III Southern-Summer School on Mathematical Biology

Roberto André Kraenkel, *IFT*

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

Lecture I

São Paulo, February 2014

Outline

1. Populations

Outline

Outline

Outline

Outline

Outline

Outline

Populations

- *Population* will be a primitive concept for us.

Populations

- *Population* will be a primitive concept for us.
  - It concerns groups of living organisms (plants, animals, micro-organisms..) which are composed of individuals with a similar dynamical behavior.

Populations

- *Population* will be a primitive concept for us.
  - It concerns groups of living organisms (plants, animals, micro-organisms..) which are composed of individuals with a similar dynamical behavior.
  - We postulate that every living organism has arisen from another one, *omne vivum ex vivo*, to use the formulation of G.E. Hutchinson.

Populations

- *Population* will be a primitive concept for us.
  - It concerns groups of living organisms (plants, animals, micro-organisms..) which are composed of individuals with a similar dynamical behavior.
  - We postulate that every living organism has arisen from another one, *omne vivum ex vivo*, to use the formulation of G.E. Hutchinson.Therefore populations reproduce.
  - Note: we will study populations and not the individuals.

Populations

- *Population* will be a primitive concept for us.
  - It concerns groups of living organisms (plants, animals, micro-organisms..) which are composed of individuals with a similar dynamical behavior.
  - We postulate that every living organism has arisen from another one, *omne vivum ex vivo*, to use the formulation of G.E. Hutchinson.Therefore populations reproduce.
  - Note: we will study populations and not the individuals.
- Populations change in size, they grow or decrease due to birth, death, migration.

Populations

- *Population* will be a primitive concept for us.
  - It concerns groups of living organisms (plants, animals, micro-organisms..) which are composed of individuals with a similar dynamical behavior.
  - We postulate that every living organism has arisen from another one, *omne vivum ex vivo*, to use the formulation of G.E. Hutchinson.Therefore populations reproduce.
  - Note: we will study populations and not the individuals.
- Populations change in size, they grow or decrease due to birth, death, migration.

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

The basic framework

The basic framework

- We want to study laws that govern population changes in space and time

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time.

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).
  - We will first study unstructured populations, but let us not forget that structured populations may also be important. Here "structure"means classes of age, size, sex,...

ICTP SAIFR

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).
  - We will first study unstructured populations, but let us not forget that structured populations may also be important. Here "structure"means classes of age, size, sex,...
- *Secondo* : we need to describe the time variation of the population.

ICTP SAIFR

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).
  - We will first study unstructured populations, but let us not forget that structured populations may also be important. Here "structure"means classes of age, size, sex,...
- *Secondo* : we need to describe the time variation of the population. We will use derivatives to do so.

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).
  - We will first study unstructured populations, but let us not forget that structured populations may also be important. Here "structure"means classes of age, size, sex,...
- *Secondo* : we need to describe the time variation of the population. We will use derivatives to do so. Alternatively, we could also work with stochastic processes or discrete-time formulations...

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).
  - We will first study unstructured populations, but let us not forget that structured populations may also be important. Here "structure"means classes of age, size, sex,...
- *Secondo* : we need to describe the time variation of the population. We will use derivatives to do so. Alternatively, we could also work with stochastic processes or discrete-time formulations...
- *Terzo* : we need to know what causes these time variations. Which biological processes. Then we have to translate in mathematical language how these biological processes affect the time-changes of the population.

The basic framework

- We want to study laws that govern population changes in space and time
- We begin by restricting our study to how populations change in time. We call these changes *dynamical*. Our basic framework is
- *Primo*: a population is described by its number of individuals (in some cases, however, by the biomass).
  - We will first study unstructured populations, but let us not forget that structured populations may also be important. Here "structure"means classes of age, size, sex,...
- *Secondo* : we need to describe the time variation of the population. We will use derivatives to do so. Alternatively, we could also work with stochastic processes or discrete-time formulations...
- *Terzo* : we need to know what causes these time variations. Which biological processes. Then we have to translate in mathematical language how these biological processes affect the time-changes of the population.

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
- $$\frac{dN(t)}{dt} = rN(t)$$
- where $N(t)$ is the number os individuals in the population and r is the intrincsic growth rate of the population, sometimes called the *Malthusian parameter*.

Exponential Growth

The solution

Exponential Growth

The solution

The solution to the Malthusian equation is just:

Exponential Growth

The solution

The solution to the Malthusian equation is just:

$$N(t) = N_0 e^{rt}$$

Exponential Growth

The solution

The solution to the Malthusian equation is just:

$$N(t) = N_0 e^{rt}$$

- This equation predicts exponential growth.

Exponential Growth

The solution

The solution to the Malthusian equation is just:

$$N(t) = N_0 e^{rt}$$

- This equation predicts exponential growth.
- Obviously impossible!

Exponential Growth

The solution

The solution to the Malthusian equation is just:

$$N(t) = N_0 e^{rt}$$

- This equation predicts exponential growth.
- Obviously impossible!

Back-of-the-Envelope calculation

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

Exponential Growth

- Although exponential growth is, *stricto sensu*, impossible, we can have phases of exponential growth. These are usually the initial phases of growth, when the population is unchecked.

Exponential Growth

- Although exponential growth is, *stricto sensu*, impossible, we can have phases of exponential growth. These are usually the initial phases of growth, when the population is unchecked.
- In other words, when the population becomes too large something must happen, so that the growth rate is depleted.

Exponential Growth

- Although exponential growth is, *stricto sensu*, impossible, we can have phases of exponential growth. These are usually the initial phases of growth, when the population is unchecked.
- In other words, when the population becomes too large something must happen, so that the growth rate is depleted.
- Before going into this, some examples:

Exponential Growth

- Although exponential growth is, *stricto sensu*, impossible, we can have phases of exponential growth. These are usually the initial phases of growth, when the population is unchecked.
- In other words, when the population becomes too large something must happen, so that the growth rate is depleted.
- Before going into this, some examples:

Examples

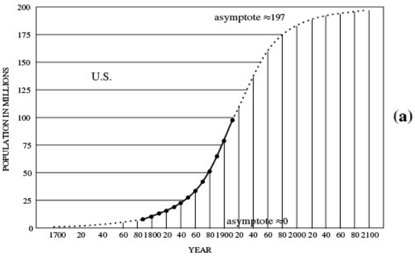


Figura : The population of USA . Until 1920, the growth is well approximated by an exponential.

Examples

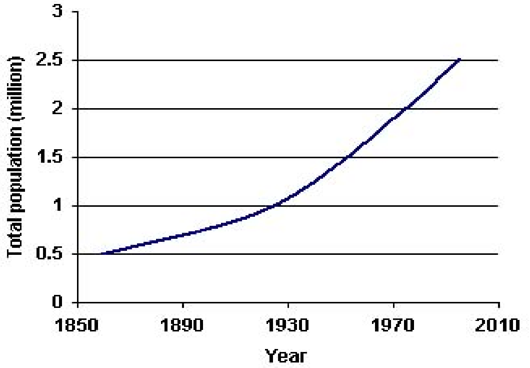


Figura : The population of Jamaica, between 1860 e 195l.

Examples

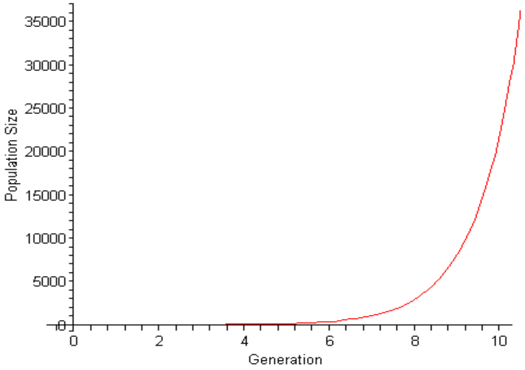


Figura : (*Escherichia coli*) on a Petri dish

Simple Models II: the logistic equation

Simple Models II: the logistic equation

- We will further postulate that there is an upper limit for the number of beings that can occupy a finite portion of space.

Simple Models II: the logistic equation

- We will further postulate that there is an upper limit for the number of beings that can occupy a finite portion of space.
- The simplest way to introduce this mathematically is to modify the Malthusian equation :

Simple Models II: the logistic equation

- We will further postulate that there is an upper limit for the number of beings that can occupy a finite portion of space.
- The simplest way to introduce this mathematically is to modify the Malthusian equation :
- $$\frac{dN}{dt} = rN(1 - N/K)$$

Simple Models II: the logistic equation

- We will further postulate that there is an upper limit for the number of beings that can occupy a finite portion of space.
- The simplest way to introduce this mathematically is to modify the Malthusian equation :
- $$\frac{dN}{dt} = rN(1 - N/K)$$
- 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.
- For $N/K \ll 1$, we may take $1 - N/K \sim 1$ and we revover the Malthusian equation.

Simple Models II: the logistic equation

- We will further postulate that there is an upper limit for the number of beings that can occupy a finite portion of space.
- The simplest way to introduce this mathematically is to modify the Malthusian equation :
- $$\frac{dN}{dt} = rN(1 - N/K)$$
- 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.
- For $N/K \ll 1$, we may take $1 - N/K \sim 1$ and we revover the Malthusian equation.
- This equation is called the **logistic equation,** or **Verhulst's.**

Logistic equation

Figura : Pierre-François Verhulst, 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.

Solution of the logistic equation

- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.

Solution of the logistic equation

- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.
- Just take $dt = dN/(rN(1 - n/K))$,

Solution of the logistic equation

- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.
- Just take $dt = dN/(rN(1 - n/K))$, integrate both sides and

Solution of the logistic equation

- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.
- Just take $dt = dN/(rN(1 - n/K))$, integrate both sides and and get:

Solution of the logistic equation

- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.
- Just take $dt = dN/(rN(1 - n/K))$, integrate both sides and and get:
- $$N(t) = \frac{N_0 K e^{rt}}{[K + N_0(e^{rt} - 1)]}$$

Solution of the logistic equation

- It is easy to solve this equation $\frac{dN}{dt} = rN(1 - N/K)$.
- Just take $dt = dN/(rN(1 - n/K))$, integrate both sides and and get:
- $$N(t) = \frac{N_0 K e^{rt}}{[K + N_0(e^{rt} - 1)]}$$
- Here is a plot of the solution, for different values of N_0:

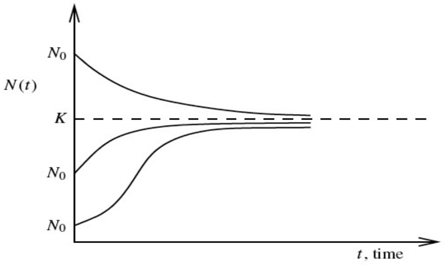


Figura : Temporal evolution of a population described by solution of the logistic equation. Each curve corresponds to a different initial condition. For all initial conditions , $t \to \infty$, we have $N \to K$

In other words...

In other words...

- The equation

$$\frac{dN}{dt} = rN(1 - N/K)$$

  has two fixed points:
  - $N = 0$
  - $N = K$,
- the first being unstable and the second stable

In other words...

- The equation

$$\frac{dN}{dt} = rN(1 - N/K)$$

  has two fixed points:
    - $N = 0$
    - $N = K$,
- the first being unstable and the second stable
- Or still: K is an attractor.

More on the logistic equation

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

$$\frac{dN}{dt} = rN(1 - N/K),$$

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

More on the logistic equation

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

$$\frac{dN}{dt} = rN(1 - N/K),$$

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

More on the logistic equation

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

$$\frac{dN}{dt} = rN(1 - N/K),$$

  models the internal competition in a population for vital resources as:
  - Space,
  - Food .

More on the logistic equation

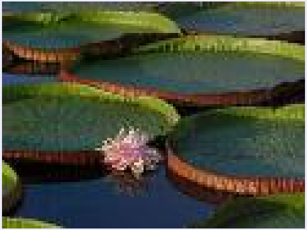
- The quadratic term (rN^2/K) in the logistic equation

$$\frac{dN}{dt} = rN(1 - N/K),$$

  models the internal competition in a population for vital resources as:
  - Space,
  - Food .
- This is called *intra-specific competition*

Logistic equation

Water lilies on a pond, compete for space:



Logistic equation

Trees in the Amazonian forest compete for light:

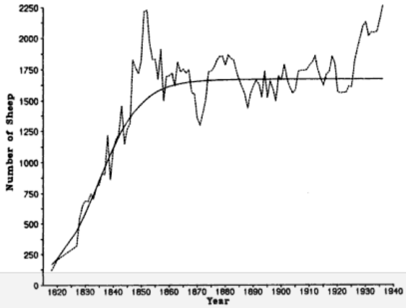
Logistic equation

But in semi-arid regions, competition is for water

Logistic equation

Here is a plot of the Tasmanian sheep population

Figure 3.2. Growth of the Tasmanian sheep population (- - -) (thousands) from 1818 to 1936 and the superimposed logistic curve $N(t) = 1670/[1 + \exp\{240.81 - 0.131\,25t\}]$ (———) (redrawn from Davidson, 1938b).



Nomenclature

Nomenclature

- The constant K that appears in the logistic equation

Nomenclature

- The constant K that appears in the logistic equation

$$\frac{dN}{dt} = rN(1 - N/K)$$

Nomenclature

- The constant *K* that appears in the logistic equation

$$\frac{dN}{dt} = rN(1 - N/K)$$

is usually known by *carrying capacity*.

Nomenclature

- The constant K that appears in the logistic equation

$$\frac{dN}{dt} = rN(1 - N/K)$$

  is usually known by *carrying capacity*.
- The carrying capacity is "phenomenological parameter"that depends on the particular environment, on the species and all circumstances affecting population maintenance.

Nomenclature

- The constant K that appears in the logistic equation

$$\frac{dN}{dt} = rN(1 - N/K)$$

  is usually known by *carrying capacity*.
- The carrying capacity is "phenomenological parameter"that depends on the particular environment, on the species and all circumstances affecting population maintenance.
- As we already saw, the population takes the value K for large times.

Glory and Misery of the logistic equation

Glory and Misery of the logistic equation

Glory

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

ICTP SAIFR

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

- It's too simple

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

- It's too simple
- It does not model more complex biological facts

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

- It's too simple
- It does not model more complex biological facts

So, why should I like the logistic equation?

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

- It's too simple
- It does not model more complex biological facts

So, why should I like the logistic equation?

It's a kind of minimal model whereupon we can build more sophisticated ones.

Glory and Misery of the logistic equation

Glory

- It's simple and its solvable.
- It allows us to introduce the concept of carrying capacity.
- It's a good approximation in several cases.

Misery

- It's too simple
- It does not model more complex biological facts

So, why should I like the logistic equation?

It's a kind of minimal model whereupon we can build more sophisticated ones.

Generalizations

Generalizations

- To go beyond the logistic, but still in the context of single species dynamics, we consider:

Generalizations

- To go beyond the logistic, but still in the context of single species dynamics, we consider:

$$\frac{dN(t)}{dt} = \mathcal{F}(N)$$

Generalizations

- To go beyond the logistic, but still in the context of single species dynamics, we consider:

$$\frac{dN(t)}{dt} = \mathcal{F}(N)$$

where $\mathcal{F}$ is a given function of N.

Generalizations

- To go beyond the logistic, but still in the context of single species dynamics, we consider:

$$\frac{dN(t)}{dt} = \mathcal{F}(N)$$

where $\mathcal{F}$ is a given function of N.

Examples

Examples

- spruce budworm model (see Murray)

$$\mathcal{F}(N) = rN(1 - N/K) - \frac{BN^2}{(A^2 + N^2)}$$

Examples

- spruce budworm model (see Murray)

$$\mathcal{F}(N) = rN(1 - N/K) - \frac{BN^2}{(A^2 + N^2)}$$

- Allee effect (see Edelstein-Keshet)

$$\mathcal{F}(N) = -aN + bN^2 - cN^3$$

ICTP SAIFR

Examples

- spruce budworm model (see Murray)

$$\mathcal{F}(N) = rN(1 - N/K) - \frac{BN^2}{(A^2 + N^2)}$$

- Allee effect (see Edelstein-Keshet)

$$\mathcal{F}(N) = -aN + bN^2 - cN^3$$

- Gompertz growth in tumors (see Kot)

$$\mathcal{F}(N) = -\kappa N \ln N/K$$

Generalizations

Generalizations

- Usually, to study these equations, we do not solve the differential equation.

Generalizations

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:

Generalizations

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:
  - We look for *fixed points*, N^*, given by $\mathcal{F}(N^*) = 0$.

Generalizations

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:
  - We look for *fixed points*, N^*, given by $\mathcal{F}(N^*) = 0$.
  - Once N^* have been determined, we study their stability.

Generalizations

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:
  - We look for *fixed points*, N^*, given by $\mathcal{F}(N^*) = 0$.
  - Once N^* have been determined, we study their stability.
  - Try out with any of the previous equations.....

Generalizations

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:
  - We look for *fixed points*, N^*, given by $\mathcal{F}(N^*) = 0$.
  - Once N^* have been determined, we study their stability.
  - Try out with any of the previous equations.....
- By these means we get a *qualitative* view of the dynamics.

Generalizations

- Usually, to study these equations, we do not solve the differential equation.
- We rather perform a qualitative analysis:
  - We look for *fixed points*, N^*, given by $\mathcal{F}(N^*) = 0$.
  - Once N^* have been determined, we study their stability.
  - Try out with any of the previous equations.....
- By these means we get a *qualitative* view of the dynamics.

Comments I

Scales

- The Malthusian equation introduced a parameter, r,

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.
  - In other words, r^{-1} defines a time scale.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of *time*$^{-1}$.
  - In other words, r^{-1} defines a time scale.
- The logistic brought in one more parameter: K.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.
  - In other words, r^{-1} defines a time scale.
- The logistic brought in one more parameter: K.
  - K defines a scale for population size.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.
  - In other words, r^{-1} defines a time scale.
- The logistic brought in one more parameter: K.
  - K defines a scale for population size.
- Scales, like these ones or still others (space scales, ...) are important.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.
  - In other words, r^{-1} defines a time scale.
- The logistic brought in one more parameter: K.
  - K defines a scale for population size.
- Scales, like these ones or still others (space scales, ...) are important.
- We should always remember that ours models are valid on certain scales.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.
  - In other words, r^{-1} defines a time scale.
- The logistic brought in one more parameter: K.
  - K defines a scale for population size.
- Scales, like these ones or still others (space scales, ...) are important.
- We should always remember that ours models are valid on certain scales.
- Let's see an example.

Comments I

Scales

- The Malthusian equation introduced a parameter, r, which has dimensions of $time^{-1}$.
  - In other words, r^{-1} defines a time scale.
- The logistic brought in one more parameter: K.
  - K defines a scale for population size.
- Scales, like these ones or still others (space scales, ...) are important.
- We should always remember that ours models are valid on certain scales.
- Let's see an example.

Comments: Human population

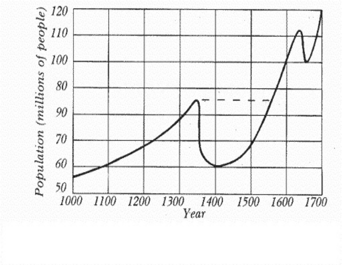


Figura : Europe's population between 1000 e 1700

Comments: Human population

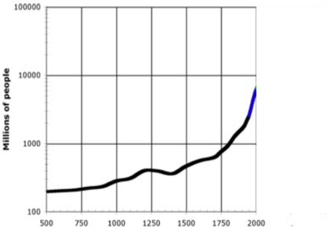


Figura : Earth population between 500 and 2000

Comments: Human population

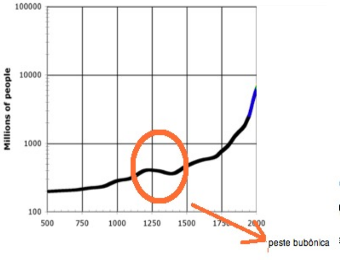


Figura : Earth population between 500 and 2000 , highlighting the effects of bubonic plague .

Comments: Human population

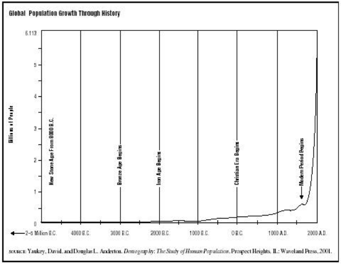


Figura : Estimated Earth's population between -4000 e 2000

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.

Comments II

What about interactions?

- Until now we considered populations of different species as independent.

Comments II

What about interactions?

- Until now we considered populations of different species as independent.
- However, it a fact that species make part of large interaction networks...

Comments II

What about interactions?

- Until now we considered populations of different species as independent.
- However, it a fact that species make part of large interaction networks...
  - Different animals compete for resources

Comments II

What about interactions?

- Until now we considered populations of different species as independent.
- However, it a fact that species make part of large interaction networks...
  - Different animals compete for resources
  - Some species are prey on others

Comments II

What about interactions?

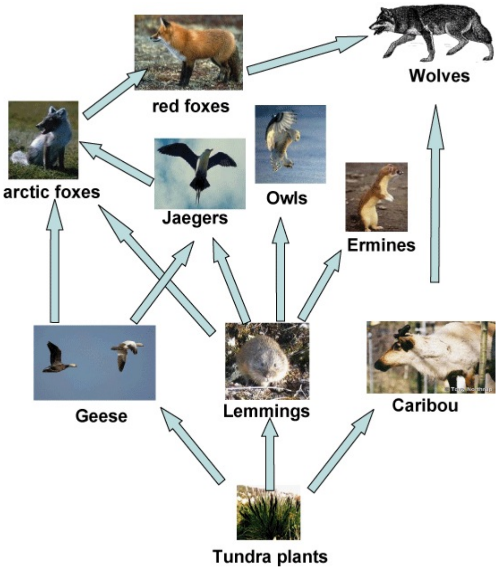
- Until now we considered populations of different species as independent.
- However, it a fact that species make part of large interaction networks...
  - Different animals compete for resources
  - Some species are prey on others
- Thus:

Comments II

What about interactions?

- Until now we considered populations of different species as independent.
- However, it a fact that species make part of large interaction networks...
  - Different animals compete for resources
  - Some species are prey on others
- Thus:"*populations are in fact inter-dependent..*".
- The networks involved can be quite complex.

Trophic network, Arctic region



Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors,

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.
- Decoupling can also occur when there many couplings!

ICTP SAIFR

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.
- Decoupling can also occur when there many couplings!
  - Say, species (A) consumes (preys on) many others.

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.
- Decoupling can also occur when there many couplings!
  - Say, species (A) consumes (preys on) many others.
  - It's coupling with each of the prey species will be "weak".

ICTP SAIFR

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.
- Decoupling can also occur when there many couplings!
  - Say, species (A) consumes (preys on) many others.
  - It's coupling with each of the prey species will be "weak".
  - Changes in the prey species do not affect strongly species (A).

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.
- Decoupling can also occur when there many couplings!
  - Say, species (A) consumes (preys on) many others.
  - It's coupling with each of the prey species will be "weak".
  - Changes in the prey species do not affect strongly species (A).
  - If, further, (A) is not the unique prey of some predator, than, it may be well described by a sinlge species dynamics.

Comments II

What are the single species good for?

- Certain species have their dynamics effectively uncoupled from the others.The population level is determined by limiting factors, but these factors are not directly affected by the population.
- Decoupling can also occur when there many couplings!
  - Say, species (A) consumes (preys on) many others.
  - It's coupling with each of the prey species will be "weak".
  - Changes in the prey species do not affect strongly species (A).
  - If, further, (A) is not the unique prey of some predator, than, it may be well described by a sinlge species dynamics.

Comments II: example

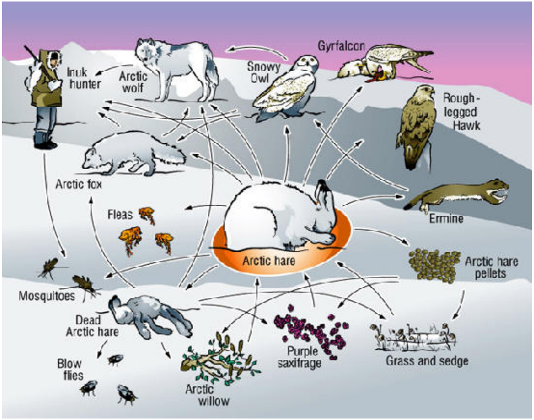


Figura : Simplified trophic network in the Arctic

Comments II: example

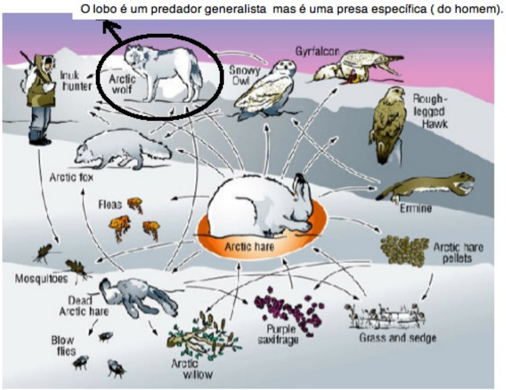


Figura : The wolf preys on many species, but its is itself a prey of a specialist predator. The coupling with human population can be strong.

Comments II: example

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

Comments II: example

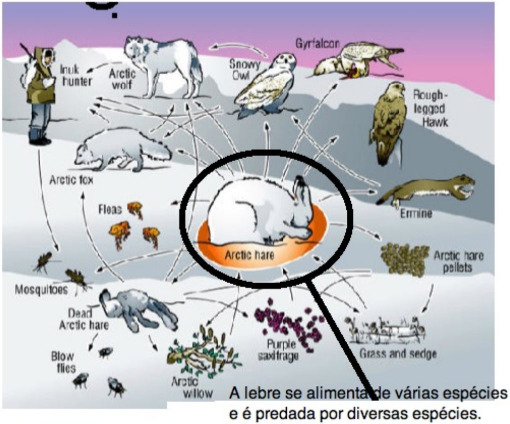


Figura : The Arctic hare is a generalist that is prey to other generalists. Single species models may apply.

Discrete time models

- In the models considered so far, time is continuous..

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.
- Certain plants, or insects.. There is no point to speak about continuous time.

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.
- Certain plants, or insects.. There is no point to speak about continuous time. We rather say "in year one population was N_1, in year two, N_2, and so on.

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.
- Certain plants, or insects.. There is no point to speak about continuous time. We rather say "in year one population was N_1, in year two, N_2, and so on.
- So, it is natural to consider:

$$N_{t+1} = \alpha N_t$$

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.
- Certain plants, or insects.. There is no point to speak about continuous time. We rather say "in year one population was N_1, in year two, N_2, and so on.
- So, it is natural to consider:

$$\underbrace{N_{t+1} = \alpha N_t}$$

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.
- Certain plants, or insects.. There is no point to speak about continuous time. We rather say "in year one population was N_1, in year two, N_2, and so on.
- So, it is natural to consider:

$$\underbrace{N_{t+1} = \alpha N_t}_{\text{Equivalent to the Malthusian equation}}$$

Discrete time models

- In the models considered so far, time is continuous.. Quite natural!
- We this suppose that birth and death, increase or decrease of populations occurs all the time.
- That's not true for all species.
- Certain species have well defines generations.often regulated by the seasons of the year.
- Certain plants, or insects.. There is no point to speak about continuous time. We rather say "in year one population was N_1, in year two, N_2, and so on.
- So, it is natural to consider:

$$\underbrace{N_{t+1} = \alpha N_t}_{\text{Equivalent to the Malthusian equation}} \qquad \text{or} \qquad N_{t+1} = \mathcal{F}(N_t)$$

Time delay

Time delay

- Our basic model

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

assumes that the rate of change of N at time t depends only on N at time t.

Time delay

- Our basic model
$$\frac{dN}{dt} = \mathcal{F}(N(t))$$
assumes that the rate of change of N at time t depends only on N at time t.
- We say that the model is **local** in time.

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

  assumes that the rate of change of N at time t depends only on N at time t.
- We say that the model is **local** in time.
- However,

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

assumes that the rate of change of N at time t depends only on N at time t.

- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .

Time delay

- Our basic model
$$\frac{dN}{dt} = \mathcal{F}(N(t))$$
assumes that the rate of change of N at time t depends only on N at time t.
- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .
- For instance, a part of the population might not be mature for reproduction.

Time delay

- Our basic model
$$\frac{dN}{dt} = \mathcal{F}(N(t))$$
assumes that the rate of change of N at time t depends only on N at time t.
- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .
- For instance, a part of the population might not be mature for reproduction.
- So, we are sometimes led to consider model like :

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

assumes that the rate of change of N at time t depends only on N at time t.

- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .
- For instance, a part of the population might not be mature for reproduction.
- So, we are sometimes led to consider model like :

$$\frac{dN}{dt} = \mathcal{F}(N(t-\tau))$$

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

assumes that the rate of change of N at time t depends only on N at time t.

- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .
- For instance, a part of the population might not be mature for reproduction.
- So, we are sometimes led to consider model like :

$$\frac{dN}{dt} = \mathcal{F}(N(t-\tau))$$

- They are called non-local in time.

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

assumes that the rate of change of N at time t depends only on N at time t.

- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .
- For instance, a part of the population might not be mature for reproduction.
- So, we are sometimes led to consider model like :

$$\frac{dN}{dt} = \mathcal{F}(N(t-\tau))$$

- They are called non-local in time.
- Usually, complicated .

Time delay

- Our basic model

$$\frac{dN}{dt} = \mathcal{F}(N(t))$$

assumes that the rate of change of N at time t depends only on N at time t.

- We say that the model is **local** in time.
- However, the rate of change of the population might not respond instantaneously to variations in the population size .
- For instance, a part of the population might not be mature for reproduction.
- So, we are sometimes led to consider model like :

$$\frac{dN}{dt} = \mathcal{F}(N(t-\tau))$$

- They are called non-local in time.
- Usually, complicated .

- Just try to solve:

- Just try to solve:

$$\frac{dN}{dt} = -\frac{\pi}{2T} N(t - T)$$

- Just try to solve:

$$\frac{dN}{dt} = -\frac{\pi}{2T} N(t-T)$$

- Good look.

More....

- Many other aspects have not been discussed

More....

- Many other aspects have not been discussed
- Interacting species

More....

- Many other aspects have not been discussed
- Interacting species
- The spatial distribution of the population....

More....

- Many other aspects have not been discussed
- Interacting species
- The spatial distribution of the population....
- We will study them in the coming lectures.

More....

- Many other aspects have not been discussed
- Interacting species
- The spatial distribution of the population....
- We will study them in the coming lectures.

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).**

ICTP SAIFR

Online Resources

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

Thank you for your attention