VIII Southern-Summer School on Mathematical Biology

Roberto André Kraenkel, *IFT*

http://www.ift.unesp.br/users/kraenkel

Lecture II

São Paulo, January 2019

Outline

Outline

Outline

Outline

Outline

Outline

Outline

Interacting Species

Interacting Species

- We saw that populations (animals, plants, bacteria, etc)

Interacting Species

- We saw that populations (animals, plants, bacteria, etc) do live in networks of trophic interactions that might be quite complex .

Interacting Species

- We saw that populations (animals, plants, bacteria, etc) do live in networks of trophic interactions that might be quite complex .
- Sometimes – as we saw – certain species can be considered effectively non-interacting or self-interacting.

Interacting Species

- We saw that populations (animals, plants, bacteria, etc) do live in networks of trophic interactions that might be quite complex .
- Sometimes – as we saw – certain species can be considered effectively non-interacting or self-interacting.But in many instances, not.

Interacting Species

- We saw that populations (animals, plants, bacteria, etc) do live in networks of trophic interactions that might be quite complex .
- Sometimes – as we saw – certain species can be considered effectively non-interacting or self-interacting.But in many instances, not.Let us see the simplest cases of interacting species.

Interacting Species

- We saw that populations (animals, plants, bacteria, etc) do live in networks of trophic interactions that might be quite complex .
- Sometimes – as we saw – certain species can be considered effectively non-interacting or self-interacting.But in many instances, not.Let us see the simplest cases of interacting species.
- We begin with just two species.

Interacting Species

- We saw that populations (animals, plants, bacteria, etc) do live in networks of trophic interactions that might be quite complex .
- Sometimes – as we saw – certain species can be considered effectively non-interacting or self-interacting.But in many instances, not.Let us see the simplest cases of interacting species.
- We begin with just two species.

Types of interactions

Types of interactions

- We define **three** types of basic interactions between species:
- Predation: the presence of a species **(A)** is detrimental for species**(B)**, but the presence of **(B)** favors **(A)**. Species **(A)** is the predator, and **(B)** is its prey[a].
- Competition: the presence of **(A)** is detrimental for **(B)** and vice-versa.
- Mutualism: the presence of **(A)** favors **(B)** and vice-versa.

[a] Actually, we are using the word *predation* in a broad sense. Technically, we should call this interaction **antagonism**, predation being a special case of it

Types of interactions

- We define **three** types of basic interactions between species:
- Predation: the presence of a species **(A)** is detrimental for species **(B)**, but the presence of **(B)** favors **(A)**. Species **(A)** is the predator, and **(B)** is its prey[a].
- Competition: the presence of **(A)** is detrimental for **(B)** and vice-versa.
- Mutualism: the presence of **(A)** favors **(B)** and vice-versa.

[a] Actually, we are using the word *predation* in a broad sense. Technically, we should call this interaction **antagonism**, predation being a special case of it

Nota bene

There is also the **amensalism** (negative for one species, neutral for the other) and the **comensalism** (positive for one species and neutral for the other). Not to speak of **neutralism**.

Predation

Predation

- **Predation** is a widespread interaction between species.

Predation

- Predation is a widespread interaction between species.
- Ecologically, it is a direct interaction.

Predation

- **Predation** is a widespread interaction between species.
- Ecologically, it is a direct interaction.
- Let us now proceed to describe a mathematical model for it.

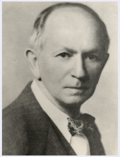
Predation

- **Predation** is a widespread interaction between species.
- Ecologically, it is a direct interaction.
- Let us now proceed to describe a mathematical model for it.
- This is known as the *Lotka-Volterra* model.

Lotka and Volterra

Muoiono gl'imperi, ma i teoremi d'Euclide conservano eterna giovinezza (Volterra)

Vito Volterra (1860-1940), an Italian mathematician, proposed the equation now known as the Lotka-Volterra one to undestand a problem proposed by his futer son-in-law , Umberto d'Ancona, who tried to explain oscillations in the quantity of predator fishes captured at the certain ports of the Adriatic sea.



Alfred Lotka (1880-1949),was an USA mathematician and chemist,born in Ukraine, who tried to transpose the principles of physical-chemistry to biology. He published his results in a book called "Elements of Physical Biology", dedicated to the memory of Poynting. His results are independent from the work of Volterra.

The Lotka-Volterra equations

Let

- $\boldsymbol{N(t)}$ be the number of predators,
- $\boldsymbol{V(t)}$ the number of preys.

In what follows, $\boldsymbol{a}$, $\boldsymbol{b}$, $\boldsymbol{c}$ e $\boldsymbol{d}$ are positive constants

The Lotka-Volterra equations

O number of prey will increase when there are no predators:

$$\frac{dV}{dt} = aV$$

The Lotka-Volterra equations

But the presence of predators should decrease the growth rate of prey:

$$\frac{dV}{dt} = V(a - bP)$$

The Lotka-Volterra equations

On the other hand the population of predators should decrease in the absence of prey :

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = -dP$$

The Lotka-Volterra equations

and presence of prey will increase the number of predators:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

The Lotka-Volterra equations

These two coupled equations ate known as

The Lotka-Volterra equations

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

Let's study them!

Lotka-Volterra: analysis

- We have **nice** equations.

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways
  - Numerical integration.

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways
  - Numerical integration. What's that?

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways
  - Numerical integration. What's that?
  - Qualitative analysis.

ICTP SAIFR

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways
  - Numerical integration. What's that?
  - Qualitative analysis. What's that?

Lotka-Volterra: analysis

- We have **nice** equations.
- But we do not know their solution.
- These equation do not have solutions in terms of elementary functions.
- What can we do?
- Two ways
  - Numerical integration. What's that?
  - Qualitative analysis. What's that?

Lotka-Volterra: qualitative analysis

- Let's get back to the equations:

Lotka-Volterra: qualitative analysis

- Let's get back to the equations:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

Lotka-Volterra: qualitative analysis

- Let's get back to the equations:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

- The second divided by the first:

Lotka-Volterra: qualitative analysis

- Let's get back to the equations:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

- The second divided by the first:

$$\frac{dP}{dV} = \frac{P(cV - d)}{V(a - bP)}$$

ICTP SAIFR

Lotka-Volterra: qualitative analysis

- Let's get back to the equations:

$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

- The second divided by the first:

$$\frac{dP}{dV} = \frac{P(cV - d)}{V(a - bP)}$$

- So that:

$$\frac{dP(a - bP)}{P} = \frac{dV(cV - d)}{V}$$

....

- $$\frac{dP(a-bP)}{P}=\frac{dV(cV-d)}{V}$$

....

- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$
- Integrate on both sides:

....

- $$\frac{dP(a - bP)}{P} = \frac{dV(cV - d)}{V}$$

- Integrate on both sides:

$$a \ln P - bP = cV - d \ln V + H$$

....

- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$
- Integrate on both sides:
$$a \ln P - bP = cV - d \ln V + H$$
where H is a constant.

....

- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$
- Integrate on both sides:
  $$a \ln P - bP = cV - d \ln V + H$$
  where H is a constant.
- In other words:
  $$c\mathbf{V}(\mathbf{t}) + b\mathbf{P}(\mathbf{t}) - a \ln \mathbf{P}(\mathbf{t}) - d \ln \mathbf{V}(\mathbf{t}) = H$$

- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$

- Integrate on both sides:

$$a\ln P - bP = cV - d\ln V + H$$

  where H is a constant.

- In other words:

$$c\mathbf{V}(\mathbf{t}) + b\mathbf{P}(\mathbf{t}) - a\ln\mathbf{P}(\mathbf{t}) - d\ln\mathbf{V}(\mathbf{t}) = H$$

- This is a relation that has to be fulfilled by the solution of the Lotka-Volterra system of equations.

....

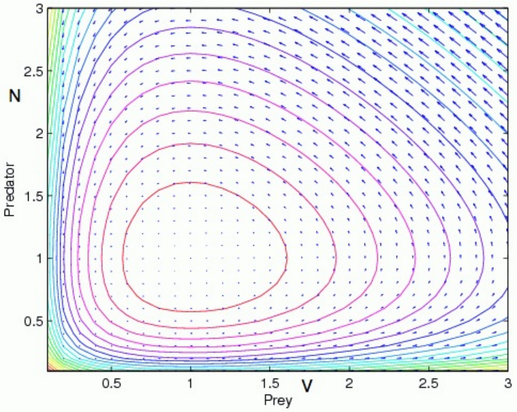
- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$
- Integrate on both sides:
  $$a \ln P - bP = cV - d \ln V + H$$
  where H is a constant.
- In other words:
  $$c\mathbf{V(t)} + b\mathbf{P(t)} - a \ln \mathbf{P(t)} - d \ln \mathbf{V(t)} = H$$
- This is a relation that has to be fulfilled by the solution of the Lotka-Volterra system of equations.
- For a given value of H we can plot on the $P \times V$ plane the geometric locus of the points that obey the above relation.

ICTP SAIFR

- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$
- Integrate on both sides:
  $$a \ln P - bP = cV - d \ln V + H$$
  where H is a constant.
- In other words:
  $$c\mathbf{V(t)} + b\mathbf{P(t)} - a \ln \mathbf{P(t)} - d \ln \mathbf{V(t)} = H$$
- This is a relation that has to be fulfilled by the solution of the Lotka-Volterra system of equations.
- For a given value of H we can plot on the $P \times V$ plane the geometric locus of the points that obey the above relation. Let's do it!.

- $$\frac{dP(a-bP)}{P} = \frac{dV(cV-d)}{V}$$
- Integrate on both sides:
  $$a \ln P - bP = cV - d \ln V + H$$
  where H is a constant.
- In other words:
  $$c\mathbf{V(t)} + b\mathbf{P(t)} - a \ln \mathbf{P(t)} - d \ln \mathbf{V(t)} = H$$
- This is a relation that has to be fulfilled by the solution of the Lotka-Volterra system of equations.
- For a given value of H we can plot on the $P \times V$ plane the geometric locus of the points that obey the above relation. Let's do it!.

Phase trajectories



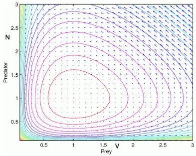
$$\frac{dV}{dt} = V(a - bP)$$

$$\frac{dP}{dt} = P(cV - d)$$

The phase trajectories of the Lotka-Volterra equations, with $a = b = c = d = 1$. Each curve corresponds to a given value of H. The curves obey: $c\mathbf{V}(\mathbf{t}) + b\mathbf{P}(\mathbf{t}) - a \ln \mathbf{P}(\mathbf{t}) - d \ln \mathbf{V}(\mathbf{t}) = H$

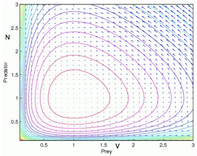
Lotka-Volterra: oscillations

Lotka-Volterra: oscillations



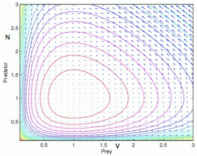
- We call the $P \times V$ plane, the phase space.

Lotka-Volterra: oscillations



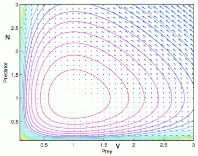
- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.

Lotka-Volterra: oscillations



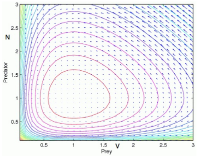
- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*

Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

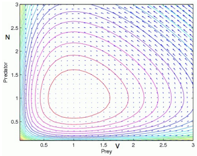
Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.

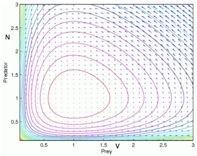
Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.
- It represents a certain number of predators and prey.

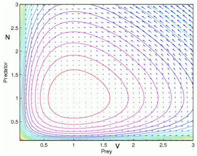
Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.
- It represents a certain number of predators and prey.
- There is a trajectory passing by this point.

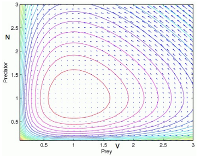
Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.
- It represents a certain number of predators and prey.
- There is a trajectory passing by this point.
- As time passes by, these populations evolve according go the trajectory in phase space.

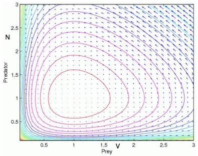
Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.
- It represents a certain number of predators and prey.
- There is a trajectory passing by this point.
- As time passes by, these populations evolve according go the trajectory in phase space.
- After a certain amount of time, they will come back to the initial point.

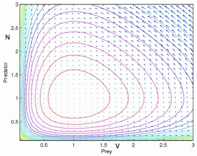
Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.
- It represents a certain number of predators and prey.
- There is a trajectory passing by this point.
- As time passes by, these populations evolve according go the trajectory in phase space.
- After a certain amount of time, they will come back to the initial point.
- This system is periodic.

Lotka-Volterra: oscillations



- We call the $P \times V$ plane, the phase space.
- The curves are called **trajectories** or the **orbits**.
- In theis case, we have *closed orbits.*
- What do they represent?

- Take a point in the phase phase.
- It represents a certain number of predators and prey.
- There is a trajectory passing by this point.
- As time passes by, these populations evolve according go the trajectory in phase space.
- After a certain amount of time, they will come back to the initial point.
- This system is periodic.

Oscillations II

Oscillations II

- Ok, the system is **periodic.**

Oscillations II

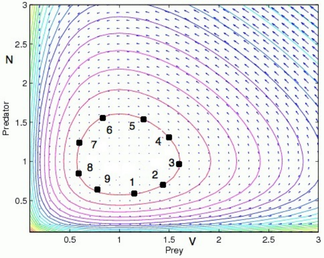
- Ok, the system is **periodic.**
- Let's take a closer look.

Oscillations II

- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:

Oscillations II

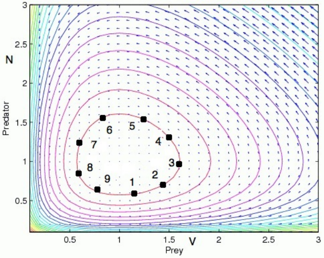
- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



ICTP SAIFR

Oscillations II

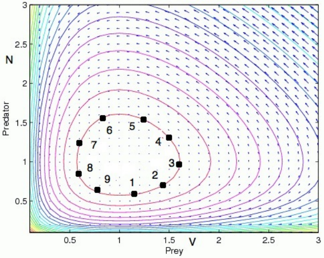
- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).

Oscillations II

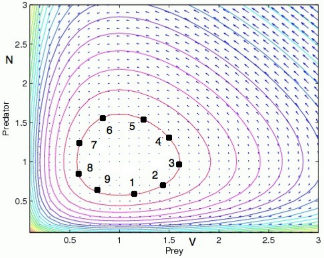
- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.

Oscillations II

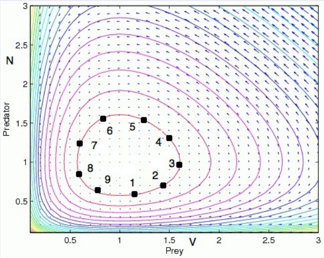
- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.

Oscillations II

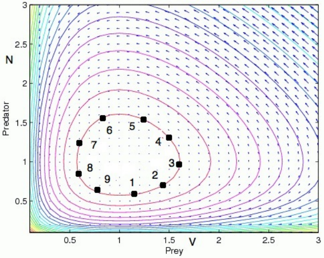
- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.
- and from 8 to 3 it increases again

Oscillations II

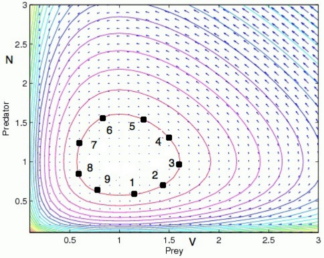
- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.
- and from 8 to 3 it increases again
- and so on.

Oscillations II

- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:

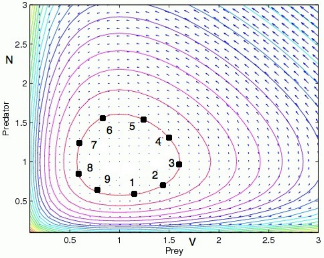


- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.
- and from 8 to 3 it increases again
- and so on.

The number of prey oscillates periodically in time.

Oscillations II

- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.
- and from 8 to 3 it increases again
- and so on.

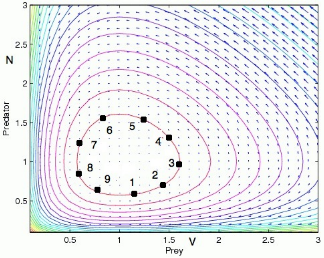
The number of prey oscillates periodically in time.

and the predators so the same.

ICTP SAIFR

Oscillations II

- Ok, the system is **periodic.**
- Let's take a closer look.
- Take a point in the $P \times V$ plane and follow it in time:



- Let us see how the variable V evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.
- and from 8 to 3 it increases again
- and so on.

The number of prey oscillates periodically in time.

and the predators so the same.

What about the solutions

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot:

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But,

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?.

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?. *The real thing!*.

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?. *The real thing!*.
- We can show a plot of them .

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?. *The real thing!*.
- We can show a plot of them . Where does it come from?

What about the solutions

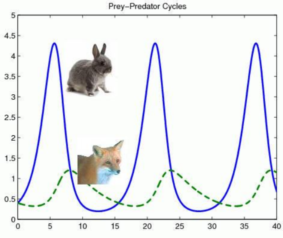
- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?. *The real thing!*.
- We can show a plot of them . Where does it come from? Numerical integration.

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?. *The real thing!*.
- We can show a plot of them . Where does it come from? Numerical integration.
- Here it is:

What about the solutions

- Until now we saw how the solutions of the de Lotka-Volterra equations behave **qualitatively**.
- That's a lot: we can predict that the "predator-prey" system presents **periodic oscillations** of the species populations.
- But, and solutions ?. *The real thing!*.
- We can show a plot of them . Where does it come from? Numerical integration.
- Here it is:



More about Lotka-Volterra

More about Lotka-Volterra

In words...

- Lotka-Volterra equations tell us that:
  - Given a small number of predators and a certain number (not small) of prey ;
  - The availability of prey makes the population of predators grow;
  - And therefore the prey population will grow slower. After a certain amount of time, it will begin to decrease ;
  - And predators attain a maximal population, and – because the lack of enough prey – it's population begins to decrease;
  - Meanwhile, prey get to a minimum and begin to recover, as the number of predators has decreased;
  - and so on....

More about Lotka-Volterra

In words...

- Lotka-Volterra equations tell us that:
  - Given a small number of predators and a certain number (not small) of prey ;
  - The availability of prey makes the population of predators grow;
  - And therefore the prey population will grow slower. After a certain amount of time, it will begin to decrease ;
  - And predators attain a maximal population, and – because the lack of enough prey – it's population begins to decrease;
  - Meanwhile, prey get to a minimum and begin to recover, as the number of predators has decreased;
  - and so on....
- Makes sense!

More about Lotka-Volterra

In words...

- Lotka-Volterra equations tell us that:
  - Given a small number of predators and a certain number (not small) of prey ;
  - The availability of prey makes the population of predators grow;
  - And therefore the prey population will grow slower. After a certain amount of time, it will begin to decrease ;
  - And predators attain a maximal population, and – because the lack of enough prey – it's population begins to decrease;
  - Meanwhile, prey get to a minimum and begin to recover, as the number of predators has decreased;
  - and so on....
- Makes sense!
- **But, is it true?**

The real world

- Does the Lotka-Volterra equations describe real situations?
- Partially.
- There are some elements that are clearly not realistic:
  - The growth of prey in the absence of predator is exponential; it does not saturate.
    - No big deal. Just put a logistic term there. We can still have oscillating solutions. Great!
  - On the other hand... the growth rate of the predator is given by $(cV - d)$.
  - The larger V, the higher the rate. This predator is voracious!
  - It would be rather natural to suppose that the conversion rate also saturates. An effect of the predators becoming satiated

The real world

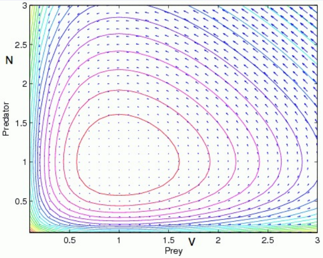
- Does the Lotka-Volterra equations describe real situations?
- Partially.
- There are some elements that are clearly not realistic:
  - The growth of prey in the absence of predator is exponential; it does not saturate.
    - No big deal. Just put a logistic term there. We can still have oscillating solutions. Great!
  - On the other hand... the growth rate of the predator is given by $(cV - d)$.
  - The larger V, the higher the rate. This predator is voracious!
  - It would be rather natural to suppose that the conversion rate also saturates. An effect of the predators becoming satiated or because there is handling time to consume prey.
  - We can modify the above equations to take this into account.
- Cycling can still be present.

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



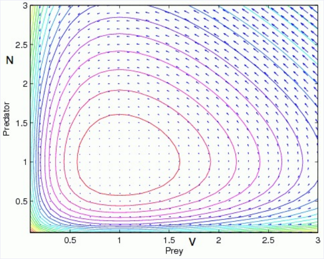
- Say you are on a certain orbit in the phase space, It has certain amplitude and period.

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



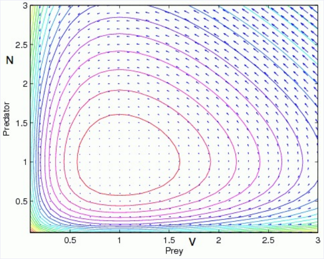
- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning:

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



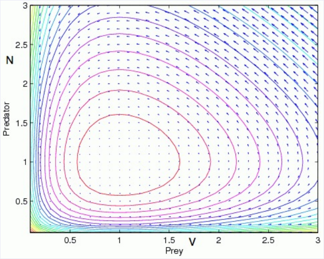
- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning: **Bad news**.

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



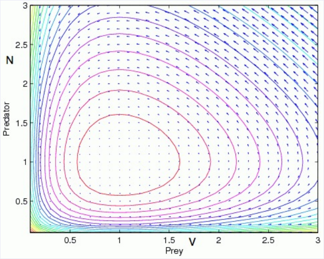
- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning: Bad news.Why?

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



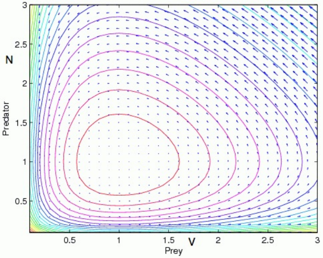
- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning: Bad news.Why?
- As real systems are under perturbations all the time, they would jump between trajectories and would not be effectively periodic.

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



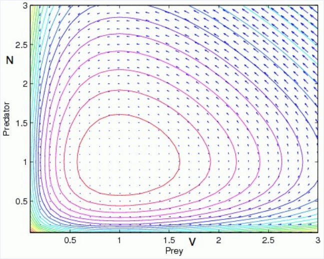
- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning: Bad news.Why?
- As real systems are under perturbations all the time, they would jump between trajectories and would not be effectively periodic.
- Real predator-prey oscillations would be better described by limit-cycles.

Glory and Misery of the Lotka-Volterra Equations

Glory

- The lesson of the Lotka-Volterra equation is: although being an oversimplified equation for predator-prey system it captures an important feature: this kind of system exhibits oscillations – which are intrinsic to the dynamics.

Misery



- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning: Bad news.Why?
- As real systems are under perturbations all the time, they would jump between trajectories and would not be effectively periodic.
- Real predator-prey oscillations would be better described by limit-cycles. What's a limit cycle???

Further beyond the Lotka-Volterra equations

- Obviously real interactions occur in interaction webs that can involve many species through predation, competition and mutualism.

Further beyond the Lotka-Volterra equations

- Obviously real interactions occur in interaction webs that can involve many species through predation, competition and mutualism.
- Simple questions:
  - Whereupon does the prey feed?
  - This is not taken into account in the Lotka-Volterra equations.
  - If resource availability for prey is approximatively constant than a (generalized) Lotka-Volterra dynamics is maybe a good model.
  - But, on the other hand, the possibility exists that the prey and its resource are dynamically coupled... In this case we need to consider at least three species.
  - But beware!!! Do not try to put all species in a model.
- In summary, the Lotka-Volterra equations are rather a staring point than a final point for predator-prey models. .

A last comment

Host-parasitoid relations

- In close relation to the predator-prey dynamics there is the relation a parasitoid and its host ,
- The parasitoid plays a role analogous to the one of the predator and the host, that of the prey.
- Although these may be seen as different biological interactions, the dynamics is similarly described.

A last comment

Host-parasitoid relations

- In close relation to the predator-prey dynamics there is the relation a parasitoid and its host ,
- The parasitoid plays a role analogous to the one of the predator and the host, that of the prey.
- Although these may be seen as different biological interactions, the dynamics is similarly described.
- Note, however, that many insect species have non-overlaping generations.
- which takes us to the realm of discrete-time equations, or coupled mappings.

What I should remember

- Two-species interactions are the building blocks of larger networks of interactions:
- In a rough way, we can divide them as:
  - **predator-prey;**
  - **competition;**
  - **mutualism.**
- Predator-Prey tend to produce oscillations.
- Just don't forget that not every oscillation comes from a predator-prey dynamics.

Bibliography

- J.D. Murray: *Mathematical Biology I* (Springer, 2002)
- G.E. Hutchinson: *An Introduction to Population Ecology* (Yale, 1978).
- N.F. Britton: *Essential Mathematical Biology* (Springer, 2003).
- N.J. Gotelli: *A Primer of Ecology* (Sinauer, 2001).
- E. Renshaw: *Modelling Biological Populations in Space and Time* (CUP 2001).
- M. Kot: *Elements of Mathematical Ecology* (CUP 2001).
- P. Turchin *Complex population Dynamics* (Princeton U.P 2003)

Online Resources

- http://ecologia.ib.usp.br/ssmb/

Thank you for your attention