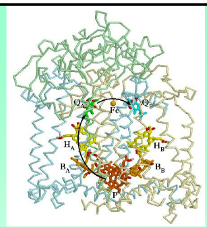
Ecology

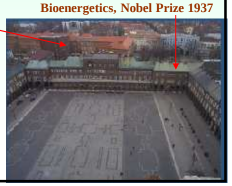


Biophysics of proteins

Simulation in Biology

Péter Maróti
Professor of Biophysics
University of Szeged, Hungary

Prof. Albert Szent-Györgyi
Bioenergetics, Nobel Prize 1937



Maróti P. és Tandori Júlia: Biofizikai Példatár, JATEPress 1996
P. Maróti, L. Berkes and F. Tölgyesi: Biophysics Problems.
A Textbook with Answers, Akadémiai Kiadó, Budapest 1998.

If the Lord Almighty had consulted me
Before embarking on creation
I should have recommended something simpler.

Alphonso the Wise (1221-1284)
King of Castile and Leon (attributed)

Population Biology, Ecological questions

Concepts and Models

Simulation ⟷ Fitting

Appropriate model, many parameters

Strict conditions, few parameters

Hypotheses for population regulation

- Populations are limited by density-independent factors such as changes in the weather.
- Populations are limited by their food supply.
- Populations regulate themselves through mechanisms such as territoriality or cannibalism.
- Populations are regulated through competition.
- Populations are regulated by predators.
- Populations are regulated by parasites or diseases.

Topics:

I. Logistic equation
one species populates alone the living space („Lebensraum”)

II. Competition (Lotka-Volterra equation)
two species compete for the common living space (food)

III. Predator-Prey Interactions (Lotka-Volterra Models)
One species is the exclusive food of the other species.

I. Logistic equation: the population does not grow to infinity

One species dominate the living space only and the equilibrium population (carrying capacity, K) is determined by the conditions.
For separate generations: the relative increase of the population density N from generation n to generation (n +1) is proportional to the actual deviation of the population from the equilibrium value K:

$$\frac{N_{n+1}-N_n}{N_n}=C\cdot(K-N_n)$$

Recursive equation

For not separate generations, the logistic equation turns to differential equation:

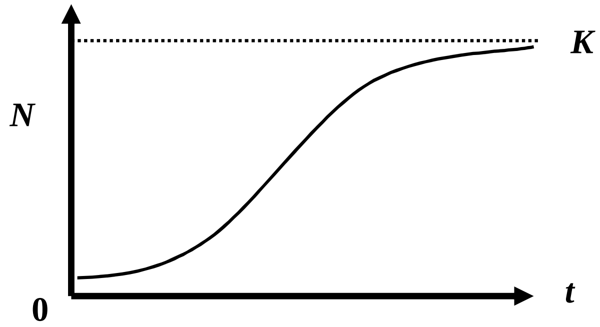
$$\frac{dN}{dt}=C\cdot(K-N)\cdot N$$

Differential equation

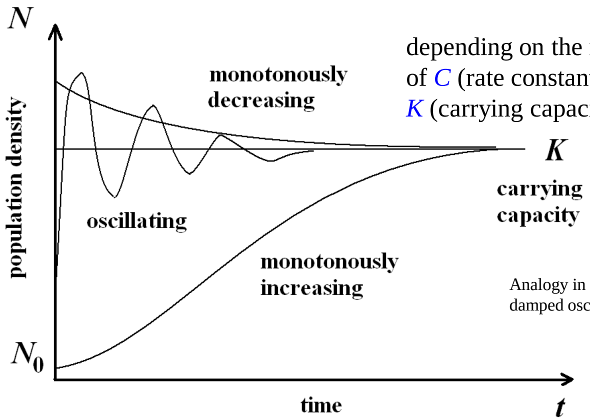
The logistic equation can be integrated by separation of the variables:

$$t=\frac{1}{C\cdot K}\cdot\ln\left|\frac{N}{K-N}\right|+B$$

where $C\cdot K$ the rate of the increase if N <<K, $C\cdot(K-N)$ is the actual rate
K population in equilibrium
B constant of integration



How does the system approach the equilibrium (if exists)?



depending on the ratio of C (rate constant) and K (carrying capacity):

Analogy in physics: damped oscillation

Homeworks

1) Growth cultures, chemostates, reactors

The equilibrium capacity of a bacterium growth culture is $K = 5\cdot 10^8$ cells/ml. In the lag phase of the growth (when the culture is dilute) the doubling time (generation time) is
$T_0 = (\ln 2)/(C\cdot K) = 40$ minutes.
How large will be the population density of the culture after 2 hours if the initial population density (concentration) is

a) $1\cdot 10^8$ cells/ml,

b) $1\cdot 10^9$ cells/ml?

2) Harvesting the species.

How many fish can be harvested without reducing the viability of the population? (When the population level becomes too low, the population will decline. This is the *Allee effect*.)

Hint:

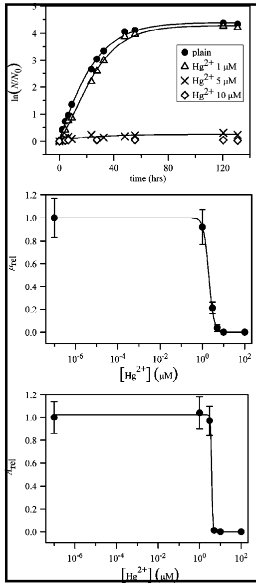
Complete the simple logistic equation with a term that considers the harvest:

$$\frac{dN}{dt} = C \cdot N\left(K - N\right) - H \cdot N$$

where H is the rate of the harvest.

a) Find the non-zero equilibrium of this model, which will depend on the value of H. What restriction on H is necessary for this equilibrium to be positive? Discuss biologically why this condition makes sense.

b) What happens to the population if H is larger than the value determined in part a?



Growth curve of photosynthetic bacteria

The anaerobic growth curves were obtained by plotting the logarithm of the relative population size, ln (N/N_0), against the time elapsed from the light exposure. Growth rate (μ), lag phase duration (λ) and the asymptotic population size (K) were determined by fitting the modified Gompertz equation to growth curves

$\ln(N/N_0) = K \cdot \exp\{-\exp[\mu \cdot e/K \cdot (\lambda - t) + 1]\}$

where N is the cell concentration at the time t, N_0 is the initial cell concentration and e (the Napier number) is the base of the natural logarithm.

II. Lotka-Volterra Competition

- The dynamics of the two species:

$$\frac{\Delta N_1(t)}{\Delta t} = r_1 N_1(t)\left(\frac{K_1 - N_1(t) - \alpha \cdot N_2(t)}{K_1}\right)$$

$$\frac{\Delta N_2(t)}{\Delta t} = r_2 N_2(t)\left(\frac{K_2 - N_2(t) - \beta \cdot N_1(t)}{K_2}\right)$$

where α and β are the interspecific competition coefficients of the two species.

N_1: population density of the first species

N_2: population density of the second species

K_1: carrying capacity of the living space for the first species

K_2: carrying capacity of the living space for the second species

r_1: growth rate of the first species ($C_1 \cdot K_1$)

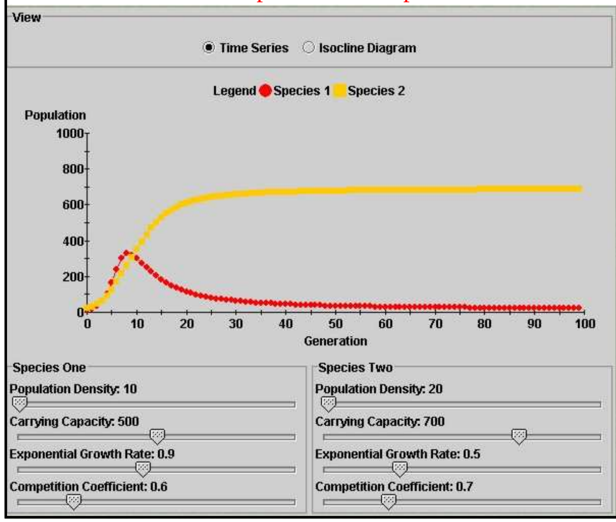
r_2: growth rate of the second species ($C_2 \cdot K_2$)

ΔN_1: increase of the population density of the first species within time Δt

ΔN_2: increase of the population density of the second species within time Δt

- **Kinetics:** Dynamics of the two populations between $t = 0$ and $t = 100$ units.

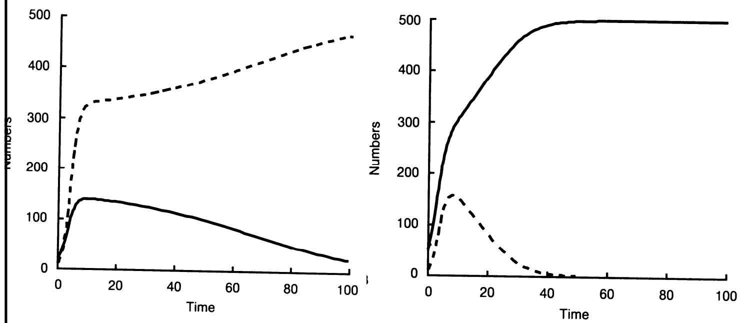
One species outcompetes the other.



$N_1(0) = 10$,
$N_2(0) = 20$,
$r_1 = 0.9$,
$r_2 = 0.5$,
$K_1 = 500$,
$K_2 = 700$,
$\alpha = 0.6$,
$\beta = 0.7$

Dynamics of competition: the outcome depends on the initial conditions.

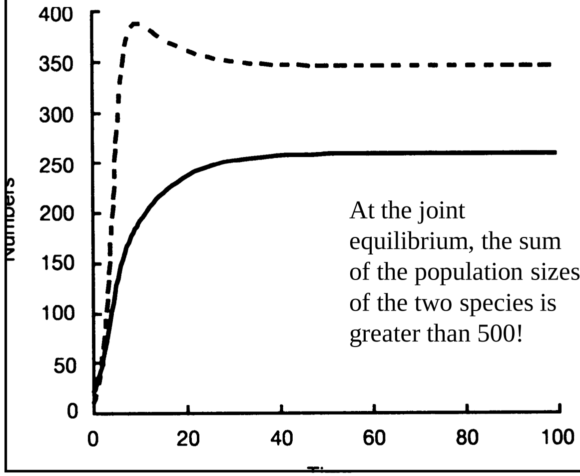
$r_1 = 0.9,\ r_2 = 0.5,\ K_1 = 500,\ K_2 = 500,\ \alpha = 1.2,\ \beta = 1.1$



The only difference between the two figures is the initial condition.

$N_1(0) = 10$, $N_2(0) = 10$ → $N_1(0) = 10$, $N_2(0) = 60$

Dynamics of competition with coexistence

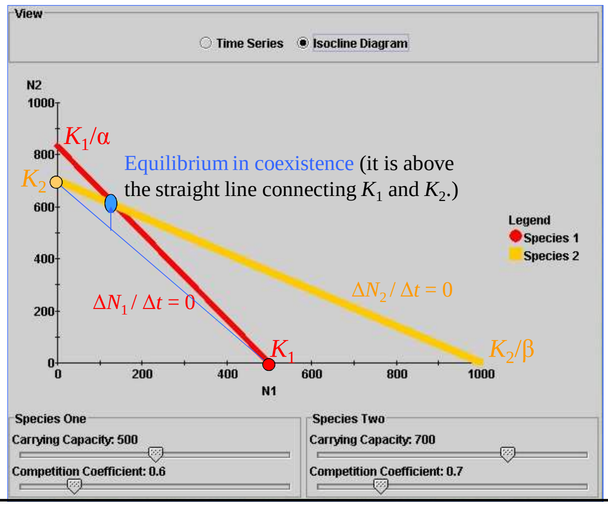


At the joint equilibrium, the sum of the population sizes of the two species is greater than 500!

$N_1(0) = 10$
$N_2(0) = 20$
$r_1 = 0.9$
$r_2 = 0.5$
$K_1 = 500$
$K_2 = 500$
$\alpha = 0.6$
$\beta = 0.7$

- **Equilibrium**: neither N_1, nor N_2 does change ($\Delta N_1 = \Delta N_2 = 0$)

$K_1 = N_1 + \alpha \cdot N_2,\quad K_2 = N_2 + \beta \cdot N_1$



Homework

The ecologist Slobodkin (1961, 1964) looked at competition between a brown hydra (*Hydra littoralis*) and a green hydra (*Chlorohydra viridissima*) in laboratory experiments. He was able to achieve coexistence only by the process he called *rarefaction*, removing a fraction of the population of both species at regular intervals by removing part of the medium in which the animals were grown.

Demonstrate how this works by adding the terms $-m \cdot N_1$ and $-m \cdot N_2$ to the Lotka-Volterra equations! Show that it is possible to have coexistence with proper choice of the the additional terms, even if the coexistence is impossible without the additional terms (i.e. one species always eliminates the other).

$$\frac{\Delta N_1(t)}{\Delta t} = r_1 N_1(t)\left(\frac{K_1 - N_1(t) - \alpha \cdot N_2(t)}{K_1}\right) - m \cdot N_1 \qquad \frac{\Delta N_2(t)}{\Delta t} = r_2 N_2(t)\left(\frac{K_2 - N_2(t) - \beta \cdot N_1(t)}{K_2}\right) - m \cdot N_2$$

III. The Lotka-Volterra-Equations for the Predator-Prey model

Lynx canadensis

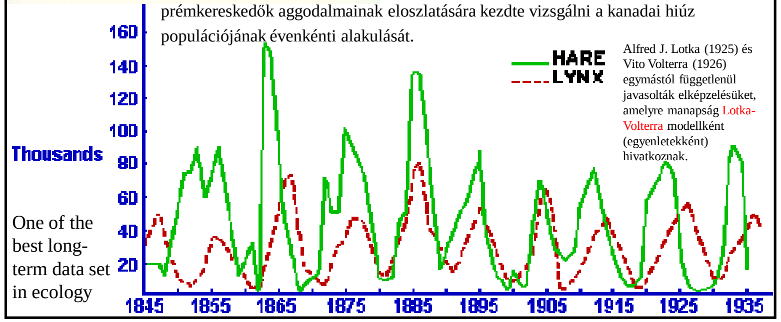
Lepus americanus

lynx

snowshoe hare

Predator-pray

Egy amerikai biztosítási ügynökség (Hudson Bay Company) a 19. században az európai prémkereskedők aggodalmainak eloszlatására kezdte vizsgálni a kanadai hiúz populációjának évenkénti alakulását.



Alfred J. Lotka (1925) és Vito Volterra (1926) egymástól függetlenül javasolták elképzelésüket, amelyre manapság Lotka-Volterra modellként (egyenletekként) hivatkoznak.

One of the best long-term data set in ecology

- Characteristics: One species (prey) is the exclusive food of the other species (predator).
- Conditions:
  - The prey lives under unlimited (food) conditions (e.g. it is grass-eating and the grass supply is inexhaustible),
  - The increase of the predator population is determined solely by the prey population,
  - The rates of reproduction of both species are independent on the age of the species,
  - The number of captured prey is proportional to the number of encounters between predators and preys.

N: actual population of the prey,
r_1: rate of increase of the population of the prey,
P: actual population of the predator,
r_2: rate of death of the predator

- If no predators are present, the population of the prey increases exponentially:

$$\Delta N(t) = r_1 N(t)\cdot\Delta t.$$

(The capacity of the living space is extremely large for the prey.)

- If no preys are available, the population of the predator decreases exponentially:

$$\Delta P(t) = -\, r_2 P(t)\cdot\Delta t.$$

- The number of encounters within unit interval of time („bimolecular process”):

$$C_1 N\cdot P,$$

where the constant C_1 offers the magnitude of the chance that a predator catches (kills and eats) a prey.

➢Taking into account both species:

$$\Delta N(t)/\Delta t = r_1 N(t) - C_1 N(t)\cdot P(t)$$

$$\Delta P(t)/\Delta t = -r_2 P(t) + C_2 N(t)\cdot P(t)$$

where the constant C_2 indicates in what extent (yield) the predator utilizes (for his own purposes, e.g. metabolism, sexual potential etc.) the captured prey.

➢ The Lotka-Volterra equations are coupled differential equations. We have to check

- the existence of the solution,
- the unicity of the solution and
- the stability of the solution (e.g. what does the noise do?).

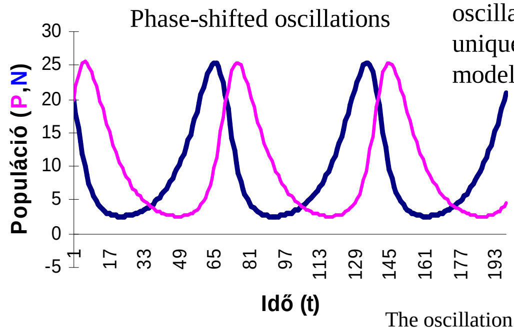
➢It can be proven, that there are solutions but cannot be obtained by analytical methods (in „closed” forms).

➢The solutions can be derived by approximate (numerical) methods. The Lotka-Volterra differential equation will be converted to difference equation and starting from time $t = 0$, we proceed with Δt steps and calculate the actual populations $N(t)$ and $P(t)$.

KINETICS

Lotka-Volterra ragadozó-zsákmány: idő trajektória

Phase-shifted oscillations



The observed oscillation is not a unique feature of the model.

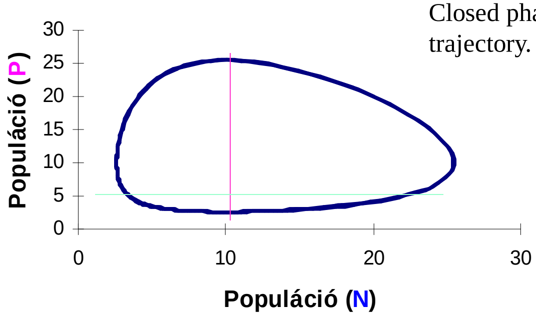
$P_0 = 20$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 20$, $r_2 = 0.1$, $C_2 = 0.01$

The oscillation does not come from the presence of the predator, the population of the prey can oscillate even in the absence of the predator and *vica cersa*.

PHASE TRAJECTORY

Lotka-Volterra ragadozó-zsákmány

Closed phase trajectory.

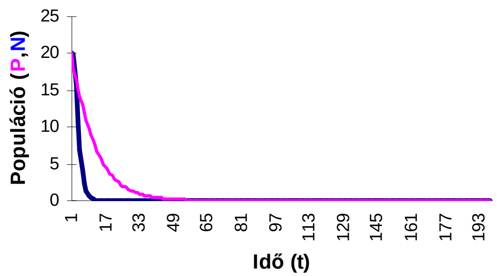


$P_0 = 20$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 20$, $r_2 = 0.1$, $C_2 = 0.01$

The variable (hidden) parameter is the time.

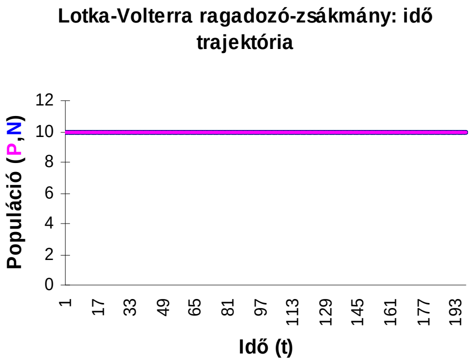
Decreasing populations. Extinction of both predator and prey.

Lotka-Volterra ragadozó-zsákmány: idő trajektória



$P_0 = 20$, $r_1 = 0.01$, $C_1 = 0.1$;
$N_0 = 20$, $r_2 = 0.1$, $C_2 = 0.01$

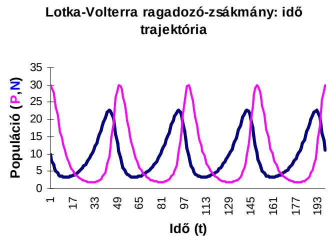
➢Stable condition means equilibrium: if $\Delta N = \Delta P = 0$, then $P = \frac{r_1}{C_1}$ and $N = \frac{r_2}{C_2}$.

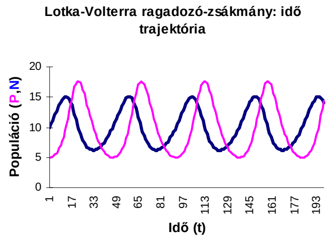


$P_0 = 10$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 10$, $r_2 = 0.2$, $C_2 = 0.02$

➢Meaning of the two equations: KINETICS

• above predator population $\boldsymbol{P = r_1/C_1}$, the prey population decreases and below predator population $\boldsymbol{P = r_1/C_1}$, the prey population increases.





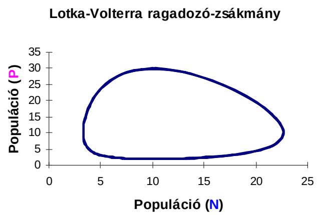
$P_0 = 30$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 10$, $r_2 = 0.2$, $C_2 = 0.02$

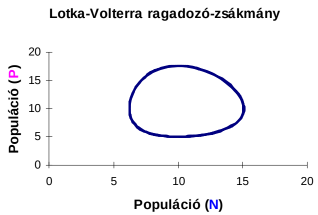
$P_0 = 5$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 10$, $r_2 = 0.2$, $C_2 = 0.02$

$r_1/C_1 = 10$

PHASES

The time is eliminated.





above

$P_0 = 30$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 10$, $r_2 = 0.2$, $C_2 = 0.02$

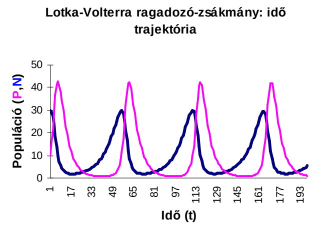
below

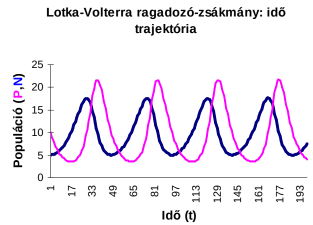
$P_0 = 5$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 10$, $r_2 = 0.2$, $C_2 = 0.02$

$r_1/C_1 = 10$

➢Meaning of the two equations: KINETICS

• above the prey population of $\boldsymbol{N = r_2/C_2}$, the predator population increases and below the prey population of $\boldsymbol{N = r_2/C_2}$, the predator population idecreases.





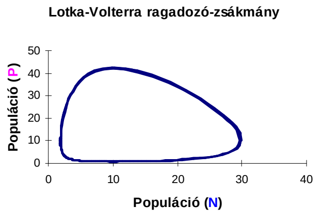
$P_0 = 10$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 30$, $r_2 = 0.2$, $C_2 = 0.02$

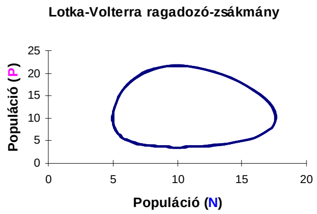
$P_0 = 10$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 5$, $r_2 = 0.2$, $C_2 = 0.02$

$r_2/C_2 = 10$

The phase diagrams are closed curves.

PHASE PLANE





$P_0 = 10$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 30$, $r_2 = 0.2$, $C_2 = 0.02$

$P_0 = 10$, $r_1 = 0.1$, $C_1 = 0.01$;
$N_0 = 5$, $r_2 = 0.2$, $C_2 = 0.02$

above $r_2 / C_2 = 10$ below

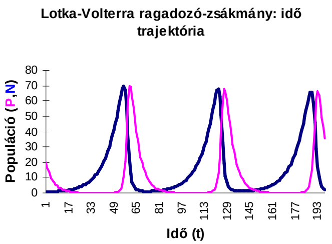
Trajektories

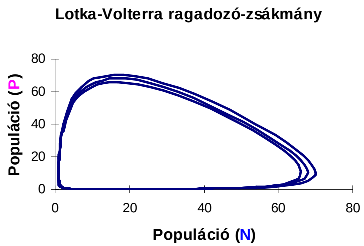
to visualize the solutions of the Lotka-Volterra model for predator-prey: simulations in planes of time and phases

Many thanks to Ms

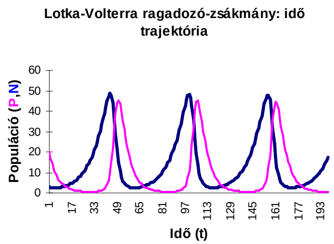
Kornélia Szebényi

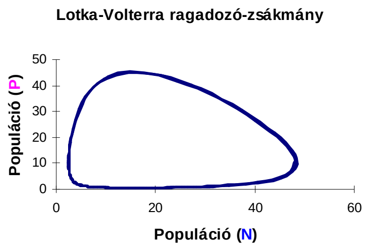
student of biophysics who calculated the time and phase trajectories with great diligence, patience and expertise.





$P_0 = 20$, $r_1 = 0.1$, $C_1 = 0.01$; $N_0 = 1$, $r_2 = 0.2$, $C_2 = 0.013$





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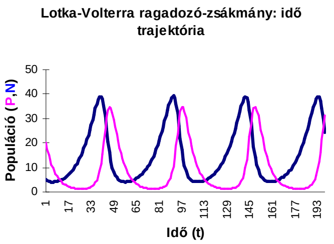

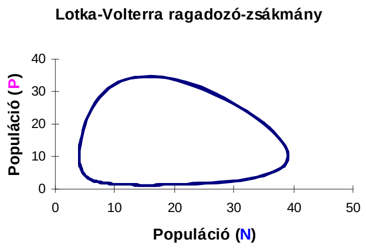

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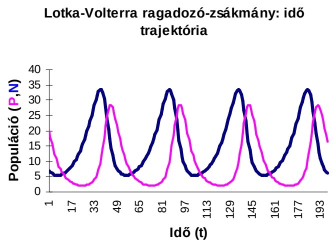

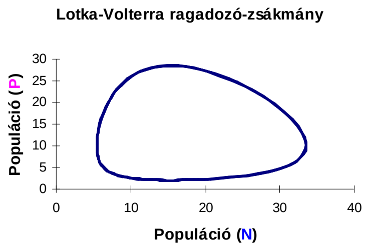

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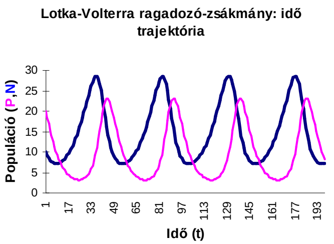

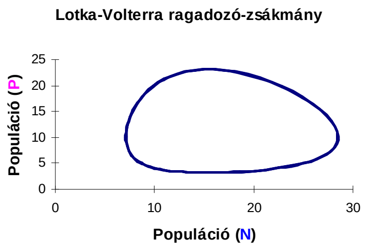

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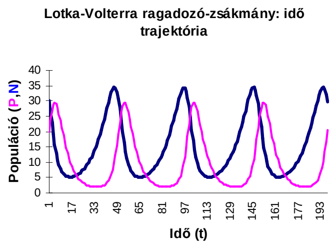

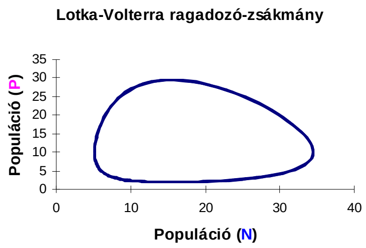

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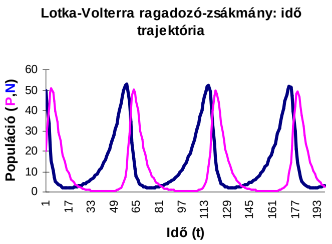

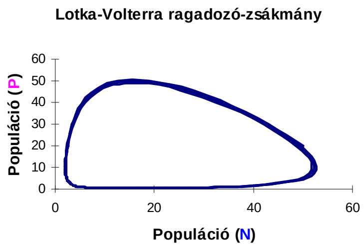

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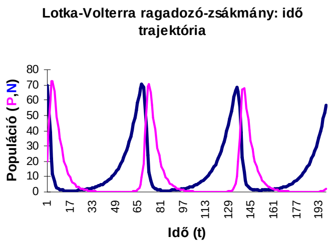

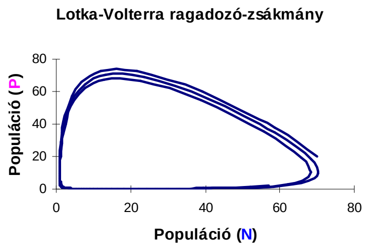

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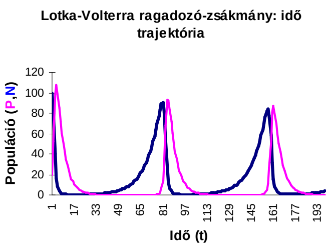

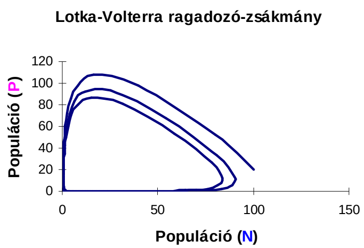

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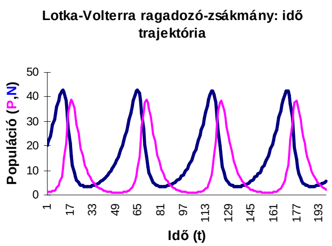
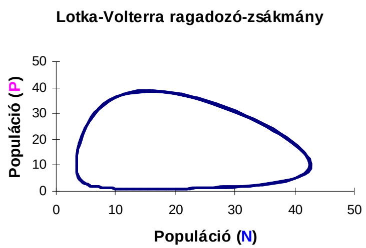
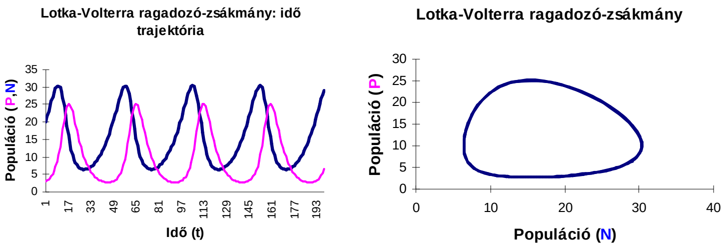
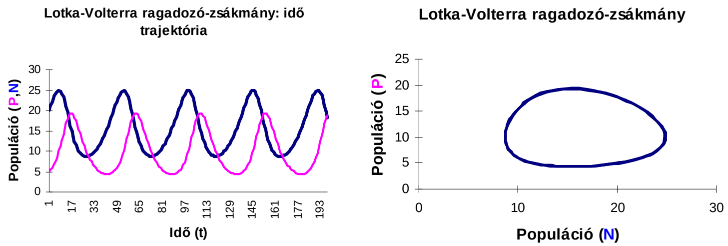




$P_0 = 1, r_1 = 0.1, C_1 = 0.01; N_0 = 20, r_2 = 0.2, C_2 = 0.013$



$P_0 = 3$, $r_1 = 0.1$, $C_1 = 0.01$; $N_0 = 20$, $r_2 = 0.2$, $C_2 = 0.013$



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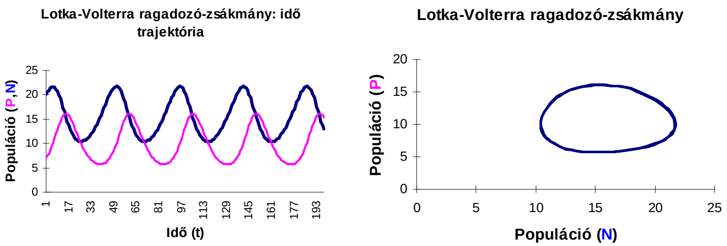

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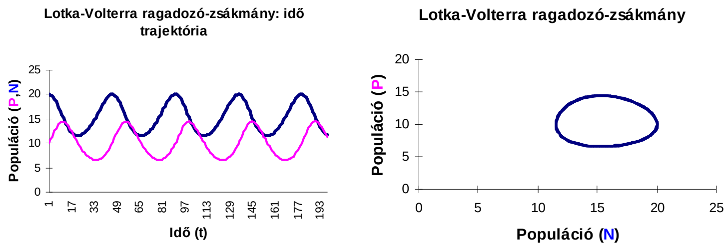

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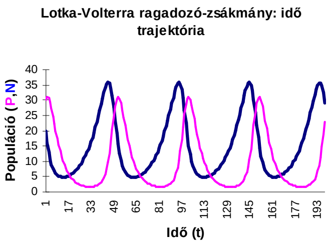
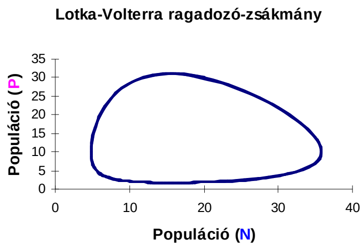
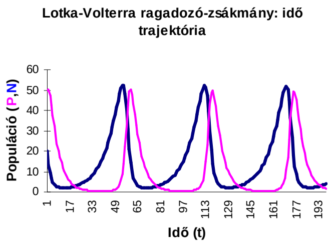
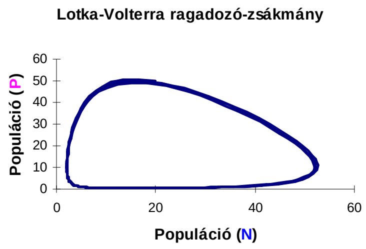


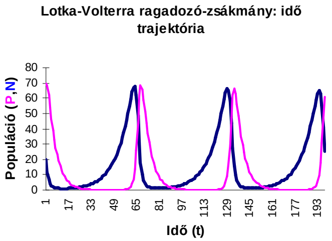


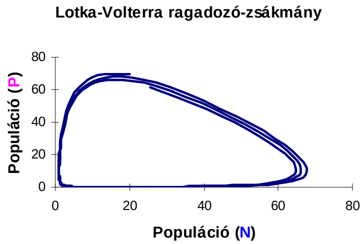
$P_0 = 30$, $r_1 = 0.1$, $C_1 = 0.01$; $N_0 = 20$, $r_2 = 0.2$, $C_2 = 0.013$



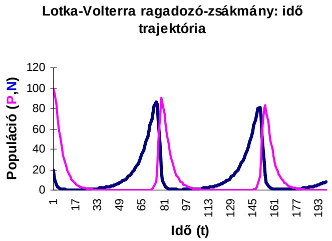


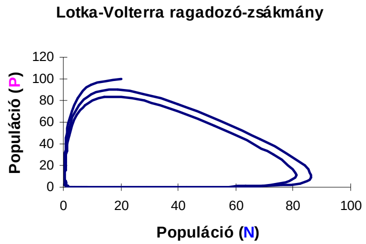
$P_0 = 50$, $r_1 = 0.1$, $C_1 = 0.01$; $N_0 = 20$, $r_2 = 0.2$, $C_2 = 0.013$





$P_0 = 70$, $r_1 = 0.1$, $C_1 = 0.01$; $N_0 = 20$, $r_2 = 0.2$, $C_2 = 0.013$

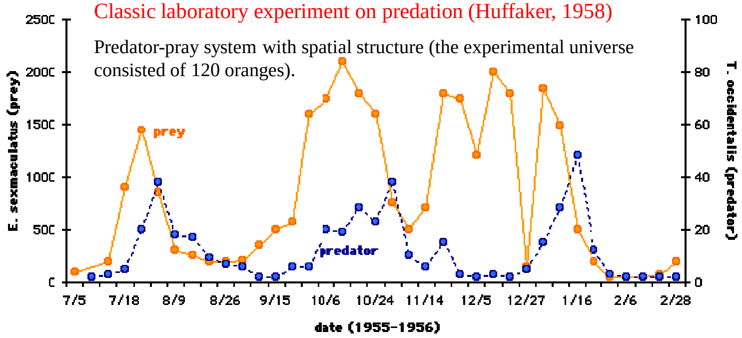




$P_0 = 100$, $r_1 = 0.1$, $C_1 = 0.01$; $N_0 = 20$, $r_2 = 0.2$, $C_2 = 0.013$

Classic laboratory experiment on predation (Huffaker, 1958)

Predator-pray system with spatial structure (the experimental universe consisted of 120 oranges).



Huffaker (1958) reared two species of mites to demonstrate these coupled oscillations of predator and prey densities in the laboratory. Using *Typhlodromus occidentalis* as the predator and the six-spotted mite (*Eotetranychus sexmaculatus*) as the prey, Huffaker constructed environments composed of varying numbers of oranges (fed on by the prey) and rubber balls on trays. The oranges were partially covered with wax to control the amount of feeding area available to *E. sexmaculatus*, and dispersed among the rubber balls. The results of one of the many permutations of his experiments are graphed below. Note that the prey population size is on the left vertical axis and the predator population is on the right vertical axis, and that the scales of the two are different.

Interpretation: It is apparent from the graph that both populations showed cyclical behavior, and that the predator population generally tracked the peaks in the prey population. However, there is some information about this experiment that we need to consider before concluding that the experimental results truly support the predictions made by the Lotka-Volterra model. To achieve the results graphed here, Huffaker added considerable complexity to the environment. Food resources for *E. sexmaculatus* (the oranges), were spread further apart than in previous experiments, which meant that food resources for *T. occidentalis* (i.e., *E. sexmaculatus*) were also spread further apart. Additionally, the oranges were partially isolated with vaseline barriers, but the prey's ability to disperse was facilitated by the presence of upright sticks from which they could ride air currents to other parts of the environment. In other words, predator and prey were not encountering one another randomly in the environment.

Conclusions: A good model must be simple enough to be mathematically tractable, but complex enough to represent a system realistically. Realism is often sacrificed for simplicity, and one of the shortcomings of the Lotka-Volterra model is its reliance on unrealistic assumptions. For example, prey populations are limited by food resources and not just by predation, and no predator can consume infinite quantities of prey. Many other examples of cyclical relationships between predator and prey populations have been demonstrated in the laboratory or observed in nature, but in general these are better fit by models incorporating terms that represent carrying capacity (the maximum population size that a given environment can support) for the prey population, realistic functional responses (how a predator's consumption rate changes as prey densities change) for the predator population, and complexity in the environment.

Predation in natural systems

One of the difficulties of relating the theory to interactions between predator and pray in natural systems is finding a relatively contained (in space) system where there is a single predator feeding on a single prey. In most natural systems, predators have alternate prey, and the spatial extent is important (see the Huffaker's experiment, 1958). A way to limit the role of spatial extent is to look at an island, which may also serve to limit the number of alternate prey.

The predator-pray interaction between wolves and moose on Isle Royale (located in Lake Superior) has been long studied and can provide insight into the dynamics of predator-pray systems in nature. It is relatively easy to demonstrate that wolves in fact kill moose, but showing that wolves are responsible for regulating the moose population is more difficult; the wolves might only be killing moose that would die anyway. To demonstrate that wolves regulate the moose population, one must show that, as the density of moose increase, the number of deaths from wolf predation also increases. (In all the models, the predation terms include this effect.) The data do not provide a clear-cut answer.

Homework

A farmer discovered a pest eating his crops. After spraying with a pesticide, the farmer found to his great surprise that the level of the pest increased! How can it occur?

Hint:

Assume that the pest was being eaten by a predator and that the pesticide affected both the predator and the pest. Also assume that the interaction between the pest and the predator can be described by a continuous time Lotka-Volterra model.

Summary

We know what can regulate populations:
- finite size of food supply („Lebensraum”),
- cannibalism,
- competitors,
- predators (or parasitoids),
- diseases etc.,

but we do not know what actually does regulate populations.

We have two possibilities:

1) Dynamics observed in the nature ↔ model-calculation.

Drawback: can clearly reject a proposed explanation of regulation but cannot prove one.

2) Field experiment: removal of a putative competitor or augmentation of the food supply, etc.

Drawback: some potential regulating mechanisms

a) cannot be manipulated at all (e.g. diseases), or

b) can be manipulated in time (e.g. long-lived organisms as trees or tortoises) or in space with great difficulties.