS}{dT} = \alpha S(1 - S/K) - \frac{M_1}{B_1}\frac{X_1 S}{(A_1+S)} - \frac{M_2}{B_2}\frac{X_2 S}{(A_2+S)} - ... - \frac{M_n}{B_n}\frac{X_n S}{(A_n+S)}$$

$$\frac{dX_i}{dT} = \frac{M_i X_i S}{(A_i+S)} - D_i X_i \ , \quad i = 1,..,n,$$

examined in [2, 16, 19, 25]. After the transformations

$$s = S/K, \quad \lambda_i = \frac{A_i D_i}{K(M_i - D_i)},$$

$$t = \alpha T, \quad m_i = \frac{M_i - D_i}{\alpha},$$

$$\alpha_i = A_i/K, \quad x_i = \frac{M_i X_i}{\alpha K B_i},$$

in [19], the system takes the corresponding form in (1.1)-(1.2) if $m_i = 1$. For the biological backround of this system see: [18].

The two dimensional system obtained by restriction of system (1.1)-(1.2) to a coordinate plane, where only one predator is present is examined in [7, 13, 14, 19, 21, 25, 30].

We are specially interested in solutions where all the predators coexist and call such solutions inner solutions. More precisely: a solution is called *inner* if the closure of the corresponding trajectory does not intersect the n-dimensional subspaces where one predator is absent.

We review and give some results from which one can determine the existence or absence of inner solution (extinction of one predator). We also discuss the behaviour of these inner solutions and try to find parameter regions where there is only one simple periodic inner solution (it is then stable), where there is a period doubling bifurcation, and where the inner solutions are chaotic (there are no inner equilibrium points). In [5] it is proved that the probability in the parameter space of finding coexistence is rapidly decreasing when the dimension of the system is increasing.

Inner solutions of the three dimensional system have also been examined in [2, 11, 16, 18, 19, 20, 25]. The system with periodic variations in the coefficients has also been examined in [6]. Analogous systems, where the prey is a substrate or nutrient and has linear growth instead of logistic are examined in [3, 15, 17] and with periodic variations, day-night in [26] or periodic death (washout) in [3]. A good suvey of results on related systems can be found in [27].

In section 2 we find bounded regions such that all solutions will enter them and remain there. In section 3 we will discuss the main properties of the two dimensional case (system of one predator-one prey) and in section 4 the properties of the three dimensional system. In section 5 we introduce a model for the Poincaré map in the three dimensional case and examine the conditions under which it works. In section 6 we study situations when the model map does not work. In section 7 we also consider the three dimensional case and discuss the stability properties of the limit cycles in the two dimensional coordinate planes and the effects of their stability on the existence of inner solutions. In section 8 we discuss the properties of the four dimensional system. Section 9 is devoted to the numerical methods of our experiments. Sections 10 and 11 contain the proofs of the main theorems.

2 Dissipativity of the system

A system is *dissipative* (see V. A. Pliss [24]) if there is a bounded set such that any solution eventually enters it and remains there. (This is not to be confused with the other common definition of dissipativity requiring the divergence being negative). The system (1.1)-(1.2) is dissipative:

Theorem 2.1 *Let* $V = x_1/q_1 + x_2/q_2 + ... + x_n/q_n + s$*, where* $q_i = a_i - \lambda_i + 2, \quad i = 1, ..., n$*. All solutions of the system (1.1)-(1.2) starting in* $x_i, s \geq 0,\ i = 1, .., n$*, enter the region* $\{(x_1, .., , x_n, s) | \, V \leq 1, \ \ x_i, s \geq 0\}$ *and remain there.*

The proof of the theorem uses the ideas of [8] and is based on the fact that

$$V' = (s-1)\left(\frac{x_1(s+\lambda_1)}{q_1(s+a_1)} + ... + \frac{x_n(s+\lambda_n)}{q_n(s+a_n)}\right) + (1-V)s < 0$$

for $V > 1$ and $s < 1$.

The following theorem gives another result for the region, where the solutions remain.

Theorem 2.2 *Any solution of (1.1)-(1.2), where* $a_i, \lambda_i < 0.1$*, enters the region* $x_1 + x_2 + ... + x_n < 1.6$ *and thereafter remains there.*

The proof of this theorem is given in section 11. This theorem implies that any attractor must be in the region $x_1 + x_2 + ... + x_n < 1.6, s < 1$. Note that Theorem 2.1. already says that an attractor must be in $x_1 + x_2 + ...x_n < 2.1$ in this case.

3 Behaviour of the two dimensional system

Let us consider the system (1.1)-(1.2) in a two dimensional coordinate plane where only one predator is present, for example, let $x_2 = ... = x_n = 0$.

After rescaling the time the two dimensional system can be written in the form

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

where $x = x_1,\ \lambda = \lambda_1,\ a = a_1$.

The system always has two equilibria: the origin and the point $(0, 1)$. The origin is always a saddle with stable mainfold on the positive x-axis. The unstable manifold contains the part of the s-axis between the origin and the point $(0, 1)$. For $\lambda > 1$ the equilibrium $(0, 1)$ is a sink attracting the whole $P = \{(x, s)|x > 0,\ s > 0\}$. For $\lambda < 1$ the point $(0, 1)$ becomes a saddle. Then there is also a third equilibrium $((1-\lambda)(\lambda+a), \lambda)$ in P. It attracts the whole P for $2\lambda + a > 1$. For $2\lambda + a < 1$ there is a unique periodic solution in P which attracts all P except for the source $((1 - \lambda)(\lambda + a), \lambda)$ inside itself. This is proved in [4, 13, 14, 21, 30]. Most of the results, however, can also be obtained as corollaries from [31]-[33]. At $2\lambda + a = 1$ there is Hopf bifurcation. For more details of the two-dimensional behaviour see [7, 13, 14, 19, 21, 25, 30].

In [6, 30] the relaxation behaviour of the trajectories is also studied when a small parameter is introduced.

4 Behaviour of the three dimensional system

Consider the four dimensional subsystem of (1.1)-(1.2) written in the form

$$\begin{aligned} x' &= \frac{s - \lambda_1}{s + a_1}\, x, \\ y' &= \frac{s - \lambda_2}{s + a_2}\, y, \qquad (4.1) \\ s' &= (1 - s - x/(s + a_1) - y/(s + a_2) - z/(s + a_3))\ s. \end{aligned}$$

The system always has two equilibria: the origin and the point $(0,0,1)$. The origin is always a saddle the stable manifold of which contains the xy-plane. The unstable manifold is the line from the origin to the point $(0,0,1)$. If $\lambda_1, \lambda_2 > 1$, the point $(0,0,1)$ attracts the whole set $\{(x,y,s)|x,y,s > 0\}$. If $\lambda_1 < 1$ there is an equilibrium $((1-\lambda_1)(\lambda_1 + a_1), 0, \lambda_1)$ in the xs-plane, which is a sink if $2\lambda_1 + a_1 > 1$ and $\lambda_2 > \lambda_1$, a saddle with one dimensional unstable manifold if $2\lambda_1 + a_1 > 1$ and $\lambda_2 < \lambda_1$, a saddle with two dimensional unstable manifold if $2\lambda_1 + a_1 < 1$ and $\lambda_2 > \lambda_1$, and a source if $2\lambda_1 + a_1 < 1$ and $\lambda_2 < \lambda_1$. The limit cycle in the xs-plane is always stable in that plane but can be stable or unstable saddle for the three dimensional system. When $\lambda_2 < 1$ we have an analogous situation in the ys-plane.

Suppose now that $a_1 > a_2$ (case $a_2 < a_1$ is analogous). In [21] is proved that if $\lambda_1 < \lambda_2$ then all solutions in $\{(x,y,s)|x,y,s > 0\}$ approach the plane $y = 0$ and if

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

then all solutions in $\{(x,y,s)|x,y,s > 0\}$ approach the plane $x = 0$. Thus there is nothing interesting inside the set $\{(x,y,s)|x,y,s > 0\}$ under these parameter conditions. Hence, we will assume the opposite

$$\lambda_2 < \lambda_1 < \frac{a_1\lambda_2(a_2+1)}{a_1a_2 + \lambda_2(a_1 - a_2) + a_2}. \tag{4.2}$$

We observe that (for $a_1 > a_2$)

$$a_1\lambda_2(a_2+1))(a_1a_2 + \lambda_2(a_1 - a_2) + a_2)^{-1} < \lambda_2 a_1/a_2 \ .$$

Experiments show that it is worth to conjecture that for fixed λ_2, a_2 and a_1, if $\lambda_2 < (1-a_2)/2$, then there exist λ_a and λ_b such that $\lambda_2 \leq \lambda_a < \lambda_b \leq (\lambda_2 a_1)/a_2$ and such that if $\lambda_1 < \lambda_a$, then all solutions in $x,y,s > 0$ tend to $y = 0$ and if $\lambda > \lambda_b$, then all solutions tend to $x = 0$ and for $\lambda_a < \lambda < \lambda_b$ there exists an inner solution which is periodic or chaotic. These parameter regions are illustrated in figures 1 and 2 for some fixed a_1 and a_2. There we have approximatively plotted for fixed a_1 and a_2 the regions in the $\lambda_1\lambda_2$-parameter plane, where the predator x becomes extinct (region 4), where the predator y becomes extinct (region 1), where the attractor is a simple periodic trajectory (region 2) and where the attractor is more complicated (region 3). On the boundary between the regions 2 and 3 there is a period doubling bifurcation. We have considered that one of the predators becomes extinct if the corresponding coordinate becomes less than 10^{-10} before we have iterated the map 100 times and even less for the following iterate of the Poincaré map. We have started our trajectory from the point $(0.25, 0.25, 0.1)$ and taken the first intersection with the defintion range of the Poincaré map as the initial value. That means that the regions 1 and 4 may in reality be slightly larger than those in the figures.

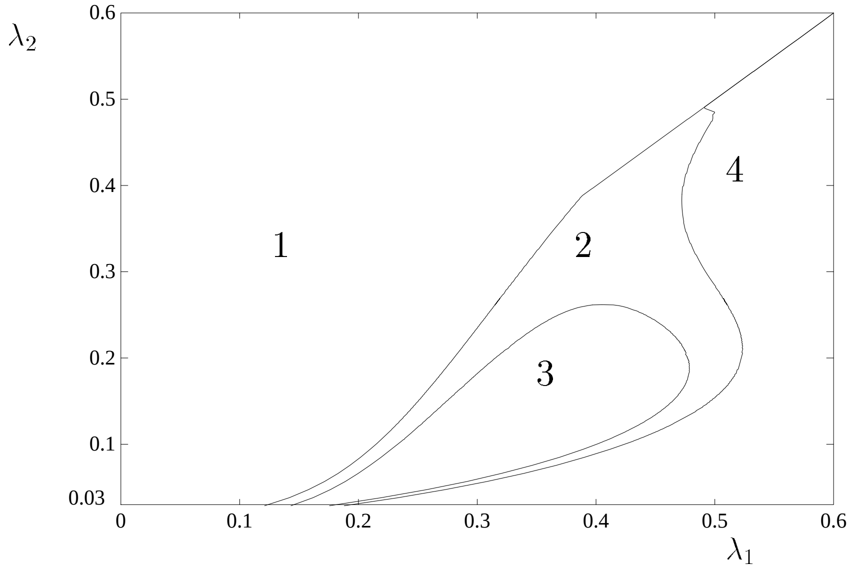

Figure 1: Parameter regions of coexistence for $a_1 = 0.2\,,\ a_2 = 0.02$

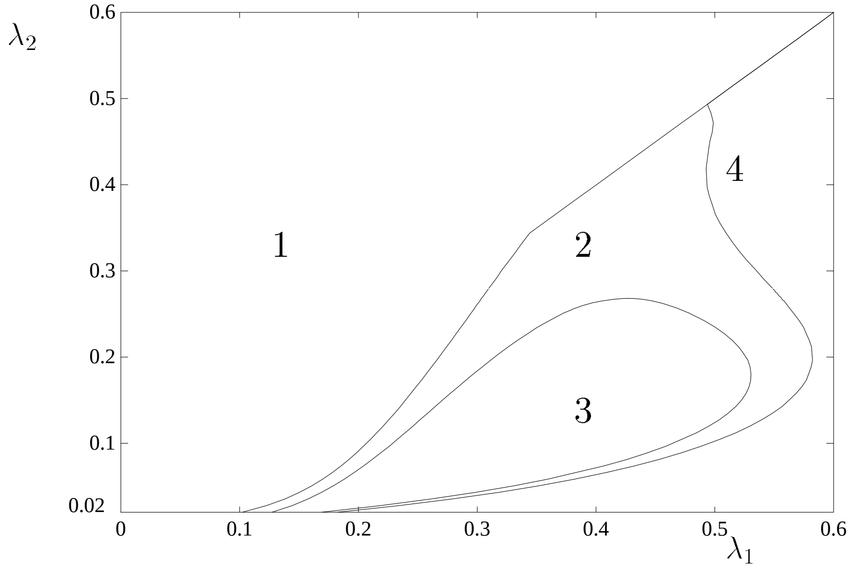

Figure 2: Parameter regions of coexistence for $a_1 = 0.3\,,\ a_2 = 0.02$

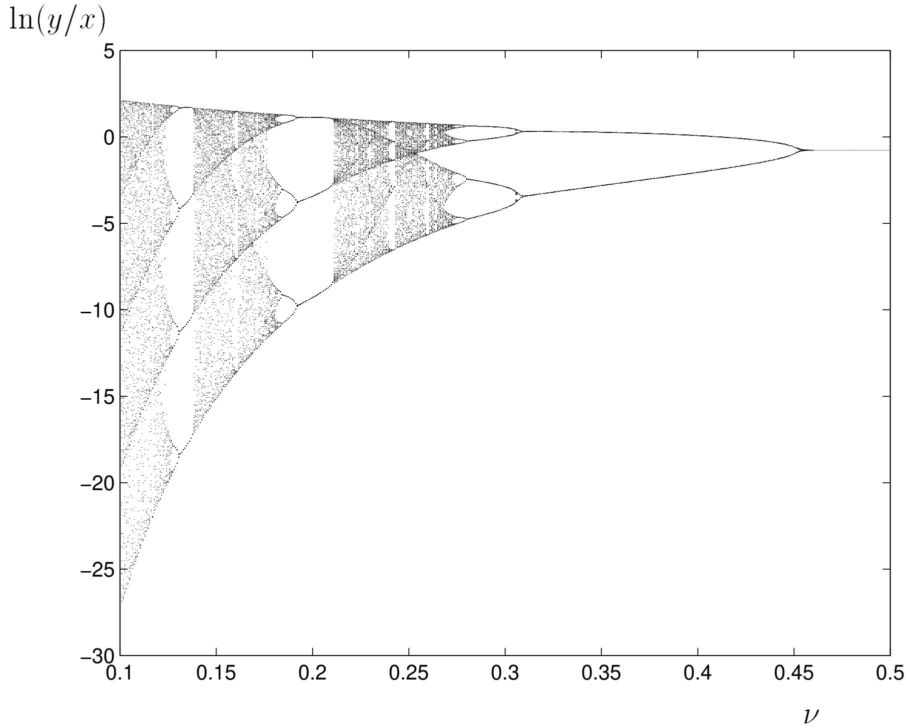

Figure 3: Bifurcation diagram for $a_1 = \lambda_1 = 0.1$, $a_2 = 0.03\nu$, $\lambda_2 = 0.04\nu$.

Figure 3 illustrates the bifurcation diagram for the three dimensional system with parameters $a_1 = \lambda_1 = 0.1$ and $a_2 = 0.03\nu$ and $\lambda_2 = 0.04\nu$. The vertical axis corresponds to the $\ln(y/x)$-coordinates of some iterates of a point under the Poincaré map in the surface $s = 0.1$, $s' < 0$ and the horizontal axis represents the parameter ν.

Under suitable conditions for small a_i and λ_i all inner solutions will intersect a two-dimensional set D defined by $u_- < x + y < u_+$ and $s =$constant in the region $s' < 0$ and thus their behaviour is described by the Poincaré map there. This Poincaré map at least exists and describes the behaviour of the inner solutions well in the case when all trajectories starting in D behave the following way: The s-coordinate on the trajectory first decreases to a minimum where $x + y$ is also small, then the s-coordinate increases to a value a bit less than 1 while $x + y$ still remains small, and then $x + y$ strongly increases and the s-coordinate decreases and finally the trajectory hits D. The Poincaré map is illustrated in figure 4, where P_2 is the image of P_1 which is the image of P_0 and Q_2 is the image of Q_1 which is the image of Q_0.

This behaviour of the solutions imply that the inner solutions are contained in a 'thick' cylinder containing the range of definition of the Poincaré map. We use this fact and some other properties to construct a model map for the behaviour of the solutions on the attractor in section 5. Not only experiments but also theoretical estimates (see also [8]) indicate the existence of parameter values (or functions α_i and f_i) for which the assumptions given in section 5 are fulfilled. Anyhow there are a lot of examples when a Poincaré

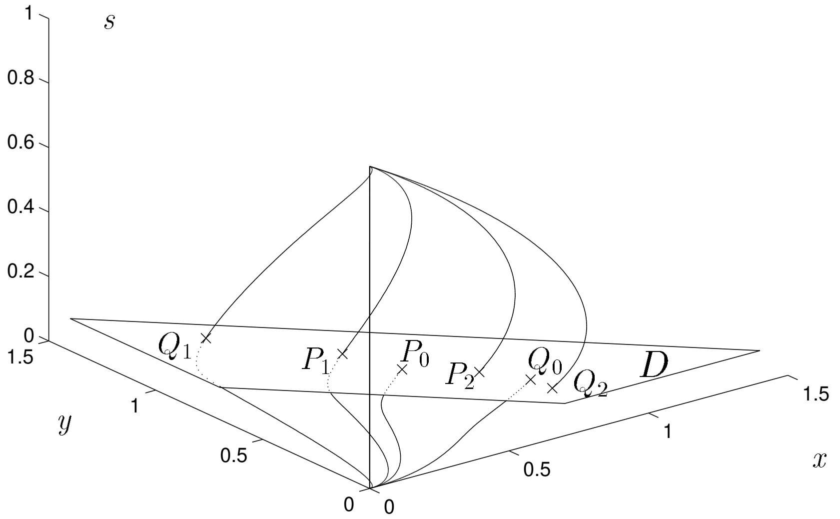

Figure 4: Illustration of Poincaré map.

map of the type given in section 5 does not work. An example of these is given in section 6.

5 A model map in the three dimensional case

Not only from numerical experiments but also from theoretical estimates (see [8] and sections 10 and 11) one can be convinced that the Poincaré map defined on D in section 4 is usually strongly contracting in the $x+y$-direction. Thus the behaviour of the Poincaré map is well described by a one dimensional map of the y/x coordinate. Here we construct such a map. If we denote by v the $\ln(y/x)$-coordinate and by u the $x+y$-coordinate, then the model map f takes the form

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

where

$$k_1 = (\gamma - \alpha)/a_1,\ k_2 = (\gamma - \alpha)/(\gamma a_2)$$

and

$$\gamma = \frac{\lambda_2 a_1}{\lambda_1 a_2},\ \alpha = \frac{(1-\lambda_2)(1+a_1)}{(1-\lambda_1)(1+a_2)}.$$

From (4.2) it follows that for the interesting parameter regions we have

$$1 < \alpha < \gamma < a_1/a_2.$$

Analysis of the map f shows that it can have an attractor, which can be a fixed point, a periodic orbit or a chaotic set. The attractor corresponds to a periodic solution or to chaotic inner solutions for the original system. We can also use the "reconstruction theorem" of F. Takens [28]-[29] to get results about the real map itself. In [8] the system (4.1) and the bifurcations leading to chaos through period doubling are examined in more detail in the case $a_1 = \lambda_1 = 0.2$ and $a_2 = 0.03\nu$ and $\lambda_2 = 0.06\nu$, where $0.2 \leq \nu \leq 1$.

To see why and how the model map is working we prove some results about the behaviour of the trajectories of the system and the orbits of the model map.

Let $s_0 < \varepsilon \min\{a_1, a_2, \lambda_1, \lambda_2\}$, $\varepsilon < 0.1$. Consider a trajectory starting at a point (x_0, y_0, s_0), where $s' < 0$. Denote the next intersection with the plane $s = s_0$ by (x_1, y_1, s_1), $s_1 = s_0$ and the next intersection with the plane $s = 1 - \varepsilon$ by (x_2, y_2, s_2). Continuing from the point (x_2, y_2, s_2) denote the next intersection with the plane $s = s_2 = 1 - \varepsilon$ by (x_3, y_3, s_3), $s_3 = s_2$ and the next intersection with the plane $s = s_0$ by (x_5, y_5, s_5), $s_5 = s_0$. Denote

$$u_i = x_i + y_i \ , \quad v_i = \ln(y_i/x_i) \ , \qquad i = 1, \ldots, 5 \ .$$

A trajectory starting at a point (x_0, y_0, s_0), $x_0 + y_0 > 0.7$ is called a *g–trajectory*, if it intersects the plane $s = 1-\varepsilon$ before it leaves the region $s' > 0$ and thereafter intersects the the plane $s = s_0$ for $x + y > 0.7$ before it leaves the region $s' < 0$.

We have strong numerical and analytical evidence that most of the trajectories are g–trajectories in a suitable range of the parameters a_i, λ_i so that the model map constructed below is appropriate. The trajectories for small s have the strongest influence on the model map and the result of that influence can be seen from the proof of the following theorem.

Theorem 5.1 *Suppose $\alpha < \gamma < a_1/a_2$, $a_1, \lambda_1 < 0.2$ and $\varepsilon < 0.1$. Then any g–trajectory satisfies*

$$v_5 = K + v_0 - qu_0 \frac{k_1 + k_2 e^{v_0}}{1 + e^{v_0}},$$

where

$$\frac{y_2 x_1}{y_1 x_2} \frac{y_5 x_3}{y_3 x_5} \left(\frac{x_3 x_1}{x_2 x_0} \right)^{\alpha - 1} < e^K < \frac{y_2 x_1}{y_1 x_2} \frac{y_5 x_3}{y_3 x_5} \left(\frac{x_3 x_1}{x_2 x_0} \right)^{\alpha(1+\varepsilon/1.4)-1} ,$$

$$q = 1 + \varepsilon_1 + \varepsilon_2 \frac{\gamma + \alpha}{\gamma - \alpha}.$$

Further, $\varepsilon_2 \to 0$ when $\varepsilon \to 0$, and $\varepsilon_1 \to 0$ when $\varepsilon,\ a_1 \to 0$.

The exact dependence of ε_1 and ε_2 on ε and a_1 can be seen in the proof of the theorem given in section 10. Both numerical experiments and analytical

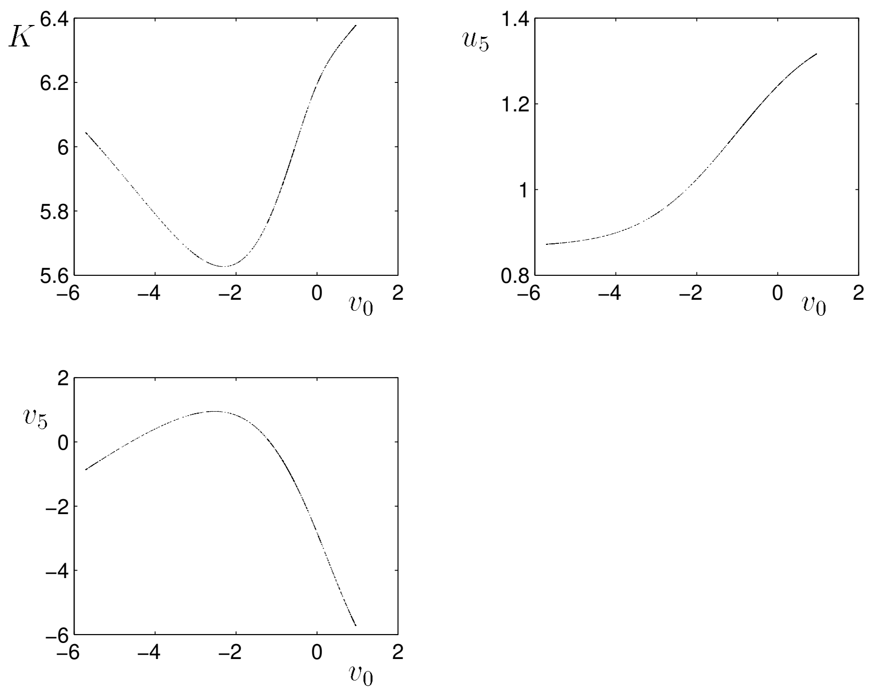

Figure 5:

estimates show that the changes in K are small compared with the other effects in the expression for v_5. Also u_0 can usually be approximated by a constant on the attractor. Because for constant parameters we cannot let $\varepsilon \to 0$ if we want to have enough g–trajectories, the model cannot be made arbitrarily good, but anyhow it reflects main properties.

In practice the model map works even with parameter values for which Theorem 5.1 does not give good estimates. In Figure 5 we see how v_5 depends on v_0 in the case $\varepsilon = 0.003$ for the parameter values $a_1 = \lambda_1 = 0.1, a_2 = 0.0075, \lambda_2 = 0.01$ on the attractor. Also the dependence of $u_5 = x_5 + y_5$ and K on v_0 is plotted. Both on the attractor.

Because K and u_5 are usually not very strongly dependent on v_0 the model map f (where these are replaced by constants β and u) describes the behaviour reasonably well.

Let us now state some immediate results for the model map, which can be used to find inner solutions of periodic or chaotic type. (Observe that from the parameter conditions it follows that $k_2 > k_1$.)

Theorem 5.2 *If $(k_2 - k_1)u > 4$ then f has two extrema: a maximum at v_- and a minimum at v_+, where $v_- < v_+$. If $\beta > uk_2$ then $v \to \infty$ and if $\beta < uk_1$ then $v \to -\infty$ when the map is iterated. If $uk_1 < \beta < uk_2$ the map has a fixed point and an attractor in a bounded set. The fixed point has a period doubling for $k_2 - k_1 = u(\beta/u - k_1)(k_2 - \beta/u)/2$.*

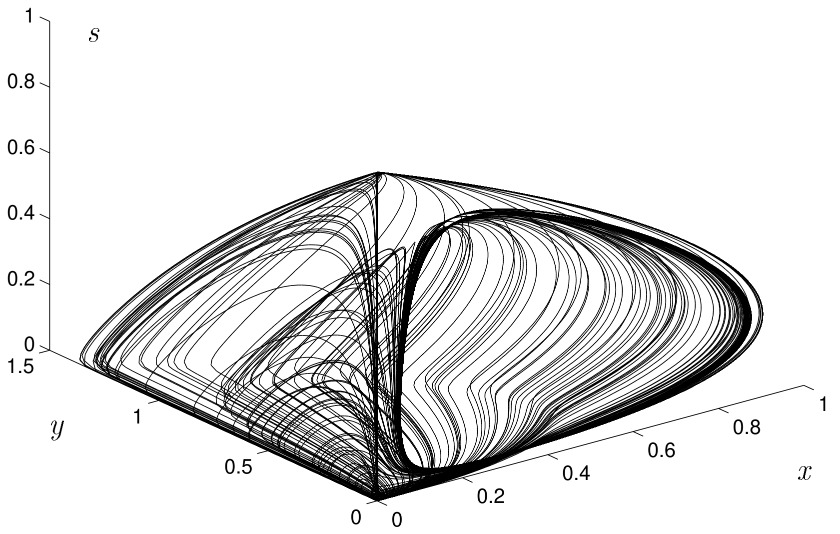

Figure 6: Part of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.06$, $\lambda_2 = 0.163$.

The statement follows by direct calculations. A chaotic attractor is thus expected after the period doubling in the region $k_2 - k_1 > u(\beta/u - k_1)(k_2 - \beta/u)/2$.

6 When the model map does not work

Figure 6 illustrates an attractor in the case when a Poincaré map of the type considered in section 6 does not work.

The problem arises because the intersection of the attractor with the plane s = constant can intersect the curve $s' = 0$ or have points very close to it. Thus the intersection of the attractor cannot be well approximated by the graph of a function of the y/x coordinate which is seen in figures 7-10. Another difficulty is connected with the fact that the Poincaré map becomes usually discontinous at points mapped to the curve $s' = 0$.

In figures 7-10 we describe the behaviour of the Poincaré map on the intersection of the attractor with the plane $s = 0.05$ in the case $a_1 = 0.25, \lambda_1 = 0.25, a_2 = 0.01, \lambda_2 = 0.02$. The points $a-f$ in figure 7 are mapped to the corresponding points in figure 8 and the pieces of the curve between two nearby points are mapped to the attractor without making folds. Analogously the points $a-e$ in figure 9 are mapped to the corresponding points in the figure 10. If we decrease a_2 and λ_2 then the type of the crosssection of the attractor is changed as shown in figures 11-13. The behaviour of the one dimensional stable manifold of the saddle equilibrium in $x = 0, y, s > 0$ clearly strongly

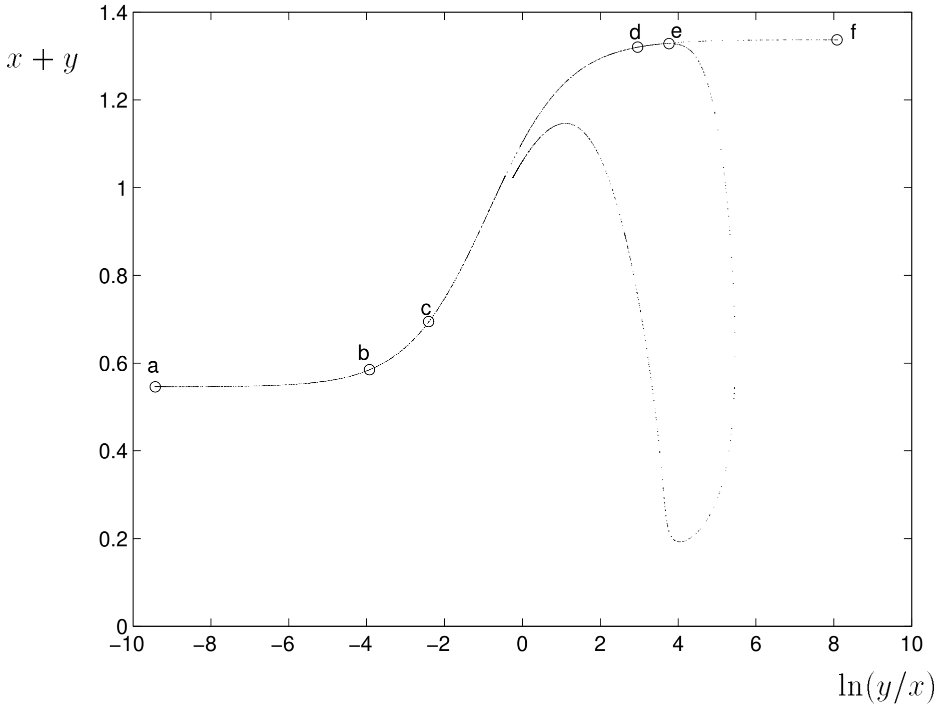

Figure 7: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.01$, $\lambda_2 = 0.02$ with the plane $s = 0.05, s' > 0$ with given points $a - f$.

effects the type of the attractor. For the parameter values in figures 7-10 the stable manifold comes from the equilibrium in the xs-plane, but for the parameter values in figure 11 it comes from the infinity. For some parameters between these it is contained in the unstable manifold of the limit cycle in the xs-plane. For parameters near to these special values the behaviour of the attractor becomes more complicated as is seen in figures 12-14.

7 Location and stability of cycles in the two dimensional coordinate planes

In this section we discuss the stability of the cycles in the planes $x = 0$ and $y = 0$ for the three dimensional system of type two predators-one prey.

The following theorem is proved in section 11. From the lemmas used in the proof we can easily find estimates for the location of the limit cycle in the plane $x = 0$.

Theorem 7.1 *Suppose $\lambda_i < 2a_i < 0.1$, $\lambda_i, a_i < \varepsilon < 0.05$, $i = 1, 2$ and*

$$\gamma > \frac{4/3 - \varepsilon \ln \varepsilon}{1 - 12\varepsilon + 2\varepsilon \ln \varepsilon}.$$

Then the limit cycle in the plane $x = 0$ is unstable.

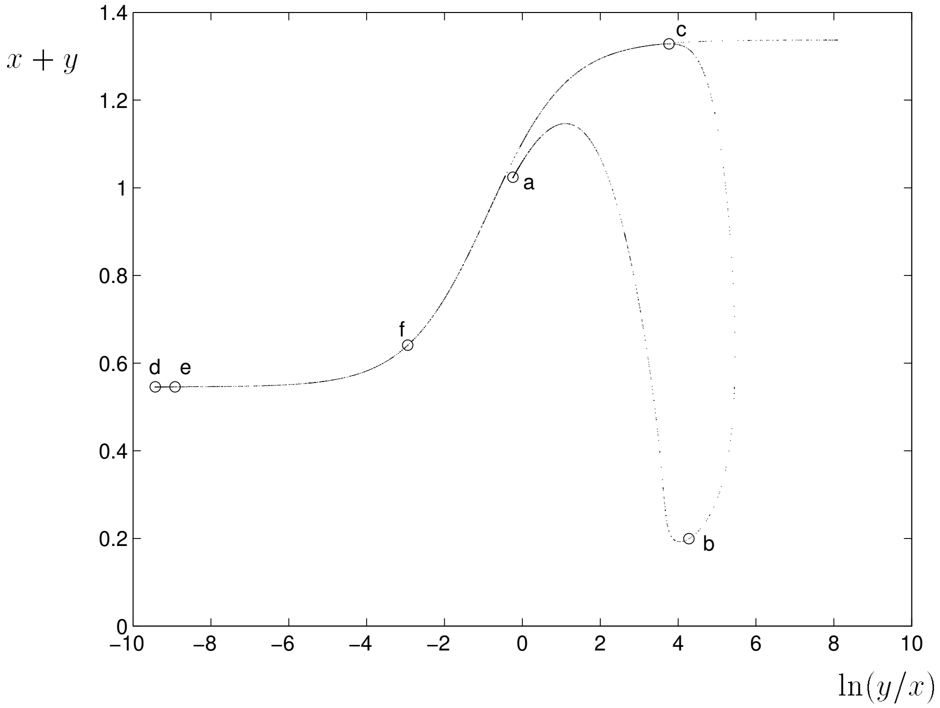

Figure 8: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.01$, $\lambda_2 = 0.02$ with the plane $s = 0.05$, $s' > 0$ with images of the points $a - f$ in the previous figure.

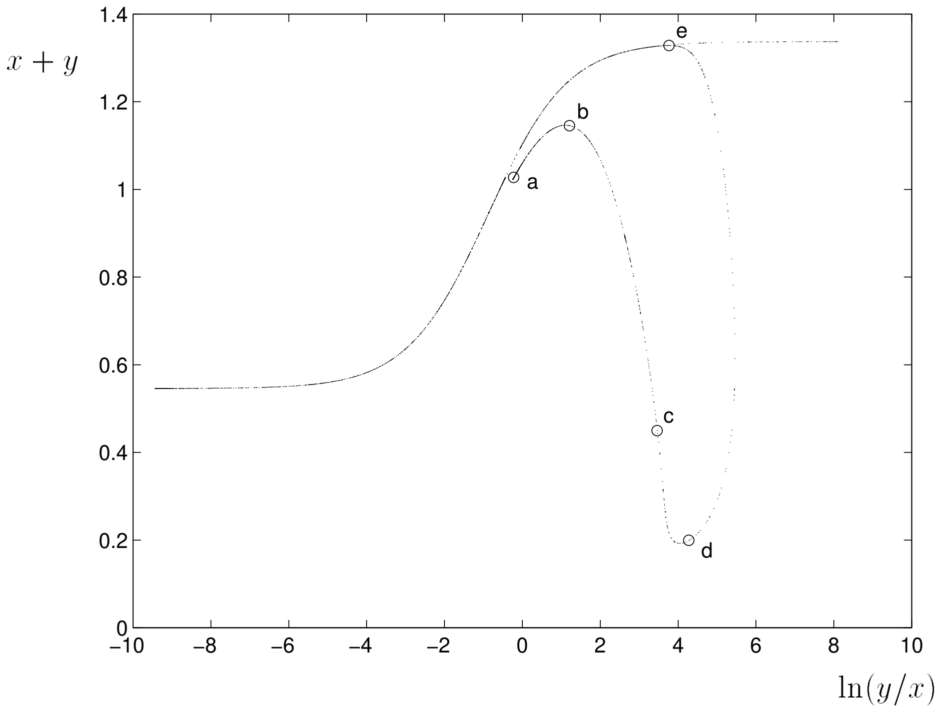

Figure 9: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.01$, $\lambda_2 = 0.02$ with the plane $s = 0.05$, $s' > 0$ with given points $a - e$.

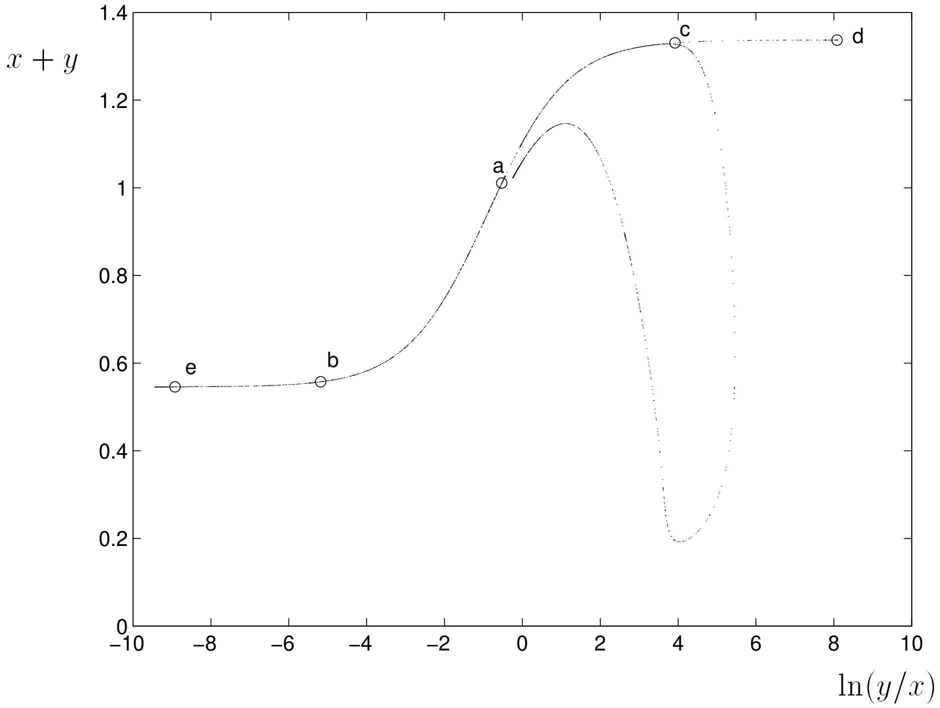

Figure 10: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.01$, $\lambda_2 = 0.02$ with the plane $s = 0.05$, $s' > 0$ with images of the points $a - e$ from the previous figure.

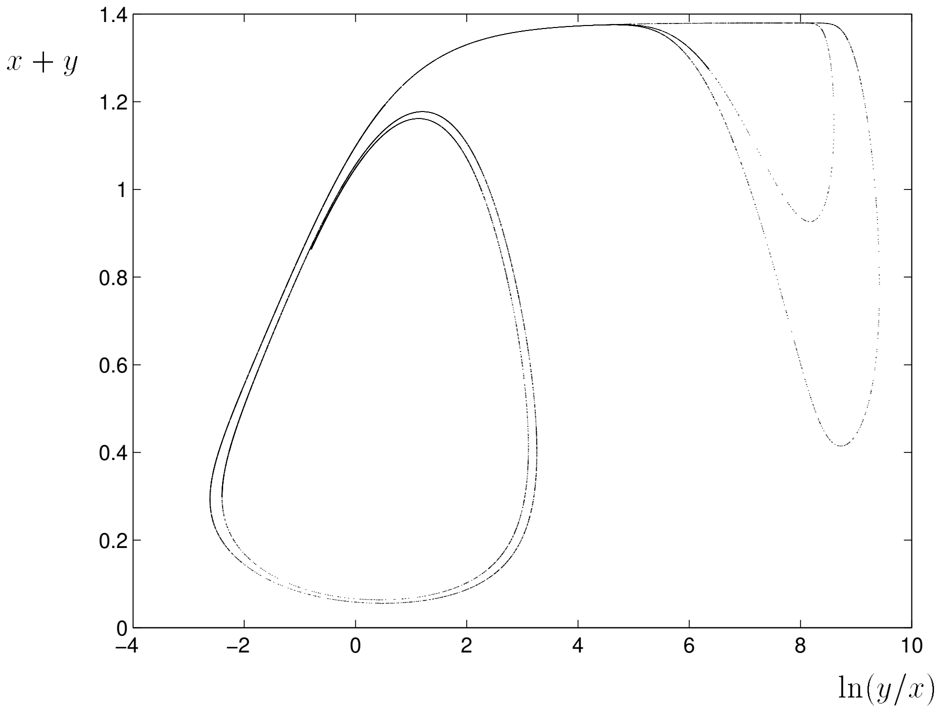

Figure 11: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.006$, $\lambda_2 = 0.012$ with $s = 0.02$, $s' > 0$.

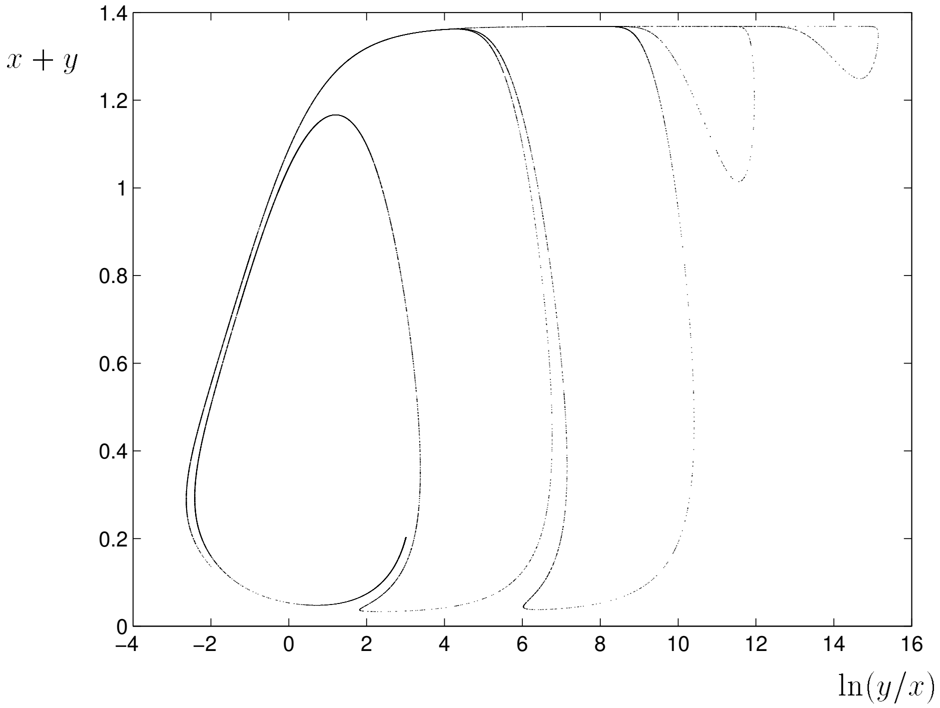

Figure 12: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.0075$, $\lambda_2 = 0.015$ with $s = 0.02$, $s' > 0$.

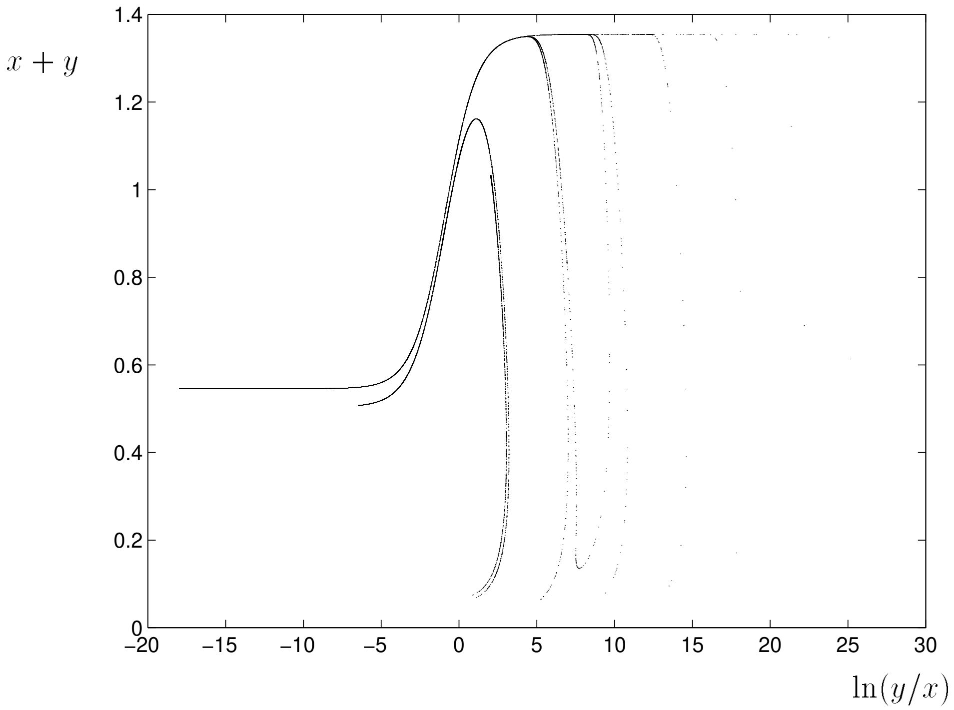

Figure 13: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.007$, $\lambda_2 = 0.014$ with $s = 0.05$, $s' > 0$.

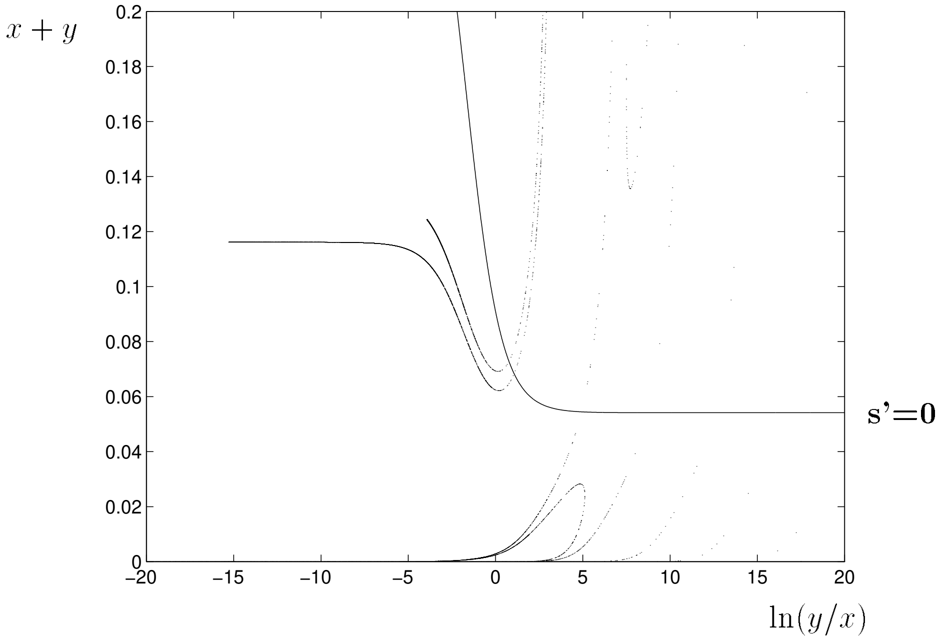

Figure 14: Intersection of the attractor for $a_1 = \lambda_1 = 0.25$, $a_2 = 0.007$, $\lambda_2 = 0.014$ with $s = 0.05$, $-20 < \ln(y/x) < 20$, $x + y < 0.2$.

This means that if the parameters are small and the difference between a_1 and a_2 is not small the limit cycle in the $x = 0$ plane will be unstable for most γ between 1 and a_2/a_1 (the region where there may be inner solutions). On the other hand if the limit cycle in the plane $y = 0$ is not intersecting the line $s = \lambda_2$ or only have a small part below it then the cycle is clearly unstable (y' is positive or mostly positive). When both cycles are unstable we usually expect inner solutions.

In connection with these results we have the following questions

Question 7.1 *Does it always mean that all other predators go extinct if one cycle in a coordinate plane is locally stable?*

The question can also be posed for the case when there is only a stable equilibrium in one of the coordinate planes and no cycle (i.e. $2\lambda_i + a_i > 1$).

Question 7.2 *Does it always mean that all other predators go extinct if one equilibrium in a coordinate plane is locally stable?*

A partial answer is given in [22]. Compare also with Figures 1-2.

8 The behaviour of the four dimensional system

Consider the four dimensional subsystem of (1.1)-(1.2) written in the form

$$
\begin{aligned}
x' &= \frac{s-\lambda_1}{s+a_1}x,\\
y' &= \frac{s-\lambda_2}{s+a_2}y,\\
z' &= \frac{s-\lambda_3}{s+a_3}z,\\
s' &= (1-s-x/(s+a_1)-y/(s+a_2)-z/(s+a_3))s.
\end{aligned}
\tag{8.3}
$$

Parameter regions for (8.3), where one predator goes extinct can be found in the same way as in [21] by only interchanging indices. Thus for example if we suppose $a_1 > a_2 > a_3$ there cannot be any inner solutions outside the region determined by the inequalities:

$$\lambda_2 < \lambda_1 < \lambda_2 a_1/a_2, \quad \lambda_3 < \lambda_1 < \lambda_3 a_1/a_3, \quad \lambda_3 < \lambda_2 < \lambda_3 a_2/a_3.$$

But even in this parameter region inner solutions are hard to find. An analog of the model map in section 5 is not seen to give any stable coexistence. This analog is the two dimensional map defined by

$$u \to \alpha_2 + u - g_2 \frac{1/\lambda_1 + e^u/\lambda_2 + e^v/\lambda_3}{1+e^u+e^v}, \quad v \to \alpha_3 + v - g_3 \frac{1/\lambda_1 + e^u/\lambda_2 + e^v/\lambda_3}{1+e^u+e^v},$$

where $g_i = (1-\gamma_i)\lambda_1/a_1$ and $\gamma_i = \lambda_i a_1/(\lambda_1 a_i)$, $i = 2, 3$. Clearly this map has no fixed points (where $u, v \neq 0$), except for some special relations between the parameters. Mostly also either $u \to 0$ or $v \to 0$.

Anyhow experimentally we can show that stable inner solutions exist for a narrow parameter region (a part of such a region is plotted in the parameter space in [12]). In Figure 15 we see a bifurcation diagram for the x-coordinate varying a parameter r, where there always seems to be inner solutions (also the y- and z-coordinates are nonzero). One value of the parameter r corresponds to a point on a straight line in the six dimensional parameter space given by the points $a_1 = 0.25$, $\lambda_1 = 0.3$, $a_2 = 0.05$, $\lambda_2 = 0.18$, $a_3 = 0.02$, $\lambda_3 = 0.13$ (here $r = 0$) and $a_1 = 0.25$, $\lambda_1 = 0.3$, $a_2 = 0.06$, $\lambda_2 = 0.2$, $a_3 = 0.025$, $\lambda_3 = 0.16$ (here $r = 1$).

Figure 16 shows an period eight solution from different perspectives in the case $r = 640/999$.

Figure 17 shows the intersection of the inner attractor with the surface $s = 0.1$, $s' < 0$ for the parameter $r = 99/499$.

In the bifurcation diagram we can observe except for period doubling also Hopf bifurcations of the Poincaré map.

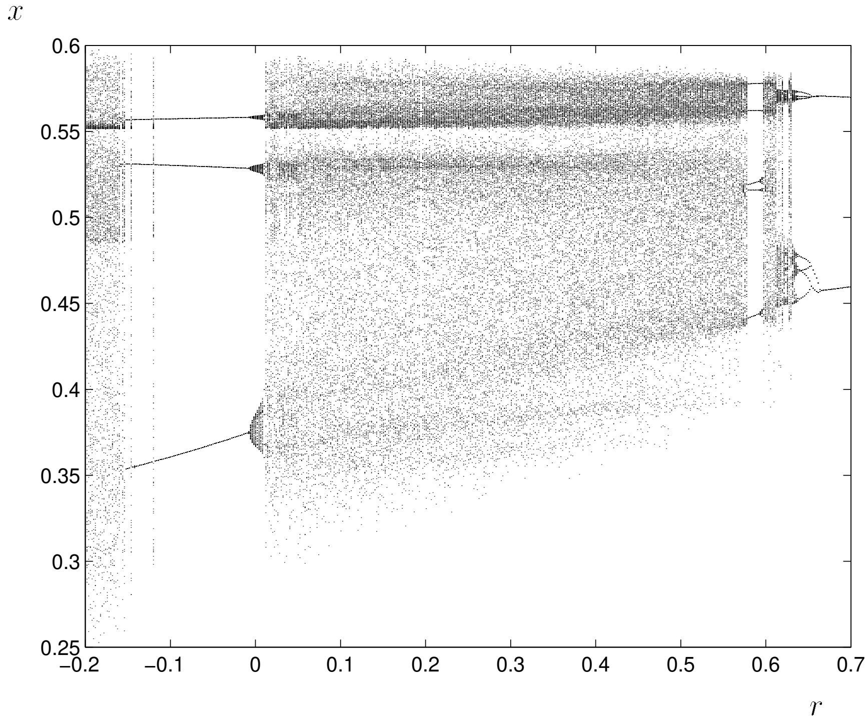

Figure 15: Bifurcation diagram in the four dimensional case.

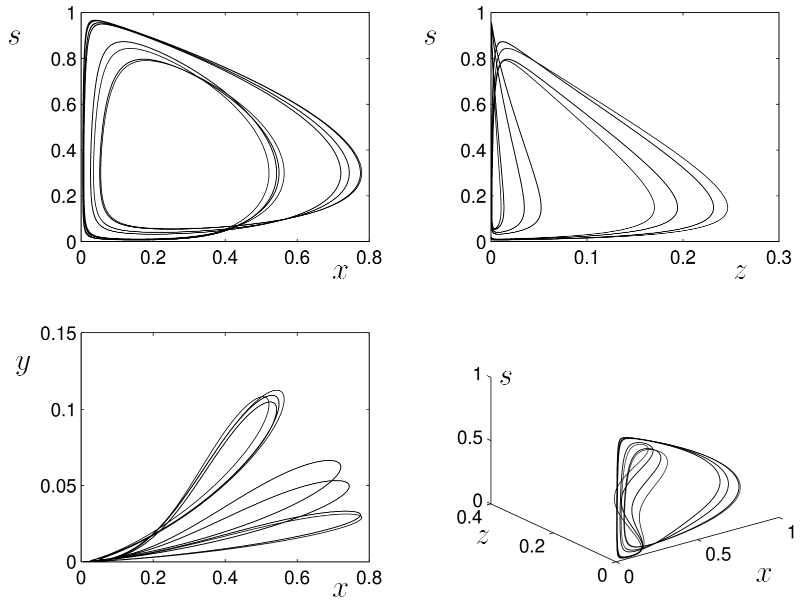

Figure 16: Period eight solution for $r = 640/999$.

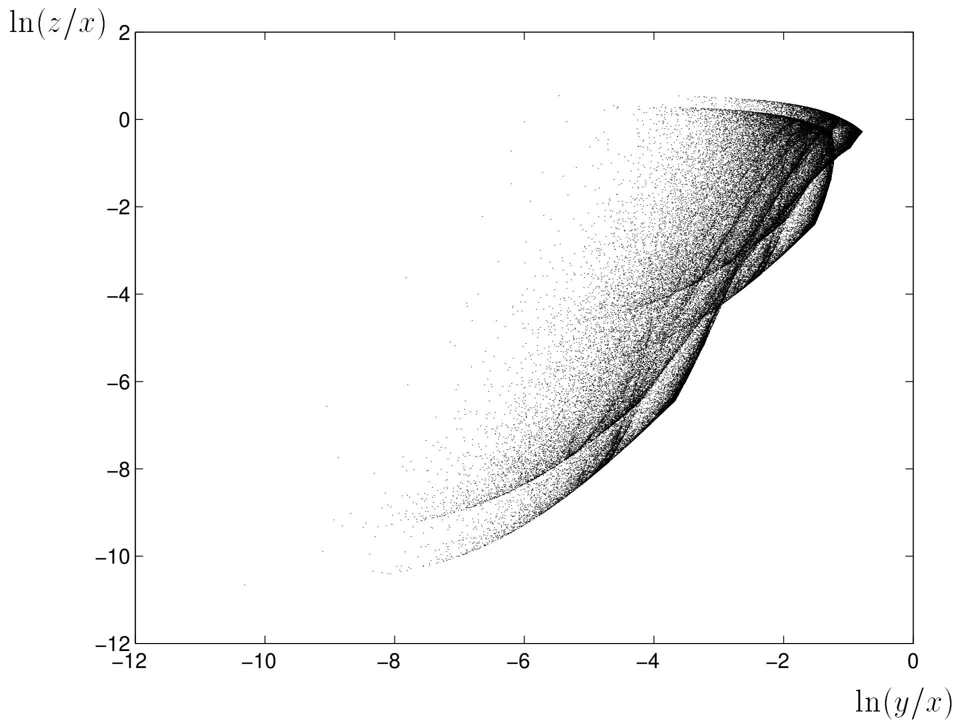

Figure 17: Intersection of the attractor with $s = 0.1$ for $r = 99/499$.

Unstable inner solutions seem to be more frequent although also they are rare. We have no examples where we have seen two different attractors. So the following question is open:

Question 8.1 *Can there be more than one attractor for the system (8.3)?*

The question is open even in the three dimensional case even if the results above do not give so much hope for the existence of many attractors in this case.

In the examples of inner solutions illustrated in the figures 15-17 two of the predators always coexist if the third is absent. So also the following question is open:

Question 8.2 *Can the system (8.3) have stable inner solutions even in the case where one of the two predators go extinct if some third predator is not present?*

9 About numerical methods.

Some of our results have been verified only numerically. For the numerical integration (using the Runge–Kutta–Fehlberg 4/5 –method) we first write the equations for the logarithms of x, y, z, and s . To speed up computations we approximate the trajectories near equilibria by the linearized flow and in the region with small s using the estimates of Lemmas 10.1 and 10.2.

For good cases well known program libraries (see [10] for references) can also be used effectively for examining the limit cycles and the period doubling etc. In bad cases (i.e. with small parameters) these have to be modified.

10 Proof of Theorem 5.1.

In this section we assume $a_i, \lambda_i < 0.2$, $i = 1, 2$, $\alpha < \gamma < a_1/a_2$ and denote by $\Gamma(s)$ the ratio $f_2(s)/f_1(s)$. Observe that $\Gamma(1) = \alpha$. Theorem 5.1. follows from the following technical theorem.

Theorem 10.1 *Consider a trajectory starting at a point (x_0, y_0, s_0), where $s_0 < \varepsilon a_i, \varepsilon\lambda_i$, $i = 1, 2$ and $\varepsilon < 0.1$ and $u_0 = x_0 + y_0 > 0.7$. Let (x_1, y_1, s_0) be the next intersection with the plane $s = s_0$ and $(x_2, y_2, 1-\varepsilon)$ and $(x_3, y_3, 1-\varepsilon)$ be the next intersections with the plane $s = 1 - \varepsilon$. Let us denote*

$$O_1 = \frac{y_1 x_0}{x_1 y_0} \quad O_3 = \frac{y_3 x_2}{x_3 y_2}.$$

Then

$$K_1 e^{-q_1(\gamma-\alpha)(x_0/a_1 + y_0/(\gamma a_2))} < O_1 O_3 < K_2 e^{-q_2(\gamma-\alpha)(x_0/a_1 + y_0/(\gamma a_2))},$$

where

$$K_1 = \left(\frac{x_3 x_1}{x_2 x_0}\right)^{\alpha-1}, \quad K_2 = \left(\frac{x_3 x_1}{x_2 x_0}\right)^{\alpha_2 - 1},$$

$$\alpha_2 = \alpha(1 + \varepsilon/1.4), \quad q_1 = (1 + 2\varepsilon)\left(1 + \frac{3\varepsilon\gamma}{\gamma - \alpha}\right)$$

and

$$q_2 = (1 - e^{-0.5/a_1})(1 - \varepsilon)\left(1 - \frac{2\varepsilon(\gamma + \alpha)}{\gamma - \alpha}\right).$$

To prove the theorem we use three lemmas. The first one gives estimates for x_1, the second one gives estimates for the ratio y_1/x_1 and the third one estimates the ratio y_3/x_3.

Lemma 10.1 *In the situation of Theorem 10.1 the following estimates are true*

(10.1) $$x_1 < x_0 e^{-(1-e^{-0.582/a_1})(1-\varepsilon)(x_0/a_1 + y_0/(\gamma a_2))}$$

and

(10.2) $$x_1 > x_0 e^{-(1+590\varepsilon/441)(x_0/a_1 + y_0/(\gamma a_2))}.$$

Proof. From the system we get the equations

$$
\begin{aligned}
&\frac{(s-\lambda_1)ds}{(s+a_1)(1-s)s} = \\
(10.3)\qquad &\left(\frac{1}{x} - \frac{1}{(s+a_1)(1-s)} - \frac{1}{(s+a_2)(1-s)}\frac{y}{x}\right) dx = \\
&\frac{dx}{x} - \frac{dx}{(1-s)(s+a_1)} - \frac{(s-\lambda_1)dy}{(1-s)(s+a_1)(s-\lambda_2)}
\end{aligned}
$$

and

$$
\begin{aligned}
&\frac{(s-\lambda_2)ds}{(s+a_2)(1-s)s} = \\
(10.4)\qquad &\left(\frac{1}{y} - \frac{1}{(s+a_2)(1-s)} - \frac{1}{(s+a_1)(1-s)}\frac{x}{y}\right) dy = \\
&\frac{dy}{y} - \frac{dy}{(1-s)(s+a_2)} - \frac{(s-\lambda_2)dx}{(1-s)(s+a_2)(s-\lambda_1)}.
\end{aligned}
$$

Integrating (10.3) and (10.4) along the trajectory in $s < \varepsilon$ from (x_0, y_0, s_0) to (x_1, y_1, s_0) the left hand side of the equations will become zero (because the s-values are the same). Thus we get the integrals

$$
(10.5)\qquad \ln\left(\frac{x_1}{x_0}\right) = \int_{x_0}^{x_1} \frac{dx}{(1-s)(s+a_1)} + \int_{y_0}^{y_1} \frac{(s-\lambda_1)dy}{(1-s)(s+a_1)(s-\lambda_2)}
$$

and

$$
(10.6)\qquad \ln\left(\frac{y_1}{y_0}\right) = \int_{y_0}^{y_1} \frac{dy}{(1-s)(s+a_2)} + \int_{x_0}^{x_1} \frac{(s-\lambda_2)dx}{(1-s)(s+a_2)(s-\lambda_1)}.
$$

Using the fact that s is small we can use these integrals to get estimates for x_0 and y_0. Because $s < \varepsilon a_i, \varepsilon\lambda_i$, $1 < \gamma < a_1/a_2$ and $\varepsilon < 0.1$ we get the estimates

$$
(10.7)\qquad \frac{1-\varepsilon}{a_1} < \frac{1}{(1+\varepsilon)a_i} < \frac{1}{(1-s)(s+a_i)} < \frac{1}{a_i} < \frac{1}{a_2},
$$

$$
\begin{aligned}
(10.8)\qquad &\frac{1-\varepsilon}{a_1} < \frac{1}{(1+\varepsilon)\gamma a_2} < \frac{\lambda_1 - s}{(a_1+s)(\lambda_2-s)(1-s)} \\
(10.9)\qquad &< \frac{1}{\gamma a_2}\frac{1}{(1-\varepsilon)(1-0.2\varepsilon)} < \frac{1+590\varepsilon/441}{a_2}.
\end{aligned}
$$

(We use that $(\lambda_1 - s)/(\lambda_2 - s)$ is an increasing function of s for $0 < s < \lambda_2$ and $(\lambda_i - s)/(a_i + s)$ is a decreasing function of s for $0 < s < \lambda_i$.) Furthermore,

$$
\begin{aligned}
(10.10)\qquad &\frac{1-2\varepsilon}{a_1} < \frac{1-\varepsilon}{1+\varepsilon}\frac{\gamma}{a_1} < \frac{\lambda_2 - s}{(a_2+s)(\lambda_1-s)(1-s)} \\
(10.11)\qquad &< \frac{\gamma}{a_1}\frac{1}{(1-\varepsilon)(1-0.2\varepsilon)} < \frac{1+590\varepsilon/441}{a_2}.
\end{aligned}
$$

Using estimates (10.7)-(10.11) in integrals (10.5)-(10.6) we get

$$x_1 < x_0 e^{(1-\varepsilon)(u_1-u_0)/a_1}, \tag{10.12}$$

$$y_1 < y_0 e^{(1-2\varepsilon)(u_1-u_0)/a_1}, \tag{10.13}$$

where $u_i = x_i + y_i$. The estimates (10.12) and (10.13) together give

$$u_1 < u_0 e^{(1-2\varepsilon)(u_1-u_0)/a_1}. \tag{10.14}$$

Using $u_0 > 0.7$, $a_1 < 0.2$ and $\varepsilon < 0.1$ in (10.14) we get $u_1 < 0.053$. Substituting $u_1 < 0.053$ into (10.12) and (10.13) and using $\varepsilon < 0.1$ we get

$$x_1 < x_0 e^{-0.582/a_1}, \quad y_1 < y_0 e^{-0.517/a_1}. \tag{10.15}$$

But using (10.15) and (10.7)-(10.9) when integrating (10.3) gives inequalities (10.1) and (10.2). Lemma is proved.

Lemma 10.2 *Consider the trajectory in Lemma 10.1. Then the ratio y_1/x_1 satisfies*

$$\frac{y_0}{x_0}\left(\frac{x_1}{x_0}\right)^{\gamma_2-1} < \frac{y_1}{x_1} < \frac{y_0}{x_0}\left(\frac{x_1}{x_0}\right)^{\gamma_1-1}, \tag{10.16}$$

where $\gamma_1 = (1-2\varepsilon)\gamma$ and $\gamma_2 = (1+2\varepsilon/0.9)\gamma$.

Proof. For $s < \varepsilon$

$$\gamma_1 = (1-2\varepsilon)\gamma < \frac{1-\varepsilon}{1+\varepsilon}\gamma < \frac{\lambda_2 - s_0}{a_2+s_0}\frac{a_1}{\lambda_1} < \Gamma(s) \tag{10.17}$$

$$< \frac{\lambda_2}{a_2}\frac{a_1+s_0}{\lambda_1-s_0} < \frac{1+\varepsilon}{1-\varepsilon}\gamma < (1+2\varepsilon/0.9)\gamma = \gamma_2. \tag{10.18}$$

($(\lambda_i - s)/(a_i+s)$ is decreasing in s for $0 < s < \lambda_i$.) By the system equations we have

$$\frac{dy}{dx} = \Gamma(s)\frac{y}{x}. \tag{10.19}$$

Integrating gives (10.16) and the lemma is proved.

Lemma 10.3 *In the situation of Theorem 10.1 the following estimates are true*

$$\frac{y_2}{x_2}\left(\frac{x_3}{x_2}\right)^{\alpha-1} < \frac{y_3}{x_3} < \frac{y_2}{x_2}\left(\frac{x_3}{x_2}\right)^{\alpha_2-1}, \tag{10.20}$$

where $\alpha = \Gamma(1)$ and $\alpha_2 = \alpha(1+\varepsilon/1.4)$.

Proof. Estimating $\Gamma(s)$ for $s > 1-\varepsilon$ we get

$$\Gamma(s) > \Gamma(1) = \alpha \tag{10.21}$$

$((s+a_1)/(s+a_2)$ and $(s-\lambda_2)/(s-\lambda_1)$ are both decreasing for $s>1-\varepsilon)$ and

$$\Gamma(s) < \frac{1-\lambda_2}{1+a_2}\frac{1-\varepsilon+a_1}{1-\varepsilon-\lambda_1} = \alpha(1+\varepsilon/1.4) = \alpha_2. \tag{10.22}$$

(We have used that $(s-\lambda_i)/(s+a_i)$ increases with s for $s>0$ and that $(1-\varepsilon+a_1)/(1-\varepsilon-\lambda_1) = ((1+a_1)/(1-\lambda_1))(1+(A-B)\varepsilon/(B(B-\varepsilon)))$ where $A=1+a_1, B=1-\lambda_1, \varepsilon<0.1$ and $a_1,\lambda_1<0.2$.) Integrating (10.19) again and using the estimates (10.22) and (10.21) we get (10.20). The lemma is proved.

Proof of Theorem 10.1. Combining (10.16) from Lemma 10.2 and (10.20) from Lemma 10.3 we get

$$K_1\left(\frac{x_1}{x_0}\right)^{\gamma_2-\alpha} < O_1O_3 < K_2\left(\frac{x_1}{x_0}\right)^{\gamma_1-\alpha_2}, \tag{10.23}$$

where

$$K_1 = \left(\frac{x_3x_1}{x_2x_0}\right)^{\alpha-1} \qquad \text{and} \qquad K_2 = \left(\frac{x_3x_1}{x_2x_0}\right)^{\alpha_2-1}.$$

Using (10.17) and (10.22) we get

$$\gamma_1-\alpha_2 = (\gamma-\alpha)\left(1-\frac{2\varepsilon\gamma+\varepsilon\alpha/1.4}{\gamma-\alpha}\right).$$

Thus we get

$$\gamma_1-\alpha_2 > (\gamma-\alpha)\left(1-\frac{2\varepsilon(\gamma+\alpha)}{\gamma-\alpha}\right).$$

Analogously using (10.18) and (10.21) we get

$$\gamma_2-\alpha < (\gamma-\alpha)\left(1+\frac{2\varepsilon/0.9\gamma}{\gamma-\alpha}\right).$$

Combining these estimates with the results of Lemma 10.1 we get

$$K_1e^{-q_1(\gamma-\alpha)(x_0/a_1+y_0/(\gamma a_2))} < O_1O_3 < K_2e^{-q_2(\gamma-\alpha)(x_0/a_1+y_0/(\gamma a_2))},$$

where

$$q_1 = (1+590\varepsilon/441)\left(1+\frac{2\varepsilon\gamma}{0.9(\gamma-\alpha)}\right)$$

and

$$q_2 = (1-e^{-0.582/a_1})(1-\varepsilon)\left(1-\frac{2\varepsilon(\gamma+\alpha)}{\gamma-\alpha}\right).$$

The theorem follows now directly from these estimates.

Let us now see how Theorem 5.1 follows from Theorem 10.1. We observe that $v_5 = v_0+\ln(O_1O_3)+\ln A$, where $A = x_1y_2x_3y_5(y_1x_2y_3x_5)^{-1}$. From the estimate of O_1O_3 from below in Theorem 10.1 we get

$$v_5 > v_0+\ln(K_1A)-q_1(\gamma-\alpha)\left(\frac{x_0}{a_1}+\frac{y_0}{\gamma a_2}\right)$$

and

$$\frac{x_0}{a_1}+\frac{y_0}{\gamma a_2}=\frac{u_0}{1+p_0}\left(\frac{1}{a_1}+\frac{p_0}{\gamma a_2}\right),\ p_0=e^{v_0}$$

and

$$q_1=1+\varepsilon_1+\varepsilon_2\frac{\gamma+\alpha}{\gamma-\alpha},\ \varepsilon_1=2\varepsilon,\ \varepsilon_2=\frac{(3\varepsilon+6\varepsilon^2)\gamma}{\gamma+\alpha}<3\varepsilon+6\varepsilon^2.$$

An estimate for v_5 from above is obtained analogously (the main difference is that here ε_1 and ε_2 depend on a_1). Theorem 5.1 follows from these estimates.

11 Proofs of Theorems 2.2 and 7.1.

Proof of Theorem 2.2. Let a be the greatest of a_i, $i=1,..,n$. Set

$$A=x_1/(s+a_1)+x_2/(s+a_2)+...+x_n/(s+a_n)$$

and $u=x_1+...+x_n$. Then $du/dt<sA$ and $ds/dt=(1-s-A)s$. Because $A\geq u/(s+a)$, $a<0.1$ and $ds/du<(1-s-A)/A$ (in $s'<0<u'$) which is greatest for smallest A, the u-value of the trajectory starting in $s'<0, u'>0$ certainly will grow slower than for the trajectory in the system

$$ds/dt=(1-s)(s+0.1)-u\ ,\quad du/dt=u. \tag{11.1}$$

Consider the function $V=s-cu-bus$, where $c=-1/1.6$ and $b=0.2$. The sign of dV/dt with respect to (11.1) on $V=1$ is determined by a fourth degree polynomial and examination shows that it is negative. Thus a trajectory starting in $V<1$ cannot leave the region.

We now show that any trajectory not on the s-axis must enter the region $V<1$. Any such trajectory starts in some region defined by $s'<-As$ for some $A>0$ which can be considered arbitrarily small. If the solution starts in the region R_1 defined by $s'<-As$ and $s<\lambda/2$ it cannot remain there forever because $u'<-\lambda u/(2a+\lambda)$. But when it leaves R_1 it enters the region $s'>-As$. A solution starting in the region R_2 defined by $s'<-As$ and $s\geq\lambda/2$ cannot remain there forever because $s'<-A\lambda/2<0$. But solutions leaving R_2 enter either the region $s'>-As$ or the region R_1. Thus any trajectory enters the region $s'\geq 0$. But clearly the region $s'\geq 0$ is inside the region defined by $u<(1-s)(s+0.1)$ which is inside the region $V<1$.

This means that any trajectory will come into $V<1$ and thereafter stay in that region. But then the $x_1+...+x_n$-value cannot be greater than 1.6.

Proof of Theorem 7.1. To prove the theorem we need some lemmas. The first five lemmas consider the position of different parts of the trajectory for the limit cycle in the ys-plane. The others give estimates for the trajectories in a neighbourhood of the limit cycle. We suppose $\lambda_i<2a_i<0.1$, $i=1,2$. In Lemmas 11.1-11.4 we will consider trajectories in the y,s-plane $x=0$ only. In these cases we will denote λ_2 and a_2 simply by λ and a.

Lemma 11.1 *A trajectory starting in the region $s \geq 0.95$ intersects $s = 0.4$ next time for an y-value, where $y > 0.846$.*

Proof. The y-value of the trajectory will certainly grow faster than for a system where $\lambda = 0.1$ and $a = 0$. But we shall show that the estimate holds even for that system. Let us again consider the function $V = s - cy - bys$ and let $c = -0.81, \quad b = 0.4$. The sign of the derivative of V with respect to the system is again determined by a fourth degree polynomial and is positive on $V = k = 0.95$ for $0.4 \leq s \leq 0.95$. On $V = k$ we have $s = (k+cy)/(1-by)$. s is decreasing in $y \in [0,1]$ and $s > 0.4$ for $y = 0.846$. Because a trajectory starting in $s \geq 0.95$ cannot intersect $s = (k+cy)/(1-by)$ for $0.4 \leq s \leq 0.95$ it intersects $s = 0.4$ only when $y > 0.846$.

Lemma 11.2 *A trajectory starting in $s = 0.4$, $y > 0.846$ intersects $s = 0.2$ next time for an y-value, where $y > 1$.*

Proof. The proof is analogous to the proof of Lemma 11.1, where we choose $c = -0.66961$, $b = 0.7$, $k = 0.72961$.

Lemma 11.3 *Any trajectory starting in $s = 0.2$, $y > 1$ intersects $s = 0.1\lambda$ for $y > 0.83$.*

Proof. Because the y-value is increasing for $\lambda < s < 0.2$, clearly the trajectory intersects $s = \lambda$ for $y > 1$. For $s < \lambda$ and $s' < 0$:

$$\frac{ds}{dy} > \frac{0.135 - y}{s - \lambda}\frac{s}{y}$$

because $H(s) < H(\lambda) < 0.135$, where $H(s) = (1-s)(s+a)$. Thus the trajectory cannot intersect the solution of $ds/s = (0.135 - y)dy/y$ through $s = \lambda$, $y = 1$:

$$0.135\ln(y) - y + \lambda\ln(s) - s = \lambda\ln(\lambda) - \lambda - 1.$$

To find where the solution intersects $s = 0.1\lambda$ we have to solve

$$L_1(y) = 0.135\ln(y) - y = \lambda(\ln(10) - 9/10) - 1 = L_2(\lambda).$$

Because $L_1'(y) < 0$ for $y > 0.135$ and $L_2'(\lambda) > 0$ the greatest y-solution is obtained for the greatest $\lambda = 0.1$. This solution is clearly greater than 0.83.

Lemma 11.4 *A trajectory starting at a point $(y_0, 0.1\lambda)$ on $s = 0.1\lambda$, where $y_0 > 0.83$, intersects $s = 0.1\lambda$ next time at a point $(y_1, 0.1\lambda)$, where*

$$y_1 < 0.83e^{-\frac{0.69}{a}}. \qquad (11.2)$$

Proof. From

$$\frac{ds}{s} = \frac{H(s) - y}{y} dy$$

follows

$$\int_{y_0}^{y_1} \frac{H(s) - y}{y} dy = 0.$$

In $s < 0.1\lambda$ we have $H(s) < s + a < 1.2a$ from which follows $H(s)/y - 1 < 1.2a/y - 1$ and

$$y_1 < y_0 e^{\frac{y_1 - 0.83}{1.2a}}. \tag{11.3}$$

If for $y < 0.83$

$$F(y, a) = \frac{1}{0.83} e^{\frac{0.83}{1.2a}} y e^{-\frac{y}{1.2a}} > 1,$$

then $y > y_1$. Because $F(y, a) > F(y, 0.05)$ and $F(0.001, 0.05) > 1$ we get $y_1 < 0.001$. Thus (11.2) follows from (11.3).

Lemma 11.5 *There is a neighbourhood of the point* $(0, y, 0.1\lambda_2)$, *where*

$$y < 0.8e^{\frac{-0.69}{a_2}}$$

such that if a trajectory starts at a point $(x_1, y_1, 0.1\lambda_2)$ *in that neighbourhood the* s*-coordinate of the trajectory will increase until it reaches the point* $(x_2, y_2, 0.95)$, *where*

$$1.39 y_1 < y_2 < y_1 \frac{15}{a_2^{1.34}} \tag{11.4}$$

and

$$1.39 x_1 < x_2 < x_1 \frac{15}{a_1^{1.34}} \tag{11.5}$$

Proof. In this proof we use the notations a and λ for a_2 and λ_2 resp. Suppose

$$y < 0.1 H(0.95) \quad \text{and} \quad y < 0.1a \tag{11.6}$$

on the trajectory between the two points. Then $B(s) = (H(s) - y)/H(s) > 0.9$. Because

$$\frac{dy}{y ds} = \frac{s - \lambda}{(H(s) - y - x(s + a)/(s + a_1))s} \tag{11.7}$$

$$= \frac{s - \lambda}{(B(s)H(s) - x(s + a)/(s + a_1))s}, \tag{11.8}$$

where x can be supposed arbitrarily small, and because

$$\frac{s - \lambda}{H(s)s} = -\frac{\lambda}{as} + \frac{\lambda + a}{a(1 + a)} \frac{1}{s + a} + \frac{1 - \lambda}{1 + a} \frac{1}{1 - s} \tag{11.9}$$

we get

$$
\frac{dy}{yds} < -\frac{\lambda}{as} + \left(\frac{\lambda + a}{a(1+a)} \frac{1}{s+a} + \frac{1-\lambda}{1+a} \frac{1}{1-s} \right) \frac{1}{0.9} \tag{11.10}
$$

Integrating along the trajectory (from $(y_1, 0.1\lambda)$ to (y, s)) we get

$$
\frac{y}{y_1} < \left(\frac{0.1\lambda}{s} \right)^k \left(\frac{s+a}{0.1\lambda + a} \right)^{(k+1)/0.9} \left(\frac{1-0.1\lambda}{1-s} \right)^{\frac{1-\lambda}{0.9(1+a)}}, \tag{11.11}
$$

where $k = \lambda/a$. For $s = s_2$ the right hand side of (11.11) is less than

$$
\left(\frac{0.1\lambda}{0.95} \right)^k \left(\frac{1}{a} \right)^{(k+1)/0.9} \frac{1}{(1-0.95)^{1/0.9}} = 20^{1/0.9} C^k \frac{\lambda^k}{a^{(k+1)/0.9}}, \tag{11.12}
$$

where $C = 0.1/0.95$. Using $k = \lambda/a$ we get

$$
\frac{\lambda^k}{a^{(k+1)/0.9}} = \frac{(ka)^k}{a^{(k+1)/0.9}} = k^k \frac{1}{a^{q(k)}}, \tag{11.13}
$$

where $q(k) = (k+1)/0.9 - k$. Thus we get

$$
\frac{y_2}{y_1} < 20^{1/0.9} \frac{C^k k^k a^{q(2)-q(k)}}{a^{q(2)}} = \frac{20^{1/0.9} e^{g(k,a)}}{a^{q(2)}}, \tag{11.14}
$$

where $g(k,a) = k\ln(C) + k\ln(k) + (q(2) - q(k))\ln(a) < g(k, 0.05) < g(2, 0.05)$. But now because $q(2) < 1.34$ we get

$$
\frac{y_2}{y_1} < \frac{20^{1/0.9} e^{g(2,0.05)}}{a^{1.34}} < \frac{15}{a^{1.34}}. \tag{11.15}
$$

Thus the second part of (11.4) is proved provided (11.6) holds. Let us now convince ourself that (11.6) is satisfied. Since we can suppose

$$
y_1 < 0.83 e^{\frac{-0.69}{a}}
$$

we get from (11.15)

$$
y_2 < 0.83 \frac{15}{a^{1.34}} e^{\frac{-0.69}{a}}
$$

which satisfies (11.6) for $a < 0.05$. Clearly (11.6) is satisfied at the endpoints of the trajectory and because the y-value first decreases and then increases (11.6) is satisfied on the whole trajectory. Thus we have proved the estimate from above for y_2/y_1.

The analogous estimate for x_2/x_1 can be proved in the same way. Let us now prove the estimate for y_2/y_1 from below. As above we get

$$
\frac{dy}{yds} > -\frac{\lambda}{0.9as} + \left(\frac{\lambda + a}{a(1+a)} \frac{1}{s+a} + \frac{1-\lambda}{1+a} \frac{1}{1-s} \right) \tag{11.16}
$$

After integration we get

$$(11.17)\qquad \frac{y_2}{y_1} > \left(\frac{0.1\lambda}{0.95}\right)^{\frac{\lambda}{0.9a}} \left(\frac{0.95+a}{0.1\lambda+a}\right)^{\frac{k+1}{1+a}} \left(\frac{1-0.1\lambda}{1-0.95}\right)^{\frac{1-\lambda}{1+a}}$$

Because $\lambda < 2a < 0.1$ and thus $k < 2$ we get

$$(11.18)\qquad \frac{y_2}{y_1} > \left(\frac{0.1}{0.95}\right)^{\frac{k}{0.9}} \left(\frac{0.95}{1.2}\right)^{\frac{k+1}{1.05}} (20\cdot 0.99)^{\frac{0.9}{1.05}} \frac{\lambda^{k/0.9}}{a^{(k+1)/1.05}}$$

The right hand side of (11.18) can be rewritten as

$$(11.19)\qquad BA^k \frac{(ka)^{k\eta}}{a^{\delta k+\delta}} = Be^{g(k,a)},$$

where $g(k,a) = k\ln(A) + \beta k \ln(k) + (\beta k - \delta k - \delta)\ln(a)$. For our values of k and a the minimum of g is $g(2, 0.05)$ and thus we get

$$(11.20)\qquad \frac{y_2}{y_1} > Be^{g(2,0.05)} > 1.39.$$

Again the proof for the lower estimate for x_2/x_1 is analogous and thus the proof of the lemma is finished.

Lemma 11.6 *There is a neighbourhood of the point $(0, y, 0.1\lambda_2)$ where $y > 0.8$ such that if a trajectory starts at a point $(x_0, y_0, 0.1\lambda_2)$ in that neighbourhood it will intersect $s = 0.1\lambda_2$ next time at a point $(x_1, y_1, 0.1\lambda_2)$, where*

$$(11.21)\qquad \frac{x_1}{x_0} > \left(\frac{y_1}{y_0}\right)^G$$

and $G = \frac{4}{3\gamma}$.

Proof. The proof follows from $dy/dx = \Gamma(s)(y/x)$, where

$$\Gamma(s) = \frac{\lambda_2 - s}{s + a_2}\frac{s + a_1}{\lambda_1 - s}$$

and for $s < 0.1\lambda_2$

$$\Gamma(s) > \frac{\lambda_2 - 0.1\lambda_2}{0.2a_2 + a_2}\frac{a_1}{\lambda_1} = \frac{3\gamma}{4}.$$

Lemma 11.7 *Suppose a trajectory starts at a point $(x_2, y_2, 0.95)$, where $s' > 0$ and let $(x_3, y_3, 0.95)$ be the next intersection with $s = 0.95$. Then*

$$(11.22)\qquad \frac{x_3}{x_2} > \left(\frac{y_3}{y_2}\right)^A$$

and $A = 1 - 2\varepsilon/0.95$, where $\varepsilon > \max(a_1, a_2, \lambda_1, \lambda_2)$.

Proof. The proof is analogous to the proof of Lemma (11.6). We have only to convince ourself that for $s > 0.95$

$$\Gamma(s) < \frac{0.95 + a_1}{0.95 - \lambda_1}$$

and thus

$$\Gamma(s)^{-1} > 1 - \frac{2\varepsilon}{0.95 + \varepsilon} > 1 - 2\varepsilon/0.95,$$

where $\varepsilon > a_1, \lambda_1$.

Lemma 11.8 *Suppose a trajectory goes from the point* (x_4, y_4, λ_1) *to* $(x_5, y_5, 0.1\lambda_2)$ *and lies wholly in the region* $y > 0.8$. *Then*

$$\frac{x_5}{x_4} > \left(\frac{0.1\lambda_2}{\lambda_1}\right)^{\lambda_1/(3a_1)}.$$

Proof. Because $s < 0.1$, $y > 0.8$ and $a_2 < 0.1$ we get $s' < (1 - y/(s + a_2))s < (1 - 0.8/0.2)s = -3s$ and $x' > -\lambda_1 x/a_1$. The lemma follows by integration.

Lemma 11.9 *Consider a trajectory starting at a point* $(x_0, y_0, 0.1\lambda_2)$ *and denote by* $(x_1, y_1, 0.1\lambda_2)$ *the following intersection with* $s = 0.1\lambda_2$*, by* $(x_2, y_2, 0.95)$ *and* $(x_3, y_3, 0.95)$ *the following intersections with* $s = 0.95$ *in that order, by* (x_4, y_4, λ_1) *the next intersection with* $s = \lambda_1$ *and finally by* $(x_5, y_5, 0.1\lambda_2)$ *the next intersection with* $s = 0.1\lambda_2$ *in* $s' < 0$. *There exists a neighbourhood of the point* $(0, y_0, 0.1\lambda_2)$*, where* $y_0 > 0.83$*, such that any trajectory starting in that neighbourhood with coordinates* $(x_0, y_0, 0.1\lambda_2)$ *in the notations above has the following properties:*

$$\frac{x_3 x_1}{x_2 x_0} > \frac{0.05 \cdot 0.95}{1.6 \cdot 15} a_2^{1.34} e^{0.69(A-G)/a_2}, \tag{11.23}$$

$$\frac{x_2}{x_1} > 1.39, \tag{11.24}$$

$$\frac{x_4}{x_3} > 1 \tag{11.25}$$

and

$$\frac{x_5}{x_4} > \left(\frac{0.1\lambda_2}{\lambda_1}\right)^{\lambda_1/(3a_1)}. \tag{11.26}$$

Proof. From Lemma 11.6 and 11.7 follows

$$\frac{x_1 x_3}{x_0 x_2} > \left(\frac{y_1}{y_0}\right)^G \left(\frac{y_3}{y_2}\right)^A = \left(\frac{y_1}{y_0}\right)^{G-A} \left(\frac{y_1 y_3}{y_0 y_2}\right)^A. \tag{11.27}$$

From Theorem 8.1. follows that $y_0 < 1.6$ and because the point $(x_3, y_3, 0.95)$ is in $s' < 0$ we get $y_3 > 0.05 \cdot 0.95$. Using these facts and Lemma 11.4 and 11.5 in inequality (11.27) we get inequality (11.23). Inequalities (11.24) and (11.26) follow from Lemmas 11.5 and 11.8, respectively. Because $x' > 0$ for $\lambda_1 < s < 0.95$ we get inequality (11.25). The proof of the lemma is finished.

We now use the lemmas to prove the theorem. Combining the inequalities in Lemma 11.9 we get

$$x_5/x_1 > \frac{1.39 \cdot 0.05 \cdot 0.95}{1.6 \cdot 15} a_2^{1.34} \left(e^{0.69/a_2}\right)^{A-G} \left(\frac{0.1\lambda_2}{\lambda_1}\right)^{\lambda_1/(3a_1)},$$

where A and G are from Lemmas 11.7 and 11.6. After some calculations we see that $x_5/x_1 > 1$ follows from

$$\gamma > \frac{1.2/0.9 - (\lambda_2 \ln(\lambda_2) - \lambda_2 \ln(10\lambda_1))/(3 \cdot 0.69}{1 - 2\varepsilon/0.95 + a_2(\ln(1.39 \cdot 0.05 \cdot 0.95/(1.6 \cdot 15)) + 1.34 \ln a_2)/0.69},$$

which follows from

$$\gamma > \frac{4/3 - \lambda_2 \ln \lambda_2}{1 - 12\varepsilon + 2a_2 \ln a_2}.$$

Combining Lemmas 11.1-11.5 we also get that $y_5 > 0.83$ and the limit cycle in the ys-plane intersects $s = 0.1\lambda_2$, $y > 0.83$. Thus the x-value increases when the trajectory winds near the ys-plane and the limit cycle must be unstable. The statement of the theorem now follows.

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