An integrable variant of the Lotka-Volterra system

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1st Math Young Researchers Meeting
Genoa – November 8, 2019

Outline of the talk

Modeling populations

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$$\mathbb{N} \hookrightarrow \mathbb{R}_{\geq 0}$$

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- Basic parameter: (instantaneous, per-capita) growth rate

$$k = \frac{\dot{x}}{x}$$

  An *evolution model* for the given population is determined by the choice of a particular function $k = k(t, x)$.

Malthusian growth

The easiest choice is to take $k(t,x) = \alpha$, $\alpha \in \mathbb{R}$ (constant growth, independent from the population size). The corresponding evolution equation is simply

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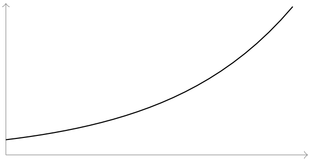
When $\alpha > 0$: exponential (or Malthusian) growth, $\alpha = (\log 2)/T$ where T is the *doubling time* for species S.



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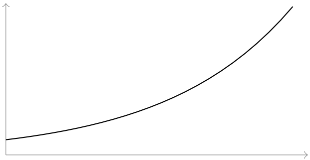

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This model is not realistic. In order to reproduce, organisms need resources; in a fixed environment resources are always bounded, so exponential growth must stop sooner or later (usually sooner).

Modeling a finite environment

To build a more refined model we introduce a new parameter, the carrying capacity of the environment:

$$N_S \in \mathbb{R}_{\geq 0}$$

It represents (a continuous approximation of) the number of individuals of species S for which the environment can supply enough resources in a sustainable way.

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- close to α when $x \ll N$,
- close to zero in a neighborhood of N,
- very large *and negative* when $x \gg N$.

Logistic model

The easiest choice which meets all these desiderata is a simple linear interpolation. The corresponding evolution equation

$$\dot{x} = \alpha x(1 - \frac{x}{N})$$

is traditionally known as the logistic equation. It can be solved by separation of variables, and the general solution reads

$$x(t) = \frac{x(0)\mathrm{e}^{\alpha t}}{x(0)(\mathrm{e}^{\alpha t} - 1) + 1}$$

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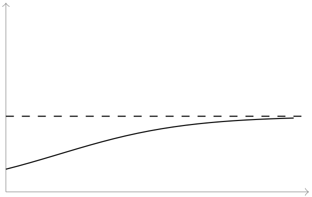

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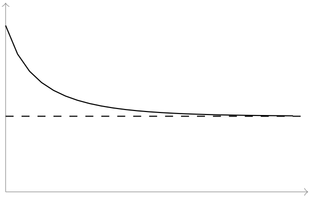

$\alpha = 1.2,\ x(0) = 2.2$

From one to two species

Now we would like to model an environment supporting *two interacting species*, 1 ("preys") and 2 ("predators"). The state space becomes $\mathbb{N}^2 \hookrightarrow \mathbb{R}^2_{\geq 0}$. Evolution equations?

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Summing up:

$$\begin{cases} \dot{x}_1 = x_1(\alpha - \beta x_2) \\ \dot{x}_2 = x_2(\gamma x_1 - \delta) \end{cases}$$

This is the (classic, 2-species) Lotka-Volterra system.

The Lotka-Volterra system

We can simplify away some parameters by rescaling the variables:

$$\tilde{x}_1 := \frac{\gamma}{\delta} x_1 \qquad \tilde{x}_2 := \frac{\beta}{\alpha} x_2 \qquad \tilde{t} := \frac{1}{\alpha} t$$

Then the LV equations become

$$\begin{cases} \dot{x}_1 = x_1(1 - x_2) \\ \dot{x}_2 = k x_2(x_1 - 1) \end{cases} \qquad (k = \delta/\alpha)$$

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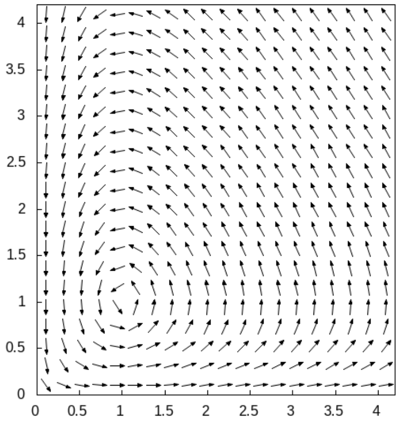
This system is notable because it is simultaneously:

- simple (quadratic interactions),
- interesting (solvable, non-obvious behaviors),
- not completely unrealistic (used e.g. by Volterra and d'Ancona to explain oscillations in fishery).

The Lotka-Volterra system

Qualitative features: single equilibrium point at $(1, 1)$, motion is oscillatory and bounded (never intersecting the axes).



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$$\cancel{\begin{cases} \dot{q} = \frac{\partial H}{\partial p} \\ \dot{p} = -\frac{\partial H}{\partial q} \end{cases}} \qquad\qquad \dot{x} = \{H, x\} \quad \checkmark$$

Poisson structures

Recall that a *Poisson structure* on a manifold M is specified by a bivector field $P \in \Gamma(M, \Lambda^2 TM)$ which satisfies the Jacobi identity:

$$P^{\ell i}\frac{\partial}{\partial x^\ell}P^{jk} + P^{\ell j}\frac{\partial}{\partial x^\ell}P^{ki} + P^{\ell k}\frac{\partial}{\partial x^\ell}P^{ij} = 0$$

The corresponding Poisson brackets are then defined by

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Symplectic structures are exactly the Poisson structures which are *invertible* (meaning that $P^\#\colon T^*M \to TM$ is invertible, in which case its inverse defines a symplectic form on M).

The LV Poisson structure

Fun fact: on a bidimensional manifold, *every* bivector is a Poisson structure! (Jacobi identity = vanishing of a 3-vector...)

$$P = \begin{pmatrix} 0 & P^{12}(x_1, x_2) \\ -P^{12}(x_1, x_2) & 0 \end{pmatrix}$$

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$$\{H, \cdot\} = x_1 x_2 \left(\frac{\partial H}{\partial x_1}\frac{\partial}{\partial x_2} - \frac{\partial H}{\partial x_2}\frac{\partial}{\partial x_1}\right)$$

to be compared with the LV vector field

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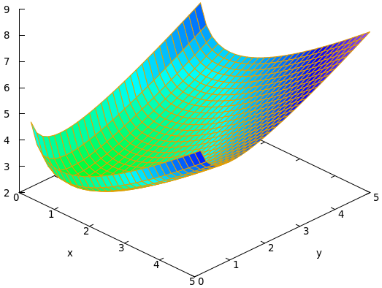
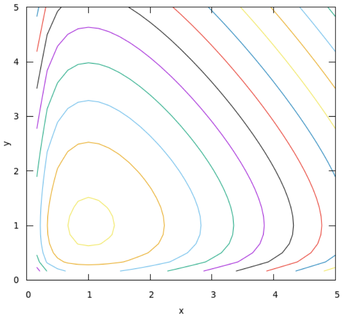
The resulting gradient system for H is solved by

$$H(x_1, x_2) = k(x_1 - \log x_1) + x_2 - \log x_2$$

This is the Hamiltonian of the classic Lotka-Volterra system.





$$k = 1.4$$

Looking for more realistic models

The LV model reduces to a Malthusian model when predators are absent ($x_2 = 0$). This is quite unrealistic, so let's try to generalize the model by incorporating a carrying capacity for preys:

$$\begin{cases} \dot{x}_1 = x_1(\alpha - \frac{\alpha}{N}x_1 - \beta x_2) \\ \dot{x}_2 = x_2(\gamma x_1 - \delta) \end{cases}$$

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(the growth of predators is already limited by the term $-\delta$).
We can again reduce the number of free parameters:

$$\begin{cases} \dot{x}_1 = x_1(1 - x_1 - x_2) \\ \dot{x}_2 = kx_2(\tau x_1 - 1) \end{cases}$$

where $k = \delta/\alpha$ as before and $\tau = N\gamma/\delta$ is the ratio between N and the amount of preys at equilibrium in the *original* model.

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Question: is this model still Hamiltonian (hence integrable)?

Integrability of 2d quadratic systems

Unfortunately, the answer is no. This follows from a result due independently to Cairo and Feix (1992) and Plank (1995):

Theorem

Suppose that the dynamical system

$$\begin{cases} \dot{x}_1 = x_1(b_1 + a_{11}x_1 + a_{12}x_2) \\ \dot{x}_2 = x_2(b_2 + a_{21}x_1 + a_{22}x_2) \end{cases}$$

has a single equilibrium point in the (open) first quadrant. Then it is Hamiltonian iff the following condition holds:

$$\frac{a_{11}}{a_{21}}\frac{b_2}{b_1}\left(1 - \frac{a_{22}}{a_{12}}\right) + \frac{a_{22}}{a_{12}}\left(1 - \frac{a_{11}}{a_{21}}\right) = 0$$

In our case $a_{22} = 0$, so the LHS reduces to $\frac{a_{11} b_2}{a_{21} b_1} = \frac{1}{\tau} \neq 0$.

An integrable perturbation

We would like a model which retains the Poisson structure of the original LV model, so let us try to perturb the LV Hamiltonian

$$H(x_1, x_2) = k(x_1 - \log x_1) + x_2 - \log x_2$$

by adding a "well-chosen" term:

$$H'(x_1, x_2) = k(\tau x_1 - \log x_1) + x_2 - \log x_2 + x_1 \log x_2$$

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The corresponding Hamilton equations read

$$\begin{cases} \dot{x}_1 = x_1(1 - x_2 - x_1) \\ \dot{x}_2 = kx_2(\tau x_1 - 1) + x_1 x_2 \log x_2 \end{cases}$$

The evolution equation for predators gains an additional term which may be interpreted as a "correction" to their growth rate. This term, being proportional to $\log x_2$, is *positive* when predators abound (> 1) and becomes quickly *very negative* when their number tends to zero.

Qualitative behavior

The nullclines of the system are

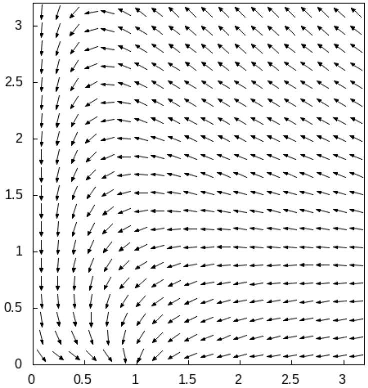
$$x_1 + x_2 = 1 \quad \text{and} \quad x_2 = \mathrm{e}^{k(\frac{1}{x_1} - \tau)}$$

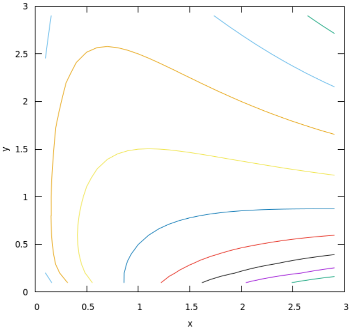
and can intersect in 0, 1 or 2 points according to the number of roots of the transcendental equation

$$k\tau x_2 + (x_2 - 1)\log x_2 = k(\tau - 1)$$

- Suppose $\tau < 1$ (the carrying capacity for species 1 is lower than their equilibrium population according to classic LV). Then it is not hard to see that the LHS is always positive and the RHS is always negative, hence there cannot be any solution and the system has no equilibrium point in the interior of the first quadrant. This means that predators cannot survive in this scenario.

Qualitative behavior, $\tau < 1$

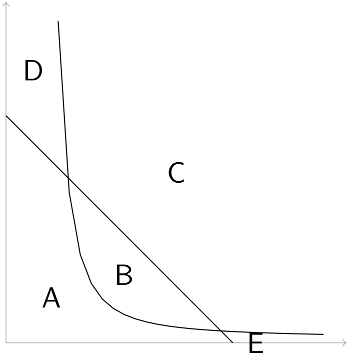




$$k = 1, \ \tau = 0.5$$

Qualitative behavior, $\tau > 1$

- When $\tau > 1$ equilibrium points are possible; in the generic case there will be two of them, dividing the phase space in five regions. One of the two equilibria is stable, the other is a saddle point. The predators are safe as long as the systems does not cross the corresponding separatrix.



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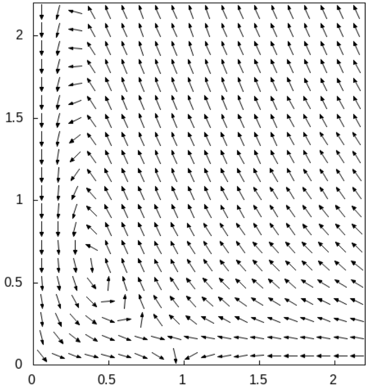

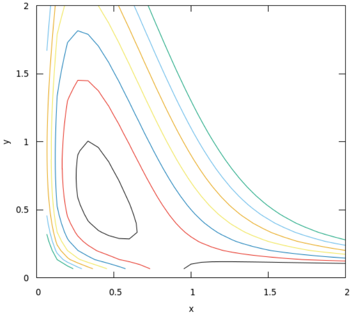

$$k = 1, \; \tau = 3$$