

# Mathematical Analysis and Numerical Simulations of General Lotka-Volterra Systems

Graß Tobias Simon

University of Vienna

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**Example**

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Simplified System

Simulations

Theoretical Results

Paradox of Pesticides

Competitive System

Simulations

Gause's Law (CEP)

Extended Models

Seasonal Variation

Delay Kernels

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## 2 The General Lotka-Volterra Equations

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  - Simulations
  - Theoretical Results
  - Paradox of Pesticides
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## 3 Extended Models

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# Hare and Lynx Population Dynamics

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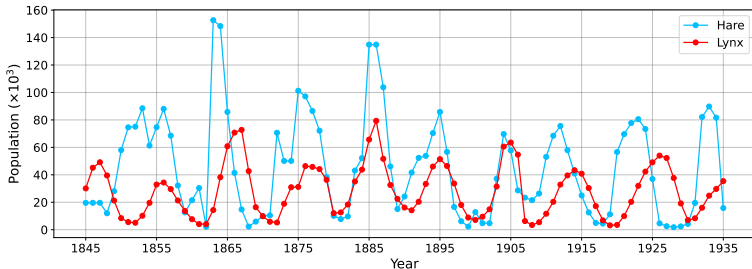
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**Figure:** Development of the population sizes of lynx and hares in the northern boreal forests of North America.

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## Definition (General Lotka-Volterra Equations)

The general Lotka-Volterra equations for a  $n$ -species model is the system

$$F_i(x) = \frac{dx_i}{dt} = x_i \left( r_i + \sum_{j=1}^n a_{ij} x_j \right) \quad (1)$$

with  $i = 1, 2, \dots, n$ . The matrix  $A = (a_{ij})_{i,j=1,2,\dots,n}$  is called the interaction matrix of the system. The vector  $\mathbf{r} = (r_1, r_2, \dots, r_n)$  contains the growth rates of the  $i$ -th species [10.25365/thesis.45530, Volterra1931].

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## Remark

- The state space of system (1) is the nonnegative orthant  $\mathbb{R}^n$ .
- If  $a_{ii} = 0$  for all  $i = 1, 2, \dots, n$  the system is called simple.

# 2-Species Predator-Prey Model

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## Definition (2-dimensional Predator-Prey Model)

The system of equations

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(r_1 - a_{12}x_2) \\ \frac{dx_2}{dt} &= x_2(-r_2 + a_{21}x_1)\end{aligned}\tag{2}$$

for  $r_1, r_2, a_{12}, a_{21} > 0$  is called simple predator-prey model and is a special case of system (1).

- The prey population  $x_1$  has an unlimited food supply.



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- The growth of  $x_1$  is exponential in the absence of their predators  $x_2$ , i.e.  $\frac{dx_1}{dt} = r_1 x_1$ .

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- The biotope is completely isolated from external influences [**theoryvsempiry**].

# Numerical Results

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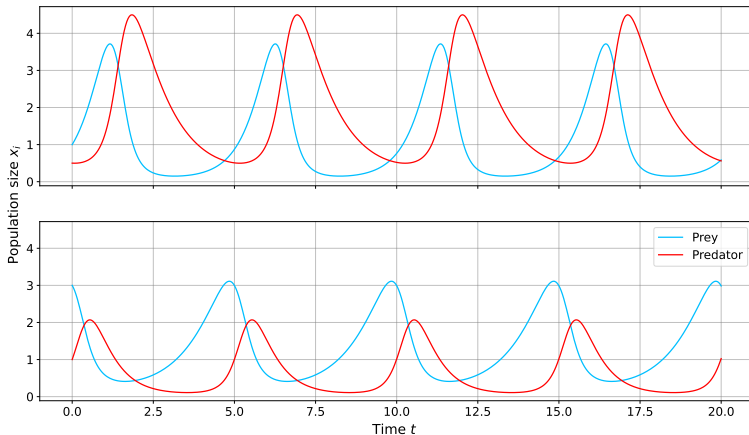
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**Figure:** Numerical solutions of the 2-species predator-prey model (2) introduced by Lotka and Volterra. The first system was solved for the initial condition  $x_1(0) = 1$ ,  $x_2(0) = 0.5$ , the second set of equations for  $x_1(0) = 3$ ,  $x_2(0) = 1$  respectively.

# Slope Field and Phase Space Representation

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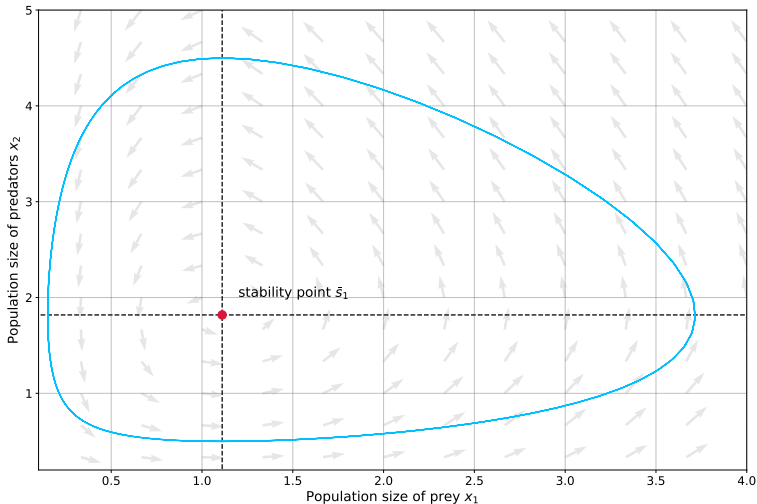
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**Figure:** Slope field of system (2) and phase trajectory of the solution with initial value  $x_1(0) = 1, x_2(0) = 0.5$ .

## Remark (Stability)

*The 2-species predator-prey model has the fixed points*

$\bar{s}_0 = (0, 0)$       unstable saddle point

$\bar{s}_1 = \left( \frac{r_2}{a_{21}}, \frac{r_1}{a_{12}} \right)$  stable center.

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## Remark (Periodicity)

*The linearized system implies periodic solutions around  $\bar{s}_1$  with natural frequency  $\omega = \sqrt{r_1 r_2}$  and phase shift  $\varphi = \frac{\pi}{2}$*   
*[stability\_2d\_predator\_preymodel, 10.25365/thesis.45530].*

## Remark (Population Mean)

*The mean values of the population sizes are*

$$\bar{x}_1 = \frac{1}{T} \int_{t_0}^{t_0+T} x_1(t) \, dt = \frac{r_2}{a_{21}}$$

$$\bar{x}_2 = \frac{1}{T} \int_{t_0}^{t_0+T} x_2(t) \, dt = \frac{r_1}{a_{12}}$$

*for  $T = \frac{2\pi}{\omega}$ . Therefore the means are independent of the initial values  $x_1(0)$  and  $x_2(0)$  [10.25365/thesis.45530].*



## Definition (2-dimensional Predator-Pest Model)

The system of equations

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(r_1 - a_{12}x_2) - \alpha \Delta(t - T) \\ \frac{dx_2}{dt} &= x_2(-r_2 + a_{21}x_1) - \beta \Delta(t - T)\end{aligned}\tag{3}$$

for  $r_1, r_2, a_{12}, a_{21}, \alpha, \beta > 0$  and

$$\Delta(t - T) = \begin{cases} \frac{1}{\epsilon}, & t \in [T, T + \epsilon] \\ 0, & \text{otherwise} \end{cases}$$

is called predator-pest model [**pesticide\_paradox**].

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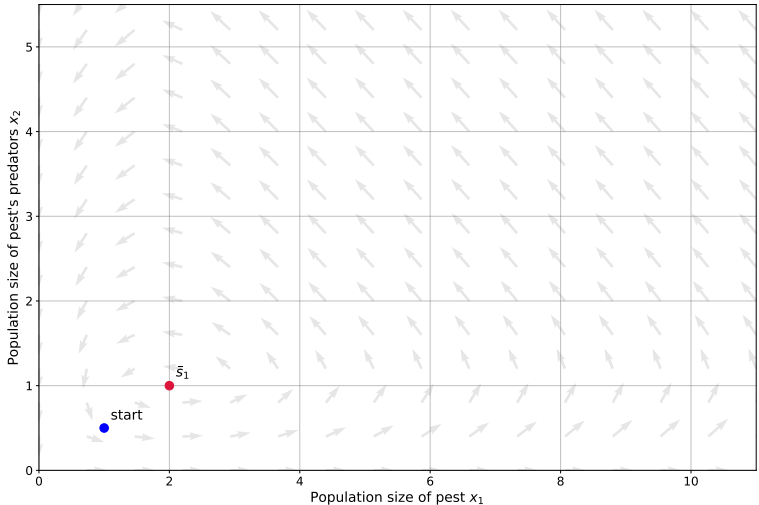
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**Figure:** Trajectories of pesticide forced orbits in the 2-dimensional predator-pest-Model for different application times.

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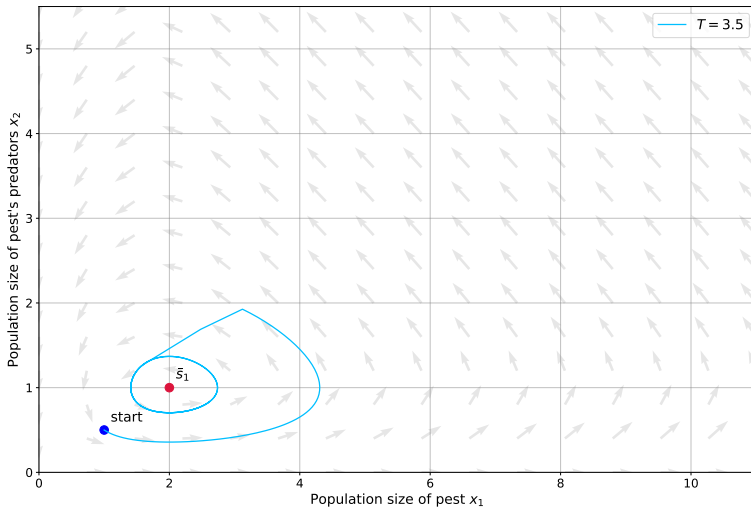
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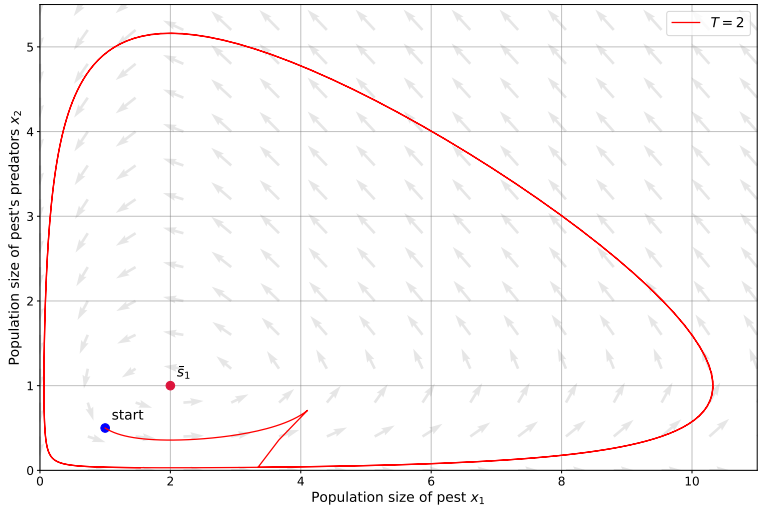
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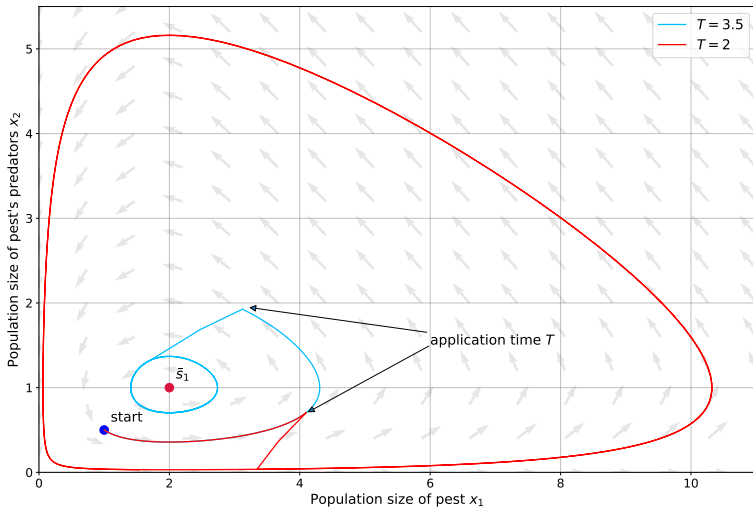
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**Figure:** Trajectories of pesticide forced orbits in the 2-dimensional predator-pest model for different application times.

## Definition (Competitive Lotka-Volterra Equations)

The competitive Lotka-Volterra equations for a  $n$ -species model is the system

$$F_i(x) = \frac{dx_i}{dt} = x_i \left( r_i - \sum_{j=1}^n a_{ij} x_j \right) \quad (4)$$

with  $i = 1, 2, \dots, n$  and  $a_{ij}, r_i > 0$  for all  $i, j = 1, 2, \dots, n$   
[stability\_2d\_predator\_preymodel].

# Lotka-Volterra's Competition Model

## Lotka-Volterra Models

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## Remark (Logistic Growth)

*The restriction to the  $i$ -th equation in system (4) gives*

$$\frac{dx_i}{dt} = x_i(r_i - a_{ii}x_i) = x_i r_i \left(1 - \frac{x_i}{K_i}\right)$$

*with  $K_i = \frac{r_i}{a_{ii}}$ , which is called the  $i$ -th carrying capacity  
[theoryvsempiry].*

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- The biotope is completely isolated from external influences [**Volterra1931, theoryvsempiry**].

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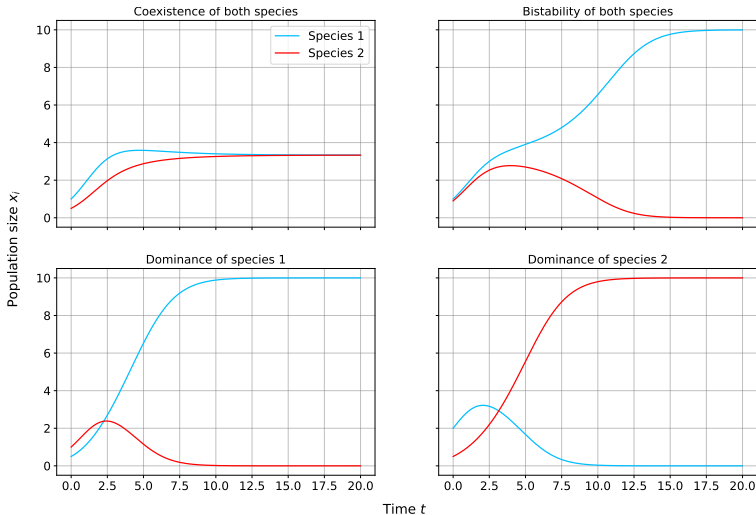
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**Figure:** Classification of the 2-dimensional Lotka-Volterra competition model.

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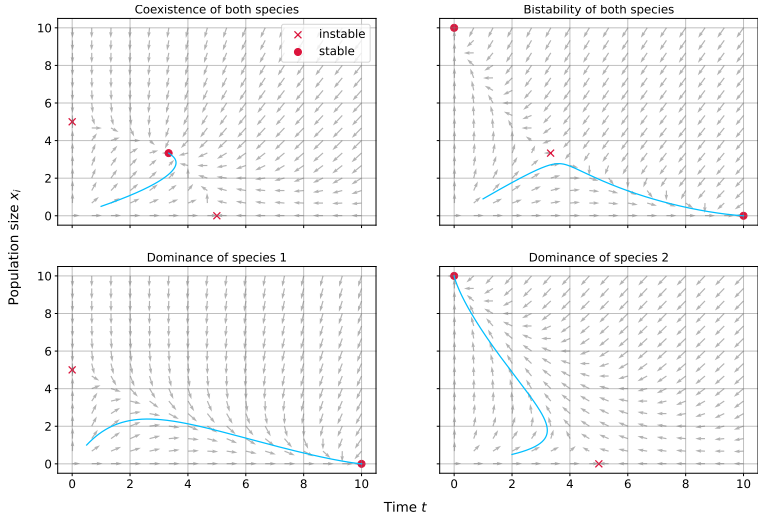
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**Figure:** Phase-space representation of the solutions of the 2-dimensional competition model.

# Competitive Exclusion Principle

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## Definition (Gause's Law (1934))

Two species or populations cannot inhabit the same niche: one will consistently out-compete the other [**gauses\_law**, **gauses\_law2**].

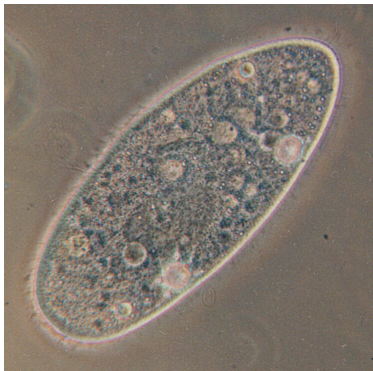


Figure: Image of paramecium aurelia.

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## Remark (Lotka-Volterra Model with seasonal Fluctuations)

*The Lotka-Volterra equations for a  $n$ -species model with seasonal term reads*

$$F_i(x) = \frac{dx_i}{dt} = x_i \left( r_i + \mu_i \sin(\nu t) + \sum_{j=1}^n a_{ij} x_j \right) \quad (5)$$

*with  $i = 1, 2, \dots, n$ . The parameter  $\mu_i$  represents the impact of the environmental change for the  $i$ -th species [predatorpreymodel].*



## Remark (Lotka-Volterra Model with Delay Kernels)

*The Lotka-Volterra equations for a  $n$ -species model with changing rate of interaction is the system*

$$F_i(x) = \frac{dx_i}{dt} = x_i \left( r_i + \sum_{j=1}^n \int_{-\infty}^t F_{ij}(t - \tau) x_j(\tau) d\tau \right) \quad (6)$$

*with  $i = 1, 2, \dots, n$ . The functions  $F_{ij}$  are non-negative continuous delay kernels representing the changing rate of interaction between species  $i$  and  $j$  with respect to the past [predatorpreymodel].*

