# III Southern-Summer School on Mathematical Biology 

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Lecture II

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## Outline

(1) Interacting Species

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(2) Predation

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(3) Lotka-Volterra

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(5) Glory and Misery of the Lotka-Volterra Equations

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(6) Further beyond the Lotka-Volterra equations

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(1) Interacting Species
(2) Predation
(3) Lotka-Volterra

4 Beyond Lotka-Volterra
(5) Glory and Misery of the Lotka-Volterra Equations

6 Further beyond the Lotka-Volterra equations
(7) Final comments

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## Types of interactions

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- 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 $(B)$ is 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.
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- 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 $(B)$ is favors (A). Species (A) is the predator, and (B) is its prey ${ }^{2}$.
- Competition: the presence of $(A)$ is detrimental for $(B)$ and vice-versa.
- Mutualism: the presence of $(A)$ favors $(B)$ and vice-versa.
> ${ }^{2}$ Actually, we are using the word predation in a wide 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.

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- 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)




#### Abstract

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

- $N(t)$ be the number of predators,
- $V(t)$ the number of preys.

In what follows, $a, b, c$ e $d$ are positive constants

## The Lotka-Volterra equations

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

$$
\frac{d V}{d t}=a V
$$

## The Lotka-Volterra equations

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

$$
\frac{d V}{d t}=V(a-b P)
$$

## The Lotka-Volterra equations

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

$$
\frac{d V}{d t}=V(a-b P)
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$$
\frac{d P}{d t}=-d P
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## The Lotka-Volterra equations

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These two coupled equations ate known as
The Lotka-Volterra equations

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\frac{d V}{d t}=V(a-b P)
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\frac{d P}{d t}=P(c V-d)
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Let's study them!

## Lotka-Volterra: analysis

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- So that:

$$
\frac{d P(a-b P)}{P}=\frac{d V(c V-d)}{V}
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- Integrate on both sides:

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- Nn other words:

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c \mathbf{V}(\mathrm{t})-b \mathrm{P}(\mathrm{t})+a \ln \mathrm{P}(\mathrm{t})+d \ln \mathrm{~V}(\mathrm{t})=H
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## Phase trajectories



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& \frac{d V}{d t}=V(a-b P) \\
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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: $c \mathrm{~V}(\mathrm{t})-b \mathrm{P}(\mathrm{t})+a \ln \mathrm{P}(\mathrm{t})+d \ln \mathrm{~V}(\mathrm{t})=H$

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from 3 to 8 it decreases.

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## More about Lotka-Volterra

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## 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....


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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 $(c V-d)$.

The larger $V$, the higher the rate. This predator is voracious!
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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.


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- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning:


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- Meaning: Bad news.


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- 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

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- 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.


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- 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.


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- 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.


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## Online Resources

- http://www.ictp-saifr.org/mathbio3
- http://ecologia.ib.usp.br/ssmb/

Thank you for your attention


[^0]:    ${ }^{a}$ Actually, we are using the word predation in a wide sense. Technically, we should call this interaction antagonism, predation being a special case of it

