A predator-prey model with non-monotonic response function

H.W. Broer, V. Naudot, R. Roussarie, K. Saleh

Abstract

We study the dynamics of a family of planar vector fields that models certain populations of predators and their prey. This model is adapted from the standard Volterra-Lotka system by a non-monotonic response function (that takes into account group defense), competition between prey and competition between predators. Also we initiate research on time-periodic perturbations, which model seasonal dependence. Partly our results are computer assisted.

We are interested in persistent features. For the planar autonomous model this amounts to structurally stable phase portraits. We focus on the attractors, where it turns out that multi-stability occurs. Further, we study the bifurcations between the various domains of structural stability. It is possible to fix the values of two of the parameters and study the bifurcations in terms of the remaining three. We find several codimension 3 bifurcations that form organizing centres for the global bifurcation set.

Studying the time-periodic system, our interest is in the chaotic dynamics. Numerically we show the existence of strange attractors near homoclinic bifurcations.

1 Introduction

This paper deals with a particular family of planar vector fields which models the dynamics of the populations of predators and their prey in a given ecosystem. The model is a variation of the Volterra-Lotka system [30, 45] given by

\[
\begin{align*}
\dot{x} &= x(a - \lambda x - yP(x)), \\
\dot{y} &= -\delta y - \mu y^2 + yQ(x),
\end{align*}
\]

(1)

where the variables $x$ and $y$ denote the density of the prey and predator populations respectively, while $P(x)$ is a non-monotonic response function [2] given by

\[
P(x) = \frac{mx}{\alpha x^2 + \beta x + 1},
\]

(2)

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where $0 \leq \alpha$, $0 < \delta$, $0 < \lambda$, $0 \leq \mu$ and $\beta > -2\sqrt{\alpha}$ are parameters. Observe that in the absence of predators, the prey dynamics has logistic growth. The coefficient $a$ represents the intrinsic growth rate of the prey, while $\lambda > 0$ is the rate of competition or resource limitation of prey. The natural death rate of the predator is given by $\delta > 0$. The function $Q(x)$ is the rate of conversion between prey and predator.

In Gause’s model [23], this function is given by $Q(x) = cP(x)$, where $0 < c$. The non-negative coefficient $\mu$ is the rate of the competition amongst predators, see [4].

Several experiments by Andrew [2], Boon and Landelout [5] and Edwards [22] indicate that non-monotonic responses are present at the microbial level when the nutrient (prey) concentration reaches a high level, in which case an inhibitory effect on the specific growth rate occurs. Another earlier example of this phenomenon is observed by Tener [43]. Indeed, lone prey (musk ox) can be successfully attacked by predators (wolves). However, small herds of musk oxen (2 to 6 animals) are attacked with less success. Furthermore, no successful attack has been observed in large herds. For more examples of populations that use the group defense strategy, see [38].

Our goal is to understand the structurally stable dynamics of (1) and in particular the attractors with their basins where we have a special interest for multi-stability. We also study the bifurcations between the open regions of the parameter space that concern such dynamics thereby giving a better understanding of the family.

We briefly address the modification of this system, where a small parametric forcing is applied in the parameter $\lambda$, as suggested by Rinaldi et al. [36]

$$\lambda = \lambda_0(1 + \epsilon \sin\left(\frac{2\pi}{\omega}t\right)),$$

where $\epsilon < 1$ is a perturbation parameter. Our main interest is with large scale strange attractors.

## 2 Strategy of research and sketch of results

We now sketch the approach of this paper.

### 2.1 Trapping domains and Reduced Morse-Smale portraits

Our study concerns the dynamics of (1) in the closed first quadrant $\text{clos}(Q)$ where $Q = \{x > 0, y > 0\}$ with boundary $\partial Q = \{x = 0, y \geq 0\} \cup \{y = 0, x \geq 0\}$, which are both invariant under the flow. We shall show that system (1) has a compact trapping domain $B_p \subset \text{clos}(Q)$: all orbits in $\text{clos}(Q)$ enter $B_p$ after finite time and do not leave it again. For the moment we restrict the attention to structurally stable (or Morse-Smale) dynamics. In the interior of $B_p$, there can be maximally two stable equilibria and possibly one saddle-point. We study these singular points using algebraic tools, occasionally supported by computer algebra. Also we numerically detect several cases with one or two limit cycles. Here we often use numerical continuation, where the algebraic detection of Hopf or Bogdanov-Takens bifurcations helps to initiate the continuation process.
Figure 1: Reduced Morse-Smale portraits occurring in system (1); A is a sink (the corresponding basin is dashed), S is a saddle-point and R a source. (a): The case where C is a sink (with corresponding basin in white). (b): The case where C is a saddle-point. In the latter case the interior of the trapping domain always contains an attractor denoted by $A_0$ with basin in white. Bi-stability only occurs in portraits [a-2] and [b-2].

Since limit cycles are hard to detect mathematically, our approach is to reduce, by surgery [31, 33] the structurally stable phase portraits to new portraits without limit cycles. Here with help of topological means (Poincaré-Hopf Index Theorem, Poincaré-Bendixson Theorem [31, 34]) we find a complete classification that is of great help to understand the original system (1). Compare with Figure 1 and see §3, in particular Theorem 1.

2.2 Organization of the parameter space

As mentioned in §1.1, our main interest is with the dense-open subset of $\mathbb{R}^5 = \{\alpha, \beta, \mu, \delta, \lambda\}$ with structurally stable dynamics. The complement of this set is the bifurcation set, which contains strata of different codimension.

It turns out that the parameters $\delta$ and $\lambda$ play a minor role and that we can describe the bifurcation set as follows. We fix $(\delta, \lambda) \in \Delta = \{\delta > 0, \lambda > 0\}$ and the bifurcation of (1) is described in the space $\mathcal{W} = \{\alpha \geq 0, \beta > -2\sqrt{\alpha}, \mu \geq 0\}$. To discuss this we introduce the projection

$$\Pi : \mathcal{W} \times \Delta \to \Delta, (\alpha, \beta, \mu, \delta, \lambda) \mapsto (\delta, \lambda),$$

studying all the fibers $\Pi^{-1}(\delta, \lambda)$. This strategy is valid as long as the fibers are transversal to the bifurcation set, where we only have to consider bifurcations of codimension less than or equal to 3. It turns out that this is the case in the complement of a smooth curve $\mathcal{C}$, compare with Figure 2-(a). Indeed, as stated in Theorem 2, the bifurcation set in $\mathcal{W}$ is constant above each open region $\Delta_1$ and $\Delta_2$, separated by $\mathcal{C}$. Above the curve $\mathcal{C}$ there is a folding of the bifurcation set whenever the fiber $\Pi^{-1}(\delta, \lambda)$ is tangent to it.

When restricting to $\Delta_1$ and $\Delta_2$ the codimension 3 bifurcations inside $\mathcal{W}$ act as organising centres. This means that when taking 2-dimensional sections in $\mathcal{W}$ we see a semi-global picture organized by the trace of the codimension 3 bifurcations, see [12, 39] for details.

For each region $\Delta_1$ and $\Delta_2$ the associated bifurcation set in $\mathcal{W}$ is depicted. Figure 2-(b) corresponds to $\Delta_1$ and Figure 2-(c) to $\Delta_2$. Figure 2-(c) shows that
Figure 2: (a): Region $\Delta = \{\delta > 0, \lambda > 0\}$. (b): Bifurcation set in $\mathcal{W} = \{\alpha \geq 0, \beta > -2\sqrt{\alpha}, \mu \geq 0\}$ when $(\delta, \lambda) \in \Delta_1$. Section $S_4 = \{\alpha = 0\}$ is the 2-dimensional section associated to the bifurcation diagram of Bazykin’s model [29]. (c): Similar to (b) for the case $(\delta, \lambda) \in \Delta_2$. Section $S_6 = \{\mu = 0\}$ covers the case of Zhu’s model [48]. For terminology see Table 1.
Figure 3: (a): Bifurcation diagram in 2-dimensional section $S_1 \subset \{\mu = 0.1\}$ of Figure 2-(b), $(\delta, \lambda) = (1.01, 0.01) \in \Delta_1$. A codimension 2 transcritical point lies on the curve $TC_1$ but is not mentioned since it occurs for $\beta < -\sqrt{\alpha}$. Note the presence of a cusp point (SN$_2$) and a Bogdanov-Takens point (BT$_2$) below $\{\alpha = 0\}$ both acting as organising centres. These points are depicted for a better understanding of the bifurcation set. (b)-(n): Associated phase portraits referring to the corresponding Reduced Morse-Smale portraits of Figure 1. Bi-stability in regions 8 and 9 both correspond to [b-2] in Figure 1. Bi-stability also holds in region 10 (corresponding to [b-1], which does not show bi-stability). The basin of attraction in white is either for C or for A$_0$. For terminology see Table 1.
<table>
<thead>
<tr>
<th>Notation</th>
<th>Name</th>
<th>Incidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>TC₁</td>
<td>Transcritical</td>
<td></td>
</tr>
<tr>
<td>TC₂</td>
<td>Degenerate transcritical</td>
<td>SN₁ + TC₁</td>
</tr>
<tr>
<td>TC₃</td>
<td>Doubly degenerate transcritical</td>
<td>SN₂ + TC₂</td>
</tr>
<tr>
<td>SN₁</td>
<td>Saddle-node</td>
<td></td>
</tr>
<tr>
<td>SN₂</td>
<td>Cusp</td>
<td>SN₁ + SN₁</td>
</tr>
<tr>
<td>BT₂</td>
<td>Bogdanov-Takens</td>
<td>SN₁ + H₁ + L₁</td>
</tr>
<tr>
<td>BT₃</td>
<td>Degenerate Bogdanov-Takens</td>
<td>BT₂ + H₂ + DL₂</td>
</tr>
<tr>
<td>NF₃</td>
<td>Singularity of nilpotent-focus type</td>
<td>SN₂ + BT₂ + L₂ + H₂</td>
</tr>
<tr>
<td>H₁</td>
<td>Hopf</td>
<td></td>
</tr>
<tr>
<td>H₂</td>
<td>Degenerate Hopf</td>
<td>H₁ + SNLC₁</td>
</tr>
<tr>
<td>L₁</td>
<td>Homoclinic (or Blue Sky)</td>
<td></td>
</tr>
<tr>
<td>L₂</td>
<td>Homoclinic at saddle-node</td>
<td>L₁ + SN₁</td>
</tr>
<tr>
<td>DL₂</td>
<td>Degenerate homoclinic</td>
<td></td>
</tr>
<tr>
<td>SNLC₁</td>
<td>Saddle-node of limit cycles</td>
<td></td>
</tr>
</tbody>
</table>

Table 1: List of bifurcations occurring in system (1). This notation will be kept throughout. All bifurcations are local except the latter four, which are global. In all cases the index indicates the codimension of the bifurcation. In the column ‘Incidence’ we put the subordinate bifurcations of the highest codimension. See [1, 20, 21, 25, 29] for details concerning the terminology and fine structure.

the bifurcation set possesses four codimension 2 curves subordinate to codimension 3 points which act as organising centres. Now we explain how to understand the bifurcations up to codimension 1.

2.3 Organising centres and 2-dimensional bifurcation diagrams

Given the organising centres of the bifurcation sets in \( W \), we take 2-dimensional sections \( S_i, i = 1, \ldots, 6, \) transversal to the codimension 2 curves as indicated in Figure 2. Each 2-dimensional section intersects codimension 0 strata in several open regions separated by codimension 1 curves. The 2-dimensional bifurcation diagrams are shown, emphasising the basins of attraction and the possible multi-stability.

We illustrate our strategy in Figure 3 by presenting one of the 2-dimensional bifurcation diagrams (in \( S_1 \), for the terminology referring to Table 1. For the other 2-dimensional diagrams see [12, 39].

2.4 Limit cycles and homoclinic loops

We describe how limit cycles can come into existence by codimension 1 bifurcations. Limit cycles may be created by Hopf bifurcation (\( H₁ \)) (see for instance regions 1 and 7 of Figure 3), by saddle-node bifurcation of limit cycles (\( SNLC₁ \)) (see regions 9 and 11 of the same Figure 3) and by homoclinic bifurcation (\( L₁ \)) (or Blue Sky catastrophe [1], see regions 1 and 12 in Figure 3). The occurrence of limit cycles is investigated numerically (continuation) with help of Matlab [26], Matcont [24] and Auto2000 [19].
As said before, all local bifurcations can be detected algebraically, which is not the case for the global bifurcations $L_1$ and SNLC$_1$. Again we resort to numerical continuation methods, using various codimension 2 bifurcations to create initial data. For example, in Figure 3, the degenerate Hopf bifurcation $H_2$ 'generates' the curve SNLC$_1$, while the Bogdanov-Takens bifurcation $BT_2$ 'generates' the curve $L_1^a$.

### 2.5 Parametric forcing

Dynamical properties of system (1) with parametric forcing (3) can be expressed in terms of the stroboscopic map

$$\mathcal{P}_\varepsilon : \mathbb{R}^2 \to \mathbb{R}^2, \quad (x, y) \mapsto \varphi^1_\varepsilon(x, y),$$

where $\varphi^1_\varepsilon$ denotes the flow of the time-periodic system written as a 3-dimensional vector field $X_\varepsilon = X_\varepsilon(x, y; \alpha, \beta, \mu, \delta, \lambda)$.

Fixed points of $\mathcal{P}_\varepsilon$ correspond to periodic solutions of $X_\varepsilon$ with period 1, and similarly invariant circles to invariant 2-tori.

We take $|\varepsilon|$ small, so that $X_\varepsilon$ is a perturbation of the autonomous system $X_0$ given in (1). As an example, we plot a few attractors for $\mathcal{P}_\varepsilon$ in Figures 4 and 5, for parameter values near the homoclinic curve $L_1^a$ in region 9 of Figure 3. We have numerical evidence for the following statements. Figure 4 shows a strange attractor that consists of 11 connected components mapped by $\mathcal{P}_\varepsilon$ to one another in a cyclic way. These components globalise in Figure 5 in a scenario called heteroclinic tangency (or boundary crisis), compare [13].

### 3 Statement of the results

We formulate the main results of this paper in a more precise way. A brief discussion is included on the behaviour of the stroboscopic map (4), based on perturbation theory. The bifurcation sets and the associated phase portraits are drawn with help of Mathematica [47], Matlab [26], Auto2000 [19] and Matcont [24].

#### 3.1 Results

The first theorem treats general properties of system (1). It contains a classification of the structurally stable case, which covers a dense-open subset of the parameter space $\mathbb{R}^5 = \{\alpha, \beta, \mu, \delta, \lambda\}$. Recall that we only consider the closed first quadrant $\text{clos}(Q)$ of the $(x, y)$-plane.

**Theorem 1** (General properties) System (1) has the following properties:

1. **(Trapping domain)** The domain

$$\mathcal{B}_p = \{(x, y) \mid 0 \leq x, \ 0 \leq y, \ x + y \leq p\},$$
Figure 4: Top: Strange attractor for \( P_\varepsilon \) for parameter values in region 9 of Figure 3 using 500 000 iterations, \( \alpha = 0.007, \beta = 0.036, \delta = 1.01, \mu = 0.1, \lambda = 0.01 \) and \( \varepsilon = 0.6 \). The attractor consists of 11 connected components mapped by \( P_\varepsilon \) to one another in a cyclic way. Left below: Magnification of box M in the figure on the top. Right below: Magnification of box N of the figure on the top.

where

\[ p > \frac{1}{\lambda} \left( \frac{1}{4\delta} (1 - \delta)^2 + 1 \right) \]

is a trapping domain, meaning that it is invariant for positive time evolution and also captures all integral curves starting in \( \text{clos}(\mathcal{Q}) \).

2. (Number of singularities) There are two singularities on the boundary \( \partial \mathcal{Q} \), namely \( (0, 0) \) which is a hyperbolic saddle-point and \( C = (1/\lambda, 0) \), which is (semi-) hyperbolic with \( \{ x > 0, y = 0 \} \subset W^s(C) \). In \( \mathcal{Q} \) there can be no more than three singularities and the cases with zero, one, two and three singularities all occur.

3. (Classification of the Reduced Morse-Smale case) Exactly six topological types of Reduced Morse-Smale vector fields occur, listed in Figure 1.

Sketch of the proof of Theorem 1. Two cases are to be distinguished: either \( C \) is a sink or \( C \) is a saddle. In the latter case system (1) possesses a heteroclinic connection between \( C \) and a nearby sink \( A_0 \), see Figure 1. Each case leads to three Reduced Morse-Smale portraits. The classification of the Reduced Morse-Smale phase portraits follows from the Poincaré-Bendixson and the Poincaré-Hopf theorems [31, 34]. To explain this we assume that \( C \) is a sink, the case when \( C \) is a saddle is treated similarly. For each Reduced Morse-Smale there exists a rectangle \( T = PQRS \) included in the trapping domain \( B_p \) with the following properties. The
Figure 5: Top: Viana-like strange attractor for $P_r$ for parameter values in region 9 of Figure 3 using 500 000 iterations, $\alpha = 0.007, \beta = 0.036, \delta = 1.01, \mu = 0.1, \lambda = 0.01$ and $\varepsilon = 0.99$, compare [13]. Left below: Magnification of box L in the figure on the top. Right below: Magnification of box K in the figure on the top.

side RS is on the hypothenuse of $B_p$ and therefore transversal to the flow. The side $PQ$ is situated near C, also transverse to the flow. The sides $PS$ and $QR$ are segments of integral curve of (1) and can be chosen arbitrarily close to the coordinates axes such that the rectangle $T$ contains all singularities of (1) in $Q$, see Figure 1. In all cases, the index of the vector field associated to (1) with respect to $T$ is equal to 0. This follows from first considering the flow-box case where there are no singularities, see Figure 1 [a-1]. Next we use the fact that the index only depends on the boundary behaviour. Knowing that system (1) has no more than three singularities in $Q$, the classification of Figure 1 follows. For details see [12, 39].

The following theorem is illustrated by Figure 2.

**Theorem 2** (Organising centres) In the parameter space $\mathbb{R}^5 = \{\alpha, \beta, \mu, \delta, \lambda\}$ consider the projection $\Pi : \Delta \times W \rightarrow \Delta$, where $\Delta = \{0 < \delta, 0 < \lambda\}$ and $W = \{\alpha \geq 0, \beta > -2\sqrt{\alpha}, \mu \geq 0\}$. There exists a smooth curve $\mathcal{C}$ that separates $\Delta$ into two open regions $\Delta_1$ and $\Delta_2$.

For all $(\delta, \lambda) \in \Delta_1$ the corresponding 3-dimensional bifurcation set in $W$ has four organising centres of codimension 3:

1. One transcritical point (TC$_3$),
2. Two nilpotent-focus type points (NF$_3^a$ and NF$_3^b$) connected by a smooth Hopf curve (H$_2$) and by a smooth cusp curve (SN$_2$) containing TC$_3$,
3. One Bogdanov-Takens point (BT) connected to NF by a smooth Bogdanov-Takens curve (BT).

Furthermore, the points NF, collide when (δ, λ) approach C and disappear for (δ, λ) ∈ Δ. The organising centers TC and BT remain.

The proof of Theorem 2 is a straight-forward application of classical normal form theory [6, 25, 42] to the system and with help of computer algebra (Mathematica [47]).

Remarks.

1. All bifurcations that occur in system (1) are known to have finite cyclicity, for definitions and details see [37]. From this it follows that in any compact region of the parameter space, such that the projection under Π is bounded away from the curve C, there is a uniform bound on the number of limit cycles [37]. Although no theoretical information is known on this bound, numerically we find that in our case it is equal to 2.

2. From the above remark and Theorem 1 we can give a complete classification of all Morse-Smale types.

3.2 The time-periodic system

As announced in §2.5, we here discuss the general relationship between the autonomous system X₀ and the time-periodic perturbation X for |ε| small.

We consider a number of dynamical properties of Pɛ, as these follow from more or less classical perturbation theory [3, 13, 14, 25]. First of all the hyperbolic periodic points (including fixed points) of P₀ persist for Pɛ, for ε ≪ 1, including their local stable and unstable manifolds. We note that globally the stable and unstable manifolds generically will behave different by separatrix splitting, giving rise to homoclinic tangle. Secondly, the local bifurcations are persistent, in particular this holds for the saddle-node and cusp of periodic points but also for the Hopf bifurcations of these. In the latter case (for which the 3-dimensional vector field X gives Neimark-Sacker bifurcations), we encounter resonances due to the interaction of internal periodicity and that of the forcing. The strong resonances are more involved [3, 13, 14, 28, 36, 41], but in the case of weaker resonances, near the Hopf curve, the limit cycle turns into a Pɛ-invariant circle. In a corresponding 2-dimensional section in W, the associated rotation number is rational in a dense-open array of Arnol’d tongues emanating from the Hopf curve. Here the circle dynamics is of Kupka-Smale type [34], which corresponds to frequency locking with the periodic forcing. For a large measure set outside the tongues the invariant circles are quasi-periodic with Diophantine rotation number. The invariant circles break up further away from the Hopf curve in a complicated way, compare with [13]. The saddle-node bifurcation of limit cycles in X₀ turns into a quasi-periodic saddle-node bifurcation for Pɛ [7, 8] with all the ensuing dynamical complexity [15, 16, 17], also compare with [11].
a systematic study of the attractors of $P_\varepsilon$ as a function of the parameters, we expect the same complexity as described in [9, 13, 14, 46], for more background also compare with [18, 32, 35]. In this investigation the present study of the autonomous system provides a skeleton.

In this paper we restrict to the numerical detection of a few attractors of $P_\varepsilon$ near homoclinic connections in the autonomous system $X_0$.

More precisely we consider the 2-dimensional bifurcation diagrams of $X_0$, looking for the loci of homoclinic orbits (L$_1$ in Figure 3 and L$^a_1$, L$^b_1$ in Figure 3). These loci can be continued in the $\varepsilon$-direction for $\varepsilon \geq 0$. In particular we look in a neighbourhood of L$_1$ where complicated dynamics related to homoclinic tangencies are to be expected, compare with Figures 8, 9 and 10. A more systematic approach of this and related time-periodic systems is subject of future research.

3.3 Biological aspects

Now we discuss the possible biological consequences and interpretations of our results regarding model (1). Globally speaking there are three possibilities for the coexistence of predators and prey. In the first case the parameters are below the transcritical curve TC$_1$, compare with Figures 5, 12 and 15, which implies that C is a saddle-point. Therefore, independent of the initial values in $Q$, both prey and predators survive. Compare with regions 3 and 5 in Figure 3. In the second case, only the prey survives, compare with region 4 in Figure 3. In the last case, depending of the initial values in $Q$, only the prey survives or both prey and predators survive (bi-stability). As an example see region 12 in Figure 3.

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References


