Dynamical Systems and Chaos
Part II: Biology Applications

Lecture 6: Population dynamics

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Living things are dynamical systems

- Dynamical systems theory can be applied to a very broad range of phenomena.
- Biological systems are not exceptions.
- However, they possess certain properties that must be accounted for:
  1. **Complex systems**: many components, spatial organization etc. Aggregated approach (population dynamics) or detailed modelling.
  2. **Systems with reproduction**: auto-catalytic characteristics. Tendency to avoid global equilibrium.
  3. **Open system**: always interact with the environment by interchanging matter and energy.
  4. **Hierarchy of regulation**: regulated by the complex multi-level regulatory mechanisms.

Biological modeling

- Usually positive variables $X > 0$ (exceptions: e.g., electrical potentials).
- Positive parameters (if not complex, e.g. $r = R - S$, reproduction R vs. senescence S).
- Highly nonlinear systems.
- Different time scales.
- Many component systems ($\Rightarrow$ inevitable approximation of reality).

Ecological Population

- Population is a group of organisms (belonging to the same species) that live together in the same habitat (ecological niche) and can interbreed.
- Populations are usually described by a number, its *density*. Thus an ODE (1D) can describe the population dynamics.
- However, there can be more complex models with separate dynamical laws for different sub-groups, sorted, for instance, by age (2D, 3D etc).
- Individual based models (usually, not ODE's).

Population dynamics

- The density of a population changes over time.
- The primary sources for the change are:
  - Births (natality)
  - Deaths (mortality)
  - Immigration (influx)
  - Emigration (outflux)

$$\text{Change in Density} = (\text{Births} + \text{Immigration}) - (\text{Deaths} + \text{Emigration})$$

- There are other impacts (biotic and abiotic) on the density—*secondary ecological events*:
  - Density-independent: climate conditions, high temperature, low humidity etc.
  - Density-dependent: predation, parasitism, contagious disease.

Malthus model

The model of exponential (unlimited) growth.

$$\frac{dx}{dt} = rx\,,$$

where $r = R - S$, R – reproduction rate (natality), S – senescence rate (mortality).

The solution of the exponential growth model is:

$$x(t) = C_0 \mathrm{e}^{rt}\,,$$

C_0 is a constant.

Malthus model dynamics

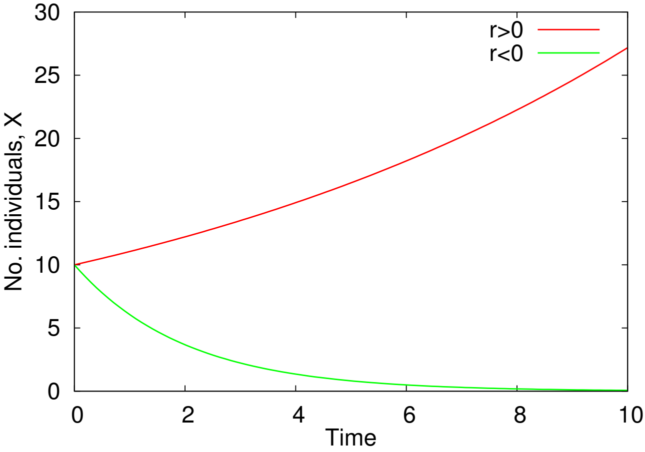


Figure: The dynamics of the Malthus model depending on the coefficient r for a single initial condition.

Verhulst model (logistic equation)

The growth of a population with the limitation

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right),$$

where K and r are positive constants.
The solution of the equation is:

$$x(t) = \frac{x_0 K \mathrm{e}^{r\cdot t}}{K - x_0 + x_0 \mathrm{e}^{r\cdot t}},$$

where x_0 is the initial condition, i.e. $x_0 = x(t = 0)$.

Verhulst model dynamics

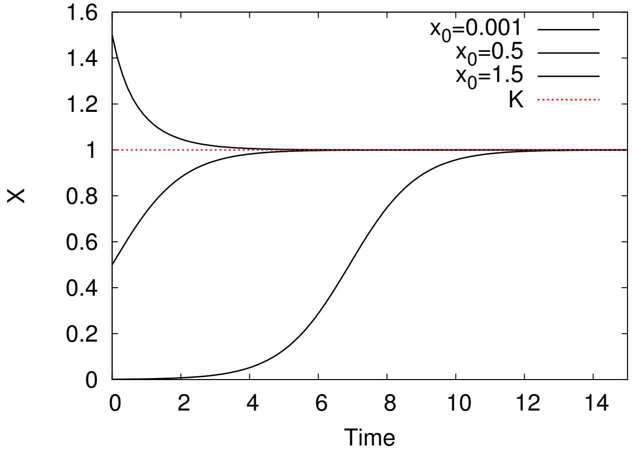


Figure: The Verhulst equation dynamics depending on the intial conditions x_0. $K = 1$, $r = 1$.

Verhulst equation

- The equation has two important properties:
  1. for small x it demonstrates the exponential growth.
  2. for large x it reaches the limit K.
- K is the *environmental carrying capacity* (food resources, space limit etc.)
- The equation has $-\frac{r}{K}x^2$ term reflecting the intraspecific competition.
- As the density grows, the intraspecific competition becomes more intensive, resulting in mortality increase and natality drop.

r- and K-selection

r-selection

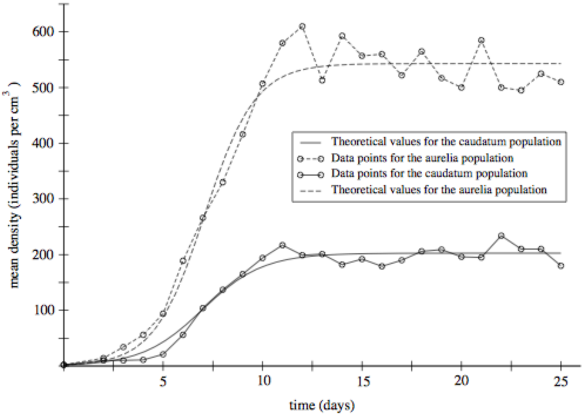
- Opportunist strategy: exploitation of unstable environments and transient resources.
- r-species produce lots of offsprings in a short space of time, rapidly disperse into new habitats as conditions become unfavorable.
- Short life cycle, small body size, high mobility, high reproduction rate r (hence r-strategy).

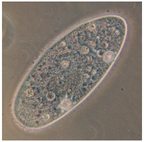
K-selection

- Stable habitats, long life cycles, larger body size, low growth rate.
- Pressure is on the intraspecific competition and efficient use of resources, i.e. focus on $-\frac{r}{K}x^2$ term.

Evidence

- Unlimited growth (e.g. Malthus model): none, except for the initial stages of growth, which is captured by the Logistic equation too.
- Growth with limitation (e.g. Logistic equation):





Unisexual vs. bisexual populations

- Linear growth terms ($\propto r \cdot x$) correspond to **unisexual** populations (Logistic and Malthus models).
- *Paramecium* populations (shown above) can reproduce and propagate alone: by simple division of a cell into two daughter cells. Each daughter cell becomes a distinct individual.
- The growth of **bisexual** populations is better described with quadratic terms, i.e. $\propto r \cdot x^2$, since two individuals must meet in order to interbreed (syngenesis).

Populations with syngenesis

1. Growth of a population with 2 distinct sexes. The reproduction takes place only when two individuals meet. Individuals can be still described by one variable.

$$x' = rx^2$$

2. At higher population density the number of female individuals becomes a limitation. This could be reflected with the limitation denominator:

$$x' = \frac{\alpha x^2}{\beta + \tau x}$$

3. The same population with the senescence. This helps to account for the critical mass in the population.

$$x' = \frac{\alpha x^2}{\beta + \tau x} - d_s x$$

Populations with syngenesis

4. Finally, the intra-species competition gives the limitation on the higher scale, i.e. population size does not blow up to the infinity.

$$x' = \frac{\alpha x^2}{\beta + \tau x} - d_s x - \delta x^2$$

Discrete population models

- Population size changes rather at discrete steps than continously over time.
- General form for the model with evolution operator F_t that is depedent on k states at the previous time moments:

$$N_t = F_t(N_{t-1}, N_{t-2}, \ldots, N_{t-k})$$

- One generation determines completely the other (e.g. insects with fast development, zoo-plankton, fish, birds). Generations do not overlap.

$$N_{t+1} = F_t(N_t)$$

Discrete Logistic map

- Recall the Logistic equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

- Let's arrange a substitute: $dN \leftarrow N_{t+1} - N_t$ and $dt = 1$ (timestep is 1 year, month, day etc.)
- The discrete Logistic equation becomes:

$$N_{t+1} = N_t\left[1 + r\left(1 - \frac{N_t}{K}\right)\right]$$

Biological reformulation of the Logistic map

- For some N_t the RHS of the map becomes negative. Namely, for $N_t > \frac{1+r}{r}K$ the next value N_{t+1} becomes negative.
- Thus, the the RHS was proposed to be changed by some authors:
$$N_{t+1} = N_t \exp\left[r\left(1-\frac{N_t}{K}\right)\right]$$
- This new form of the map was successfully applied to some species of fish and insects.

Lamerey Diagram and stability of solutions.

- One can see the solution course by the Lamerey Diagram.
- The diagram is the plot of $N_{t+1} = F(N_t)$ vs. N_t
- *Solution* is any sequence $\{N_t\}$, $t = 0, 1, \ldots$ satisfying the map.
- *Steady state* is a solution of the form: $N_t = Const = N^*$, where $N^* = F(N^*)$

Solution of the Logistic map

- Steady state solution does not change from t to $t+1$ implying for our equation:

$$\exp\left\{r\left(1-\frac{N^*}{K}\right)\right\}=1$$

- So, the solution is:

$$N^*=K$$

- One single positive solution, which, thus, has the biological meaning of the capacity (or the growth limit) of the population.

Stability of the solution

- Applying small perturbation x_t to the stationary solution N^* we can eventually obtain formula of the linearized system:
$$x_{t+1} = \left(\frac{dF}{dN}\right)_{N=N^*} \cdot x_t + O(x_t^2)$$
- This is the geometric series with common ratio of $\left(\frac{dF}{dN}\right)_{N=N^*}$
- The common ratio:
$$\frac{dF}{dN} = \exp\left\{r\left(1 - \frac{N}{K}\right)\right\} - \frac{rN\exp\left\{r\left(1 - \frac{N}{K}\right)\right\}}{K}$$
- $$\left(\frac{dF}{dN}\right)_{N=N^*} = 1 - r$$

Stability of the solution

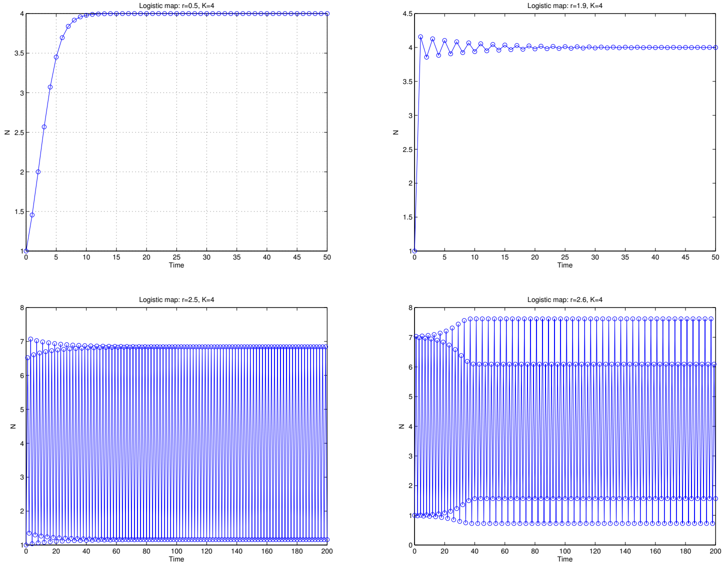
- From the convergence of the geometric series, solution $N^* = K$ is stable if:

$$|1 - r| < 1$$

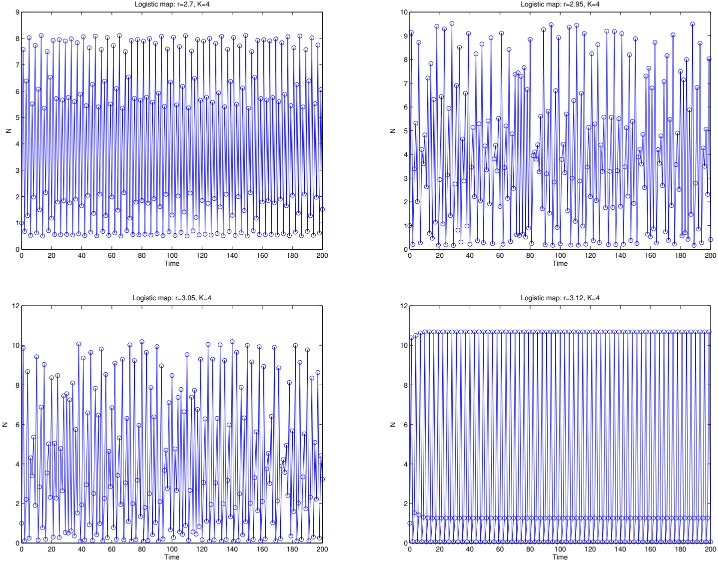
- And the solution is unstable if:

$$|1 - r| > 1$$

Solutions of the Logistic Map



Solutions of the Logistic Map



Interaction of two species: Lotka equations

- Predator-prey system (e.g. hares x and wolves y).
- Hares have non-limited food source and reproduct at constant rate k_0.
- Hares die when meet with wolves, which is proportional to xy. Wolves grow and reproduct due these meeting events.
- Wolves die proportional to y.

$$\begin{cases} \dfrac{dx}{dt} = k_0 - k_1 xy \\ \\ \dfrac{dy}{dt} = k_1 xy - k_2 y \end{cases}$$

Lotka equations

- Steady state is:

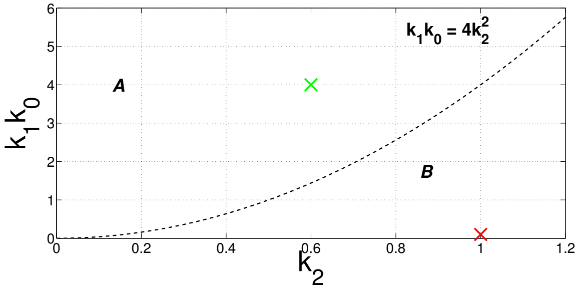
$$\bar{x} = \frac{k_2}{k_1} \wedge \bar{y} = \frac{k_0}{k_2}$$

- Roots of the characteristic equation:

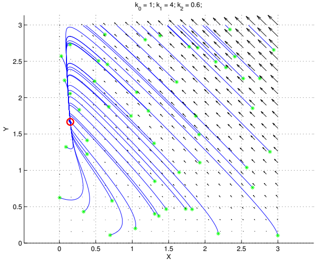
$$\lambda_{1,2} = \frac{-k_1 k_0 \pm \sqrt{(k_1 k_0)^2 - 4 k_1 k_0 k_2^2}}{2 k_2}$$

- $\operatorname{Re} \lambda_{1,2} < 0 \Rightarrow$ always stable steady state.
- If $k_1 k_0 \geq 4 k_2^2$ — stable sink. If otherwise the steady state is stable focus.

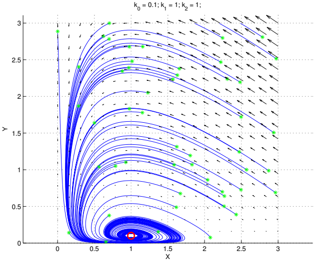
Lotka equations



NODE region A



FOCUS region B



(Lotka-)Volterra equations

- Similar to Lotka equations.
- But hares grow linearly $\epsilon_x x$ on the unlimited food supply.

$$\begin{cases} \dfrac{dx}{dt} = x(\epsilon_x - \gamma_x y) \\ \\ \dfrac{dy}{dt} = -y(\epsilon_y - \gamma_y x) \end{cases}$$

Dynamics of the Volterra equations

- Steady states are:

$$\begin{cases} \bar{x} = 0 \\ \bar{y} = 0 \end{cases} \vee \begin{cases} \bar{x} = \frac{\epsilon_y}{\gamma_y} \\ \bar{y} = \frac{\epsilon_x}{\gamma_x} \end{cases}$$

- Roots of the characteristic equation for the nonzero solution:

$$\lambda_{1,2} = \pm i\sqrt{\epsilon_x \epsilon_y}$$

- Steady state type is center = oscillations, depending on the initial conditions. But this is a nonlinear equation!
- Thus, no conclusion can be drawn from the linear analysis.
- However, one can show that ther is a *constant entity* along the solution lines of the system (constant of motion).

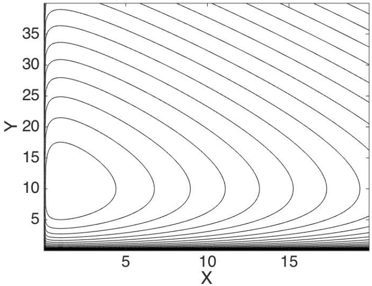
Constant of motion in the Volterra equations

- If we integrate without time: $\dfrac{dy}{dx} = -\dfrac{y(\epsilon_y - \gamma_y x)}{x(\epsilon_x - \gamma_x y}$
- We will see the constant entity K to be:

$$K = \epsilon_x \ln y + \epsilon_y \ln x - \gamma_x y - \gamma_y x$$

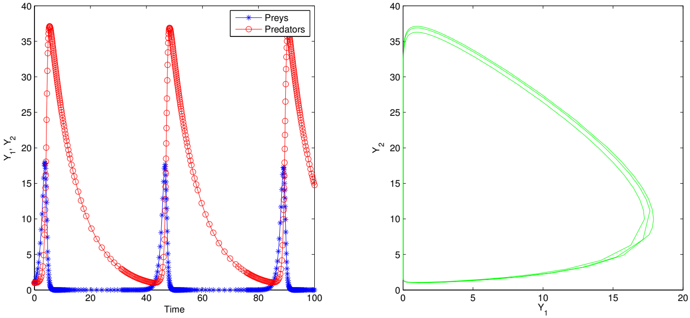
- Like in Hamiltonian systems we just need to plot levels of the constant of motion K.

Contour plot for $\epsilon_x = 1, \gamma_x = \gamma_y = 0.1, \epsilon_y = 0.1$:



Volterra equations: simulation

Simulations for $\epsilon_x = 1, \gamma_x = \gamma_y = 0.1, \epsilon_y = 0.1$:



Predator-prey oscillations

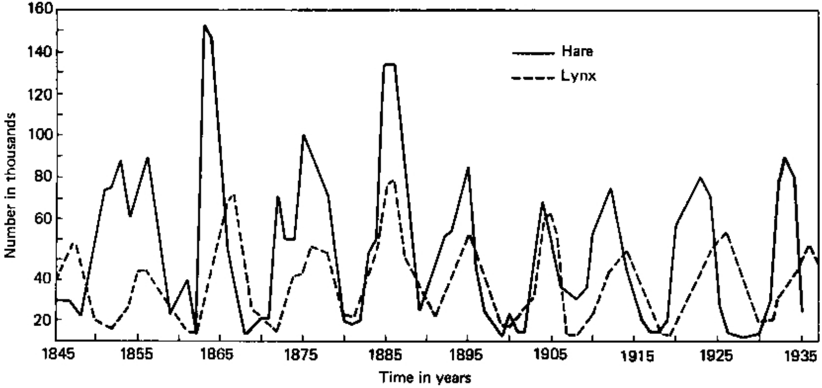
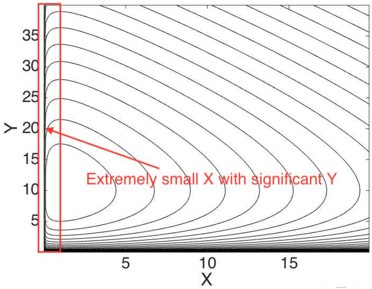


Figure 9-3. Changes in the abundance of the lynx and the snowshoe hare, as indicated by the number of pelts received by the Hudson's Bay Company. This is a classic case of cyclic oscillation in population density. (Redrawn from MacLulich 1937.)

Picture from: `http://math.ucr.edu/home/baez/week309.html`

Atto-fox problem of the Volterra equations

- For some parameters, the number of preys X can be extremely small, whereas the number of predators Y is significant. Predators can survive on small prey abundance.
- However, real populations due to fluctuations and bisexual structure can go extinct in such conditions.
- This effect was called *atto-fox problem* (atto denotes the numerical prefactor 10^{-18}) after some rabies studies (rabies virus—predator, fox—prey).



Generalized model of two-species interaction

- Volterra hypotheses and generalized equations (see the project work) for the two-species interaction.
- Kolmogorov proposed a generalized predator-prey model:

$$\begin{cases} \dfrac{dx}{dt} = k_1(x)x - L(x)y \\ \dfrac{dy}{dt} = k_2(x)y \end{cases}$$

- $k_1(x)$ is a function-coefficient of the preys (x) reproduction in the absence of predators (y). $\frac{dk_1(x)}{dx} < 0$ (limited resources).
- $L(x)$ is a number of preys consumed by a predator in a time unit. $L(x) > 0$, $L(0) = 0$.
- $k_2(x)$ is a function-coefficient of the predators' reproduction. $\frac{dk_2(x)}{dx} > 0$, $k_2(0) < 0 < k_2(\infty)$.

Kolmogorov equations

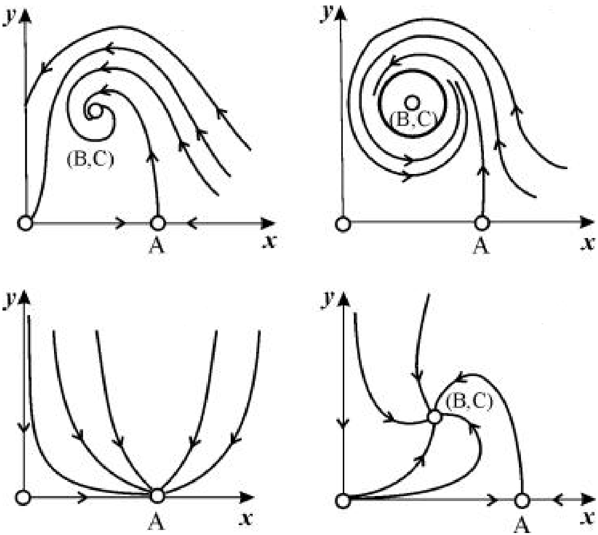
- Stationary points (two or three):

$$\text{i)} \begin{cases} x = 0 \\ y = 0 \end{cases} \qquad \text{ii)} \begin{cases} x = A \\ y = 0 \end{cases} \qquad \text{iii)} \begin{cases} x = B \\ y = C \end{cases},$$

  where $k_1(A) = 0$, $k_2(B) = 0$, and $C = \dfrac{k_1(B)B}{L(B)}$.

- i) is always saddle
- ii) is stable node $(A < B)$ or saddle $(A > B)$
- iii) is node/focus (if $\zeta = k_1(B) - \frac{dk_1}{dx}(B)B - C\frac{dL}{dx}(B) < 0$ stable, if $\zeta > 0$ unstable).

Phase portraits: Kolmogorov equations



G. Riznichenko, Mathematical modeling in biophysics. Lectures.

Useful resources

- JD Murray, Mathematical Biology, Chapter 2 (discrete 1D population models).
- Some tutorial on the population dynamics. Very descriptive. `http://www.cals.ncsu.edu/course/ent425/library/tutorials/ecology/popn_dyn.html`
- Wikipedia page about the Logistic map. Very useful with many descriptive animations. `http://en.wikipedia.org/wiki/Logistic_map`