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Published in:
Comptes Rendus Mathematique

DOI:
[10.1016/j.crma.2005.09.033](https://doi.org/10.1016/j.crma.2005.09.033)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2005

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Broer, H. W., Naudot, V., Roussarie, R., & Saleh, K. (2005). Bifurcations of a predator-prey model with non-monotonic response function. *Comptes Rendus Mathematique*, 341(10), 601-604.
<https://doi.org/10.1016/j.crma.2005.09.033>

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Ordinary Differential Equations

Bifurcations of a predator-prey model
with non-monotonic response functionH.W. Broer^a, Vincent Naudot^a, Robert Roussarie^b, Khairul Saleh^a^a University of Groningen, Department of Mathematics, P.O. Box 800, NL-9700 AV Groningen, The Netherlands^b Institut mathématiques de Bourgogne, 9, avenue Alain-Savary, B.P. 47870, 21078 Dijon cedex, France

Received 30 June 2005; accepted 11 September 2005

Presented by Étienne Ghys

Abstract

A 2-dimensional predator-prey model with five parameters is investigated, adapted from the Volterra–Lotka system by a non-monotonic response function. A description of the various domains of structural stability and their bifurcations is given. The bifurcation structure is reduced to four organising centres of codimension 3. Research is initiated on time-periodic perturbations by several examples of strange attractors. **To cite this article:** *H.W. Broer et al., C. R. Acad. Sci. Paris, Ser. I 341 (2005).*

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Résumé

Bifurcations dans un système prédateur-proie avec réponse fonctionnelle non-monotone. On considère un modèle prédateur-proie en dimension 2 dépendant de cinq paramètres adapté du système Volterra–Lotka par une réponse fonctionnelle non-monotone. Une description des différents domaines de stabilité structurelle est présentée ainsi que leurs bifurcations. La structure de l'ensemble de bifurcation se réduit à quatre centres organisateurs de codimension 3. Nous présentons quelques exemples d'attracteurs étranges obtenus par une perturbation périodique non autonome. **Pour citer cet article :** *H.W. Broer et al., C. R. Acad. Sci. Paris, Ser. I 341 (2005).*

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1. Introduction

This Note 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 system is a variation of the classical Volterra–Lotka system [7,12] given by

$$\dot{x} = x(a - \lambda x) - yP(x), \quad \dot{y} = -\delta y - \mu y^2 + cyP(x), \quad (1)$$

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 [1] given by $P(x) = mx/(\alpha x^2 + \beta x + 1)$, where $0 \leq \alpha$, $0 < \delta$, $0 < \lambda$, $0 \leq \mu$ and

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$\beta > -2\sqrt{\alpha}$ are parameters. 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 $cP(x)$ where $c > 0$ is the rate of conversion between prey and predator. The non-negative coefficient μ is the rate of the competition amongst predators [2]. See [3,5] for a more detailed discussion concerning system (1).

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 λ , i.e., $\lambda = \lambda_0(1 + \varepsilon \sin(2\pi t))$, (as suggested by Rinaldi et al. [11]) where $\varepsilon < 1$ is a perturbation parameter. Our main interest is with large scale strange attractors. For several phase portraits of the Poincaré return map (or stroboscopic map) see Fig. 3.

2. Sketch of results

The investigation concerns the dynamics of (1) in the closed first quadrant $\text{clos}(\mathcal{Q})$ where $\mathcal{Q} = \{x > 0, y > 0\}$ with boundary $\partial\mathcal{Q} = \{x = 0, y \geq 0\} \cup \{y = 0, x \geq 0\}$, which are both invariant under the flow associated to system (1). Since limit cycles are hard to detect mathematically, our approach is to reduce, by surgery [8,9], the structurally stable phase portraits to new portraits without limit cycles. In [3,5] with help of topological means (Poincaré–Hopf Index Theorem, Poincaré–Bendixson Theorem [8,10]) a complete classification of all Reduced Morse–Smale Portraits is found, which is of great help to understand the original system (1).

Theorem 2.1 (General properties). *System (1) has the following properties:*

1. (Trapping domain) The domain $\mathcal{B}_p = \{(x, y) \mid 0 \leq x, 0 \leq y, x + y \leq p\}$, where $p > 1/\lambda((1 - \delta)^2/(4\delta) + 1)$ is a trapping domain, meaning that it is invariant for positive time evolution and also captures all integral curves starting in $\text{clos}(\mathcal{Q})$;

Table 1

List of bifurcations occurring in system (1). In all cases the subscript indicates the codimension of the bifurcation. See [4,6] for details concerning the terminology

Tableau 1

Liste des bifurcations qui concernent le système (1). Pour chaque l'une d'elles, l'indice correspondant indique la codimension de la bifurcation. Voir [4,6] pour plus de détails concernant la terminologie

Notation	Name	Notation	Name
TC ₁	Transcritical	TC ₂	Degenerate transcritical
TC ₃	Doubly degenerate transcritical	SN ₁	Saddle-node
SN ₂	Cusp	BT ₂	Bogdanov–Takens
BT ₃	Degenerate Bogdanov–Takens	NF ₃	Singularity of nilpotent-focus type
H ₁	Hopf	H ₂	Degenerate Hopf
L ₁	Homoclinic (or Blue Sky)	L ₂	Homoclinic at saddle-node
DL ₂	Degenerate homoclinic	SNLC ₁	Saddle-node of limit cycles

Fig. 1. Reduced Morse–Smale portraits occurring in system (1); A is a sink, S is a saddle-point and R a source. C is either a sink or a saddle.

Fig. 1. Portraits de phase réduits réalisés par le système (1); A est un puit, S est un point de selle, R une source. C est soit un puit soit un point de selle.

Fig. 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 $(\delta, \lambda) \in \Delta_1$. (c): Similar to (b) for the case $(\delta, \lambda) \in \Delta_2$. (d): Bifurcation diagram in 2-dimensional section $\mathcal{S}_1 \subset \{\mu = 0.1\}$ of figure (b), $(\delta, \lambda) = (1.01, 0.01) \in \Delta_1$. For terminology see Table 1. See [3,5] for description of the other sections.

Fig. 2. (a) : Region $\Delta = \{\delta > 0, \lambda > 0\}$. (b) : L'ensemble de bifurcation dans $\mathcal{W} = \{\alpha \geq 0, \beta > -2\sqrt{\alpha}, \mu \geq 0\}$ lorsque $(\delta, \lambda) \in \Delta_1$. (c) : Même figure qu'en (b) lorsque $(\delta, \lambda) \in \Delta_2$. (d) : Diagramme de bifurcation pour la section $\mathcal{S}_1$ de la figure (b), $(\delta, \lambda) = (1.01, 0.01) \in \Delta_1$. Voir terminologie en Tableau 1. Voir [3,5] pour une description dans les autres sections.

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

The following theorem is illustrated by Fig. 2.

Theorem 2.2 (Organising centres). *In the parameter space $\mathbb{R}^5 = \{\alpha, \beta, \mu, \delta, \lambda\}$ consider the projection $\Pi : \Delta \times \mathcal{W} \rightarrow \Delta$, where $\Delta = \{0 < \delta, 0 < \lambda\}$ and $\mathcal{W} = \{\alpha \geq 0, \beta > -2\sqrt{\alpha}, \mu \geq 0\}$. There exists a smooth curve $\mathcal{C}$ that separates Δ into two open regions Δ_1 and Δ_2 .*

Fig. 3. Phase portraits of the Poincaré return map: On the left-hand side $(\alpha, \beta, \mu, \delta, \lambda) = (0.007, 0.036, 0.1, 1.01, 0.01)$ and $\varepsilon = 0.6$. On the right-hand side $(\alpha, \beta, \mu, \delta, \lambda) = (0.007, 0.036, 0.1, 1.01, 0.01)$ and $\varepsilon = 0.99$.

Fig. 3. Portrait de phase de l'application de retour de Poincaré : A gauche $(\alpha, \beta, \mu, \delta, \lambda) = (0.007, 0.036, 0.1, 1.01, 0.01)$ et $\varepsilon = 0.6$. A droite $(\alpha, \beta, \mu, \delta, \lambda) = (0.007, 0.036, 0.1, 1.01, 0.01)$ et $\varepsilon = 0.99$.

For all $(\delta, \lambda) \in \Delta_1$ the corresponding 3-dimensional bifurcation set in $\mathcal{W}$ 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_3) connected to NF_3^b by a smooth Bogdanov–Takens curve (BT_2).

Furthermore, the points NF_3^a , NF_3^b collide when (δ, λ) approach $\mathcal{C}$ and disappear for $(\delta, \lambda) \in \Delta_2$. The organising centres TC_3 and BT_3 remain.

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