III Southern-Summer School on Mathematical Biology

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Lecture II

São Paulo, February 2014



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- Interacting Species
- 2 Predation



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- Predation
- 3 Lotka-Volterra



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- Beyond 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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- 5 Glory and Misery of the Lotka-Volterra Equations
- 6 Further beyond the Lotka-Volterra equations
- 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 <u>detrimental</u> for species(B), but the presence of (B) is <u>favors</u> (A). Species (A) is the predator, and (B) is its <u>prey</u>^a.
- Competition: the presence of (A) is <u>detrimental</u> for (B) and vice-versa.
- Mutualism: the presence of (A) <u>favors</u> (B) and vice-versa.

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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.

COMIL

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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)



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.



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



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

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



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

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



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

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

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



and presence of prey will increase the number of predators:

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

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





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!



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- But we do not know their solution.



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So that:

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





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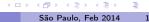
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$$a \ln P - bP = cV - d \ln V + H$$





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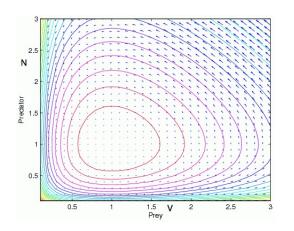
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Phase trajectories

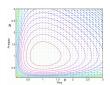


$$\frac{dV}{dt} = V(a - bP)$$

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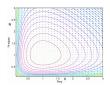
The phase trajectories of the Lotka-Volterra equations, with a=b=c=d=1. Each curve corresponds to a given value of H. The curves obey: $cV(t)-bP(t)+a\ln P(t)+d\ln V(t)=H$





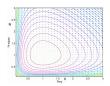
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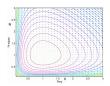
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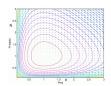
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- In theis case, we have *closed orbits*.
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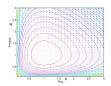




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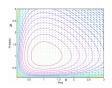
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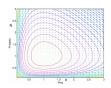
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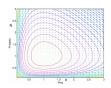
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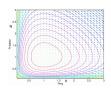
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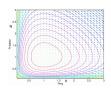
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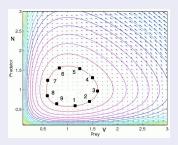
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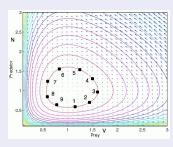


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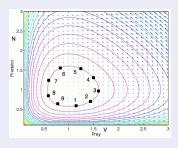
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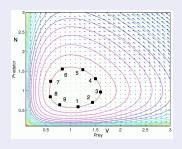


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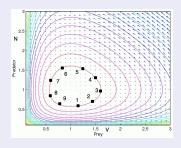


- Let us see how the variable *V* evolves (prey).
- from 1 to 3 it increases.
- from 3 to 8 it decreases.





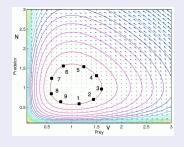
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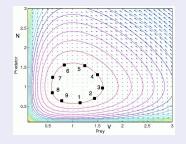
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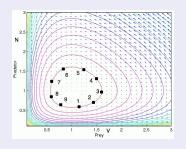


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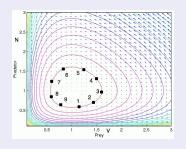
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In words...

- 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;
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 - 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).
 - \triangleright The larger V, the higher the rate. This predator is voracious!
 - It would be rather natural to suppose that the conversion rate also <u>saturates</u>. 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.

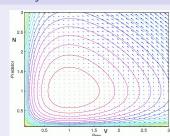
 No big deal. Just put a logistic term there. We can still have oscillating solutions. Great!
 - On the other hand... the growth rate of the predator is given by (cV d).
 - The larger V, the higher the rate. This predator is voracious!
 - It would be rather natural to suppose that the conversion rate also <u>saturates</u>. An effect of the predators becoming satiated or because there is handling time to consume prev.
 - We can modify the above equations to take this into account.
- Cycling can still be present.



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.

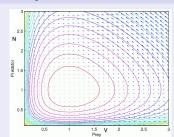




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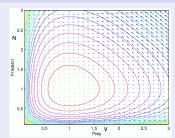
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- Say you are on a certain orbit in the phase space, It has certain amplitude and period.
- If you perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- Meaning:

Glory

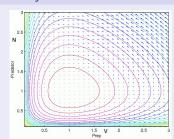
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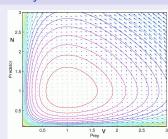
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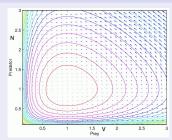
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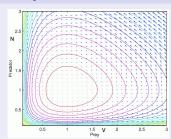
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- Real predator-prey oscillations would be better described by limit-cycles. What's a limit cycle???

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.



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

Thank you for your attention

