

Séminaire des dynamiques économiques complexes
Université de Lille 1: EQUIPPE-Labo PAINLEVE- CLERSE
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Systemes différentiels à retards en avenir certain: le modèle d'évolution déterministe de Lotka-Volterra

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contenu

- **1. La dynamique des modèles de population**
(le cadre des interactions; la formulation à deux variables d'état –deux espèces- et la généralisation à plusieurs espèces; l'existence et la stabilité d'un équilibre non nul ; une typologie des dynamiques pour deux espèces)
- **2. Le système déterministe de Lotka-Volterra**
(le modèle général d'interactions à deux espèces; une variante du modèle LV avec croissance intrinsèque logistique; les propriétés mathématiques et orbites cycliques; un exemple numérique de traitement par Mathematica; les extensions envisageables du système LV)
- **3. Système déterministe à retards de Lotka-Volterra**
(la loi logistique retardée de Verhulst-Pearl à boucle de rétroaction retardée; l'introduction d'un ou de plusieurs retards ; les nonstationarités résultantes: oscillations périodiques et instabilités; un exemple numérique de traitement par Mathematica)

1.A Framework

- Closed habitat (no migration)
- Possible interactions: 1) competition between and/or within 2 populations (biomass); 2) conflict between species (predator/prey); 3) mutual benefit of the species.

1.B Formulation for 2 and more species

$$\begin{cases} \frac{dx_1}{dt} = x_1 \left(\overset{\text{natural growth}}{a_1} + \underset{\text{overcrowding coefficient}}{b_{11}x_1} + \overset{\text{interacting coefficient}}{b_{12}x_2} \right) & \dots \text{ biomass 1} \\ \frac{dx_2}{dt} = x_2 \left(a_2 + b_{21}x_1 + b_{22}x_2 \right) & \dots \text{ biomass 2} \end{cases}$$

generalisation to n species

$$\frac{dx_i}{dt} = x_i \left(\underset{\text{intrinsic growth rates}}{a_i} + \overset{\text{interaction rates}}{\sum_{j=1}^n b_{ij}x_j} \right), \quad i = 1, \dots, n$$

or

$$\frac{d\mathbf{x}}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{a} + \mathbf{B}\mathbf{x}(t)), \quad \mathbf{x}, \mathbf{a} \in \mathbb{R}^n, \mathbf{B} \in \mathbb{R}^{n \times n}$$

1.C Existence and stability of a nonzero equilibrium

Existence of a nonzero equilibrium: the equilibrium point

$$\bar{\mathbf{x}} \in \mathbb{R}^n \text{ requires : } \mathbf{a} + \mathbf{B}\bar{\mathbf{x}} = \mathbf{0}$$

Stability of the nonzero equilibrium: the equilibrium point

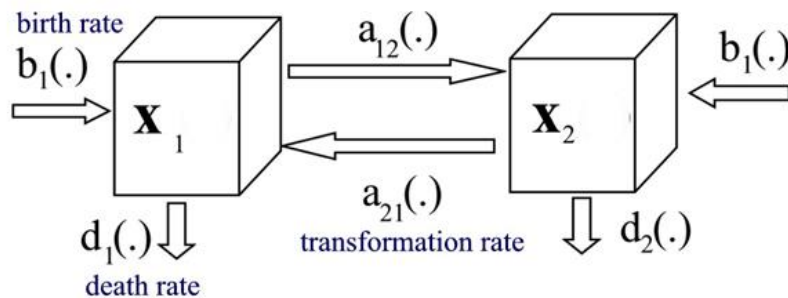
$\bar{\mathbf{x}} \in \mathbb{R}^n$ is globally stable in \mathbb{R}_+^n if there is

$\mathbf{C} = \text{diag}(c_1, \dots, c_n)$ such that $\mathbf{CB} + \mathbf{B}^T \mathbf{C}$ is negative definite.

1.D General population dynamics

	$b_{12} \cdot b_{21} < 0$	$b_{12} \cdot b_{21} > 0$		$b_{12}, b_{21} = 0$
		$b_{12}, b_{21} < 0$	$b_{12}, b_{21} > 0$	
$b_{11}, b_{22} < 0$	Predator-prey with overcrowding	Full competition within & between	Overcrowding & cooperation	Overcrowding & independence
$b_{11}, b_{22} = 0$	Lotka-Volterra	Competitive system	No overcrowding & cooperation	No overcrowding & independence
$b_{11}, b_{22} > 0$	Expansion	Expansion & competition	Mutual benefit	Expansion & independence

2.A General population system



$$\begin{cases} \frac{dx_1}{dt} = x_1 (b_1(t, x_1, x_2) - d_1(t, x_1, x_2)) \\ \frac{dx_2}{dt} = x_2 (b_2(t, x_1, x_2) - d_2(t, x_1, x_2)) \end{cases}$$

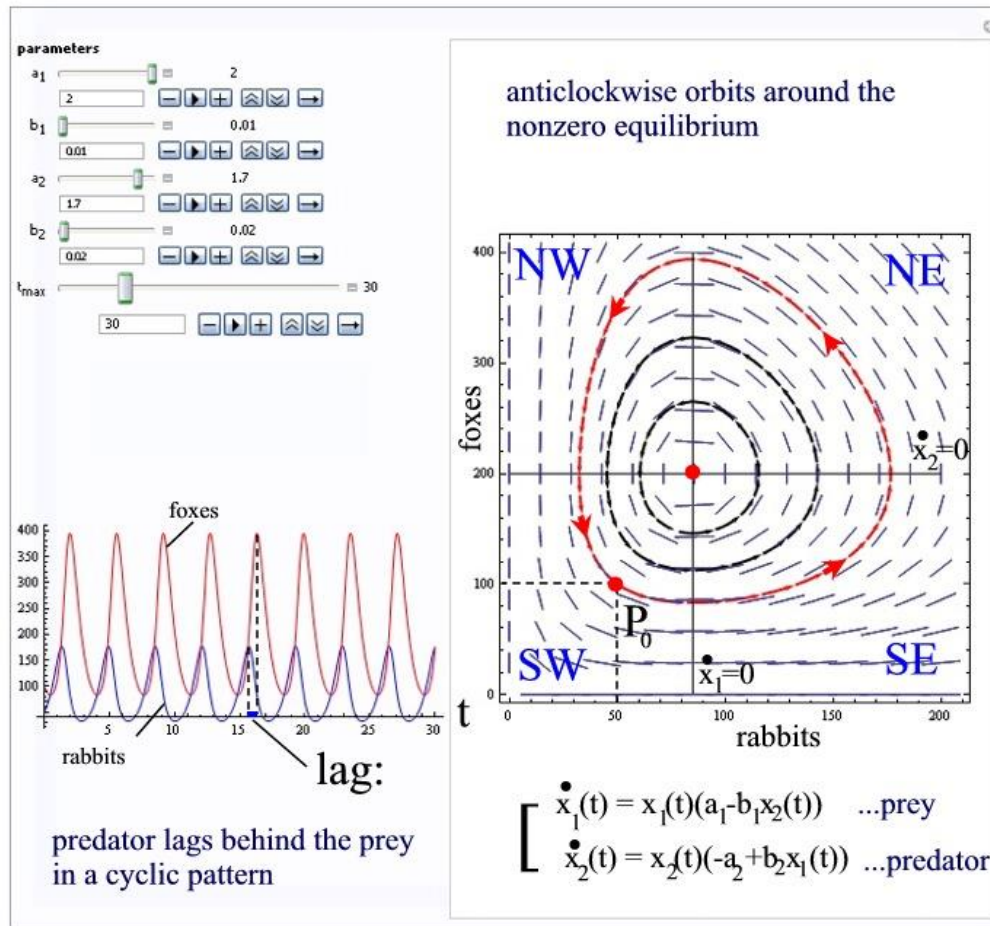
$$\begin{cases} \frac{dx_1}{dt} = x_1 (b_1 - c_1 x_2) \\ \frac{dx_2}{dt} = x_2 (c_2 x_1 - d_2) \end{cases}$$

Nonzero steady state equilibrium at :

$$\left(\frac{d_2}{c_2}, \frac{b_1}{c_1} \right)$$

Integral solutions are closed curves in the $(x_1 - x_2)$ plane to the steady state equilibrium.

2.B Numerical example with Mathematica



2.C Further developments

- Logistic intrinsic growth

$$\begin{cases} \frac{dx_1}{dt} = x_1 \left(\max \left\{ \frac{a_1(k_1 - x_1)}{k_1}, 0 \right\} - c_1 x_2 \right) \\ \frac{dx_2}{dt} = x_2 (c_2 x_1 - d_2) \end{cases}$$

Nonzero steady state equilibrium at :

$$\left(\frac{d_2}{c_2}, \frac{a_1 c_2 k_1 - a_1 d_2}{c_1 c_2 k_1} \right)$$

Integral solutions are spirals in the $(x_1 - x_2)$ plane to the steady state equilibrium.

1) Other functional responses:

$$b x_1 x_2 \quad \dots \text{Volterra} \quad x_1^g x_2 \quad \dots \text{Gause}$$

$$\frac{B \alpha x_1 x_2}{1 + B \alpha x_1} \quad \dots \text{Hotelling I}; \quad \frac{B \alpha x_1^2 x_2}{1 + B \alpha x_1^2} \quad \dots \text{Hotelling II}$$

where α : finding duration, β : catching duration; B : predation rate per time unit.

2) Other improvements: diffusion and migrations; environmental impact and pollution; seasonal effects; heterogeneous species.

2. Delay L-V system

- An autonomous competitive or cooperative LV model with delays is of the form

$$\frac{dx_i(t)}{dt} = x_i(t) \left(b_i - \sum_{j=1}^n a_{ij} x_j(t) - \sum_{j=1}^n b_{ij} x_j(t - \tau_{ij}) \right), \quad i = 1, \dots, n$$

- The permanence supposes a positive solution to the system

$$b_i - \sum_{j=1}^n a_{ij} x_j - \sum_{j=1}^n b_{ij} x_j = 0, \quad i = 1, \dots, n$$

3. Time-delay systems

- Time delays in biological systems are a source of nonstationary problems (periodic oscillations, instabilities). The loss of stability intervenes at a certain threshold.
- However, time delays can enhance stability; short delays can also stabilize unstable dynamical systems.

3.A Verhulst-Pearl's retarded logistic equation

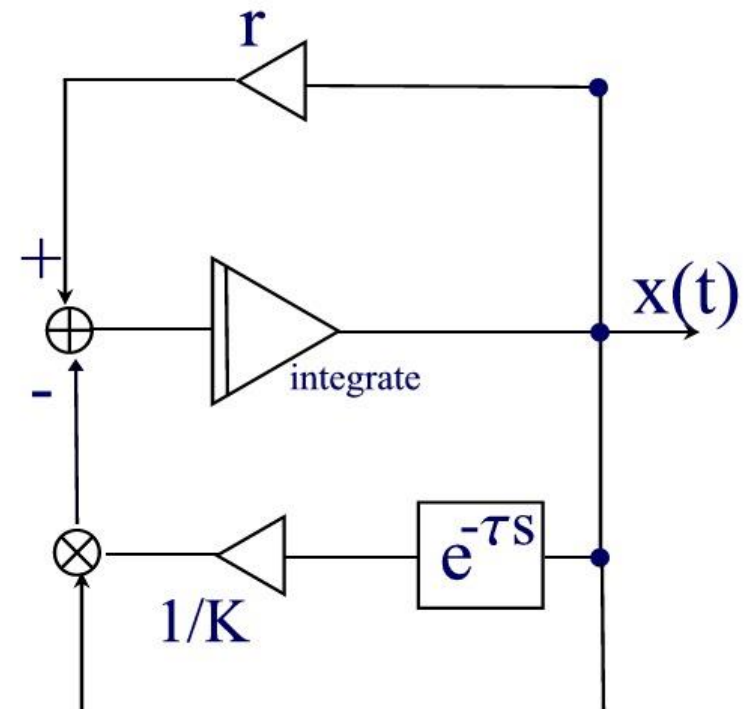
1) Specification

The population loop is controlled by a delayed retroaction loop: it takes τ units of time to respond to changes in the population density. By Hutchinson (1948), we have

$$\frac{dx}{xdt} = r \left(1 - \frac{x(t-\tau)}{K} \right)$$

where r : intrinsic growth rate; K : carrying capacity; τ time delay required to produce necessary foodstuff.]

2) Delayed reoaction loop



3.B Delay Lotka-Volterra systems

one delay:

$$\frac{d\mathbf{x}}{dt} = \text{diag}(\mathbf{x}(t))(\mathbf{a} + \mathbf{B}\mathbf{x}(t - \tau)), \quad \mathbf{a}, \mathbf{x} \in \mathbb{R}^n, \mathbf{B} \in \mathbb{R}^{n \times n}$$

several delays:

$$\frac{dx_i}{dt} = x_i \left(b_i - \sum_{j=1}^n a_{ij} x_j(t) - \sum_{j=1}^n b_{ij} x_j(t - \tau_{ij}) \right), \quad i = 1, \dots, n$$

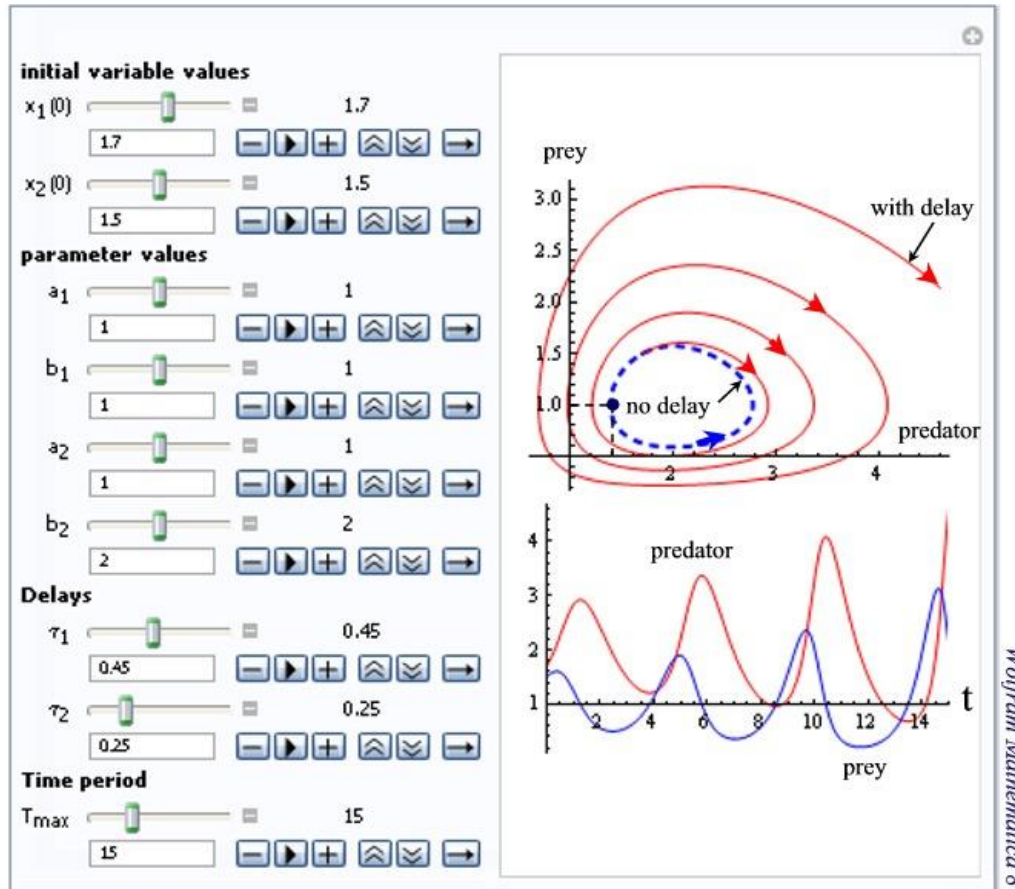
- **Example:** Let an 2 species LV model with 2 delays. The biomass of the predator (or parasite) and prey (or host) are $x_1(t)$ and $x_2(t)$ respectively

$$\frac{dx_1(t)}{dt} = x_1(t)(-1 + x_2(t - \tau_2))$$

$$\frac{dx_2(t)}{dt} = x_2(t)(2 - x_1(t - \tau_1))$$

- A stable periodic solution for the nondelay model is $H(t) \equiv 2 \ln x_1(t) + x_1(t) + \ln x_2(t) - x_2(t) = k_1$

3C. Delay L-V system with Mathematica



Conclusion: the comparable Goodwin model in economics

Goodwin growth model

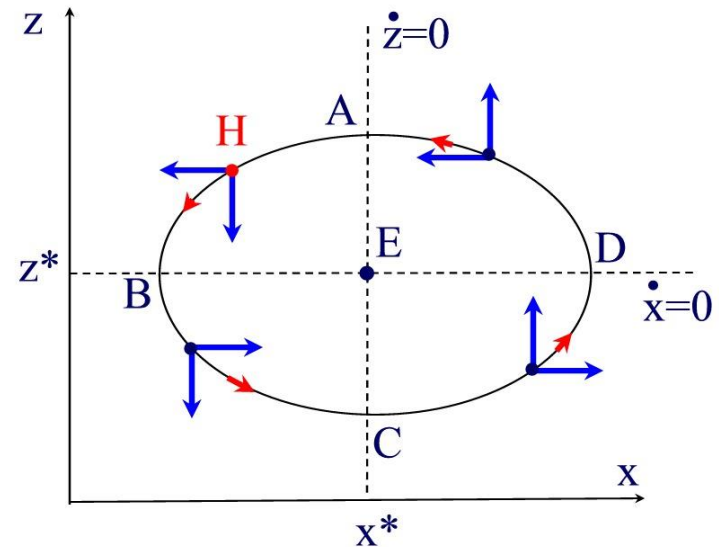
The economic system is

$$\begin{cases} \frac{dz}{zdt} = -(b + \mu) + ax(t) \\ \frac{dx}{xdt} = \frac{1}{v} - (n + \mu) - \frac{z(t)}{v} \end{cases}$$

where x is the employment rate, z a repartition variable (share of wages), n the labor supply rate, v the capital-output ratio and μ the growth rate of labor productivity.

Notes: 1) for this model, the “predator” is the share of wages and the “prey” the employment rate; 2) The inherent stability performances of this model may be loosed with some changes in the initial specification; 3) see discussion on this subject in Samuelson (Collected Scientific Papers 1971-1972)

Endogenous dynamics



critical points: $x^* = (b + \mu)/a$ and $z^* = 1 - (n + \mu)v$