# IX Southern-Summer School on Mathematical Biology Lecture I

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Populations



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- Populations
- 2 Simple Models I: Malthus



Populations

Simple Models I: Malthus

3 Simple Models II: the logistic



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- 3 Simple Models II: the logistic
- 4 Generalizations



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- Comments
  - Scales
  - More Species



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This school is about understanding the dynamical behavior of populations (how the change in size, how they use space) by means of mathematical formulations.





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# Simple Models I: Malthus



Figura: Thomas Malthus, circa 1830



# Simple Models I: Malthus

#### The simplest law

 The simplest law governing the time variation of the size of a population

0

$$\frac{dN(t)}{dt} = rN(t)$$

 where N(t) is the number os individuals in the population and r is the intrinsic growth rate of the population, sometimes called the Malthusian parameter.

This equation says that the *per capita* growth rate of the population is independent of the number of individuals in the population.





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#### Back-of-the-Envelope calculation

How long would take to cover the whole earth with a thin film of E. coli?

& OHITH

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## Examples

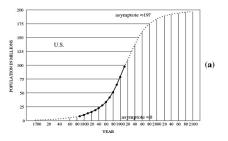


Figura: The population of USA . Until 1920, the growth is well approximated by an exponential.



## Examples

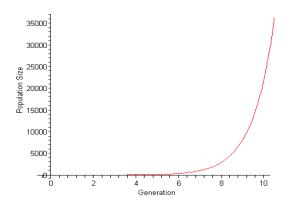


Figura: (Escherichia coli) on a Petri dish





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- The term  $-N^2/K$  is always negative ( we assume K > 0),  $\Rightarrow$  it contributes negatively to  $\frac{dN}{dt}$   $\Rightarrow$  it tends to slow down growth.
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- This equation is called the logistic equation, or Verhulst's.







Figura: Pierre-François Verhust, first introduced the logistic em 1838: "Notice sur la loi que la population pursuit dans son accroissement". On the right side, , Raymond Pearl, who "rediscovered"Verhust's work.

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• Here is a plot of the solution, for different values of  $N_0$ :



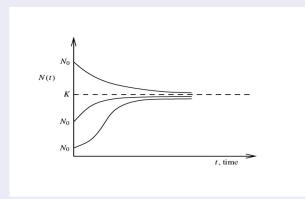


Figura: Temporal evolution of a population described by solution of the logistic equation. Each curve corresponds to a different initial condition. For all initial conditions ,  $t \to \infty$ , we have  $N \to K$ 



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- Or still: K is an attractor.



• The quadratic term  $(rN^2/K)$  in the logistic equation

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models the internal competition in a population for vital resources as:



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- This is called intra-specific competition



Water lilies on a pond, compete for space:







Trees in the Amazonian forest compete for light:



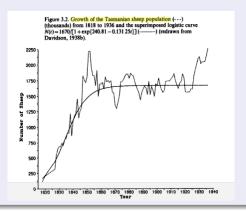


But in semi-arid regions, competition is for water





#### Here is a plot of the Tasmanian sheep population







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- The carrying capacity is "phenomenological parameter"that depends on the particular environment, on the species and all circumstances affecting population maintenance.
- ullet As we already saw, the population takes the value  ${\it K}$  for large times.



# Glory and Misery of the logistic equation



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São Paulo, Jan. 2020

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Gompertz growth in tumors (see Kot)

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## Comments: Human population

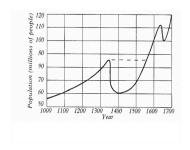


Figura: Europe's population between 1000 e 1700



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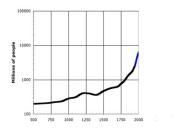


Figura: Earth population between 500 and 2000



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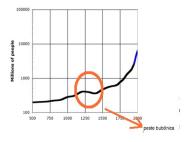


Figura: Earth population between 500 and 2000, highlighting the effects of bubonic plague .



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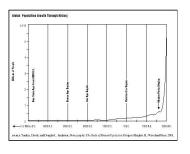


Figura: Estimated Earth's population between -4000 e 2000



# Comments: Human population

- As we look at the Human population at different space and time scales, we see different traits...
- Every mathematical model has limited validity.



#### What about interactions?

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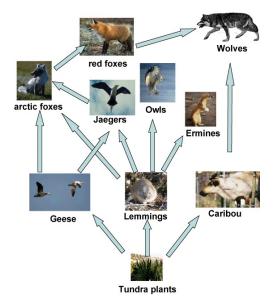
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- Thus: "populations are in fact inter-dependent..".
- The networks involved can be quite complex.



# Trophic network, Arctic region





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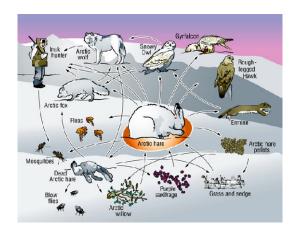


Figura: Simplified trophic network in the Arctic



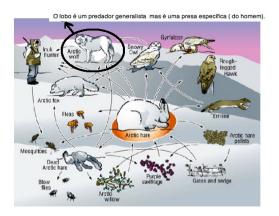


Figura: The wolf preys on many species, but its is itself a prey of a specialist predator. The coupling with human population can be strong.





Figura: The gyrfalcon depends essentially on the the artic hare.



São Paulo, Jan. 2020

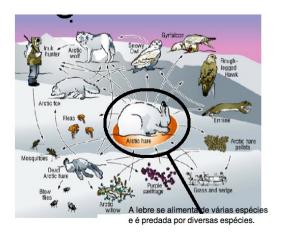


Figura: The Arctic hare is a generalist that is prey to other generalists. Single species models may apply.

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# Time delay



Our basic model



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assumes that the rate of change of  ${\it N}$  at time  ${\it t}$  depends only on  ${\it N}$  at time  ${\it t}$ .



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• Good look.



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## Bibliography

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



#### Online Resources

- http://www.ictp-saifr.org/ix-southern-summer-school-on-mathematical-biology/
- http://ecologia.ib.usp.br/ssmb/

Thank you for your attention

