

Ordinary Differential Equations

# Bifurcations of a predator-prey model with non-monotonic response function

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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  $\mu$  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  $\lambda$ , 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'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 <sub>1</sub>	Transcritical	TC <sub>2</sub>	Degenerate transcritical
TC <sub>3</sub>	Doubly degenerate transcritical	SN <sub>1</sub>	Saddle-node
SN <sub>2</sub>	Cusp	BT <sub>2</sub>	Bogdanov–Takens
BT <sub>3</sub>	Degenerate Bogdanov–Takens	NF <sub>3</sub>	Singularity of nilpotent-focus type
H <sub>1</sub>	Hopf	H <sub>2</sub>	Degenerate Hopf
L <sub>1</sub>	Homoclinic (or Blue Sky)	L <sub>2</sub>	Homoclinic at saddle-node
DL <sub>2</sub>	Degenerate homoclinic	SNLC <sub>1</sub>	Saddle-node of limit cycles

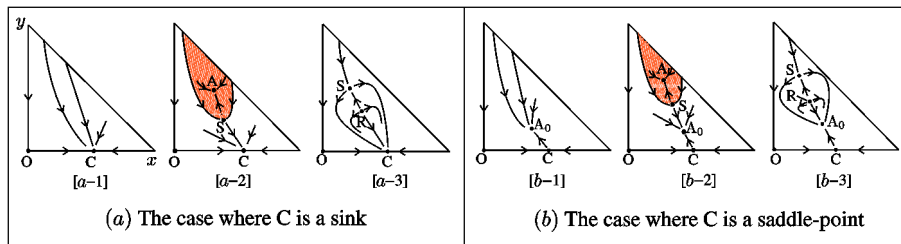


Fig. 1. Reduced Morse–Smale portraits occurring in system (1); A is a sink, S is a saddle-point and R a source. C is either a sink or a saddle.  
 Fig. 1. Portraits de phase réduits réalisés par le système (1); A est un puit, S est un point de scelle, R une source. C est soit un puit soit un point de scelle.

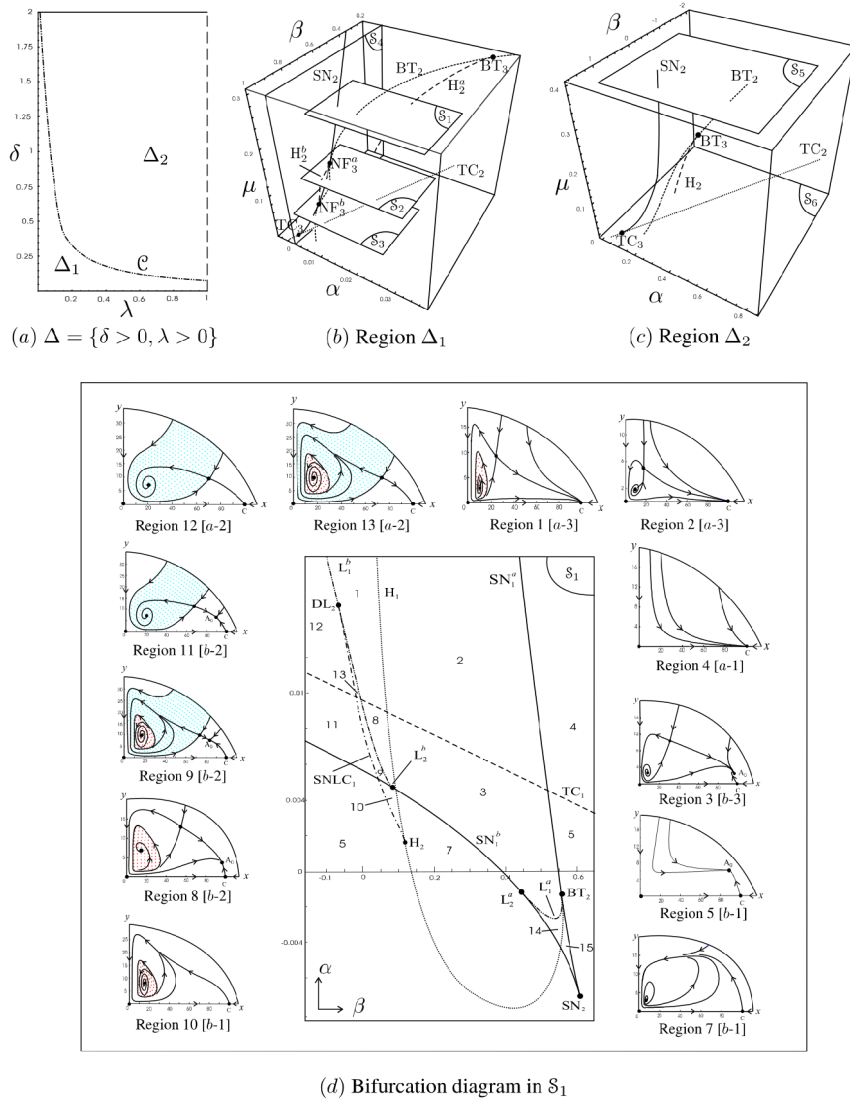


Fig. 2. (a): Region  $\Delta = \{\delta > 0, \lambda > 0\}$ . (b): Bifurcation set in  $\mathcal{W} = \{\alpha \geq 0, \beta > -2\sqrt{\alpha}, \mu \geq 0\}$  when  $(\delta, \lambda) \in \Delta_1$ . (c): Similar to (b) for the case  $(\delta, \lambda) \in \Delta_2$ . (d): Bifurcation diagram in 2-dimensional 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) : Môme 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.

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 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  $\Delta$  into two open regions  $\Delta_1$  and  $\Delta_2$ .*

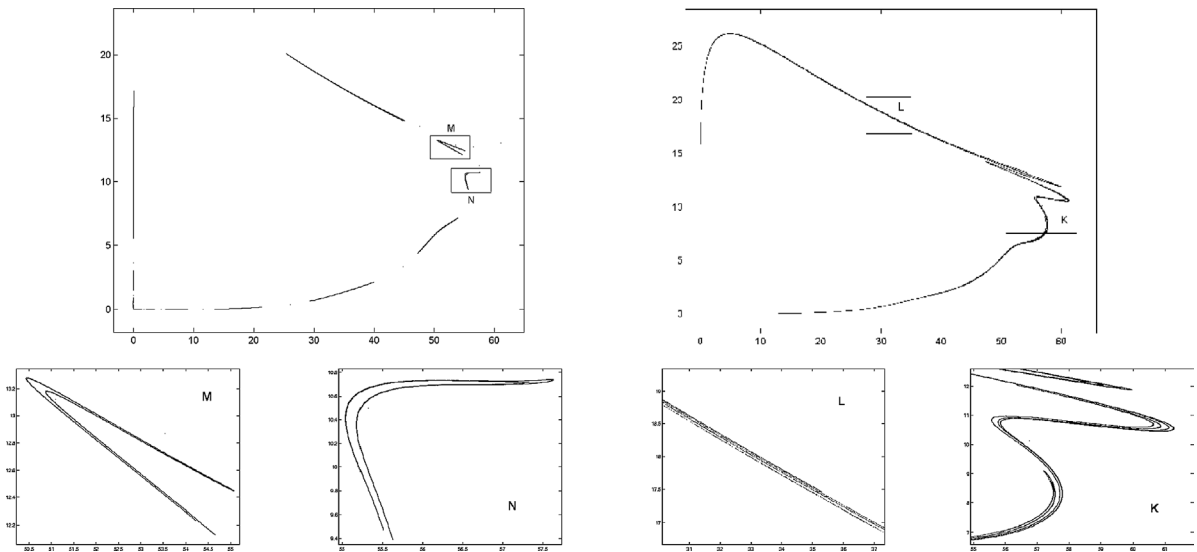


Fig. 3. Phase portraits of the Poincaré return map: On the left-hand side  $(\alpha, \beta, \mu, \delta, \lambda) = (0.007, 0.036, 0.1, 1.01, 0.01)$  and  $\varepsilon = 0.6$ . On the right-hand side  $(\alpha, \beta, \mu, \delta, \lambda) = (0.007, 0.036, 0.1, 1.01, 0.01)$  and  $\varepsilon = 0.99$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

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  $(\delta, \lambda)$  approach  $\mathcal{C}$  and disappear for  $(\delta, \lambda) \in \Delta_2$ . The organising centres  $TC_3$  and  $BT_3$  remain.

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