A Brief Overview on Population Dynamics

Seshadev Padhi

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- Provides an introduction to Classical and Modern Mathematical Models, Methods and issues in population dynamics.
- Devoted to simple models for the sake of tractability.
- Topics covered include single species models, interacting populations that include predation.
- Suitable for beginning researchers in Mathematical Modelling.

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Some useful results from ODE

Unless and otherwise stated, we assume that all the differential equations satisfy the Picard's theorem. Hence every initial value problem admits a unique solution.

Theorem (Picard's Theorem)

If g(t, u) is a continuous function of t and u in a closed and bounded region R containing a point (t_0, u_0) and satisfies the Lipschitz condition in R then there exists a unique solution u(t) to the initial value problem $u' = g(t, u), u(t_0) = u_0$ defined on an interval J containing t_0 .

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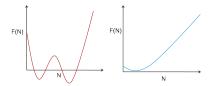
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Definition (Equilibrium Points)

Let us consider the following first order autonomous differential equation (system) $\frac{dN}{dt} = F(N)$. All the solutions of the equation F(N) = 0 are called equilibrium solutions of the above equation.

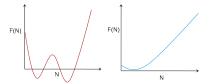
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Remark

These solutions are also some times called as equilibrium points, critical points, stationery points, rest points or fixed points.

- If N^* is an equilibrium solution of the differential equation N' = f(N) then $N(t) = N^*$ is the unique (constant) solution of the initial value problem (IVP) N' = f(N), $N(t_0) = N^*$.
- Thus, note that the equilibrium solutions are special constant solutions of the associated differential equation.

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Concept of Equilibrium

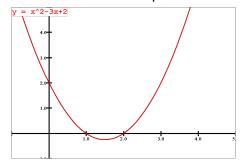
Introduction

Example:
$$x' = x^2 - 3x + 2$$

 $x^* = 2$ and $x^* = 1$ are two critical points.

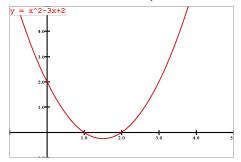
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It is easy to verify that $x^* = 2$ and $x^* = 1$ satisfy the differential equation $x' = x^2 - 3x + 2$.

Definition (Stability)

An equilibrium solution N^* is said to be Lyapunov stable, if for any given $\epsilon > 0$ there exists a $\delta > 0$ (depending on ϵ) such that, for all initial conditions $N(t_0) = N_0$ satisfying $|N_0 - N^*| < \delta$, we have $|N(t) - N^*| < \epsilon$ for all $t > t_0$.

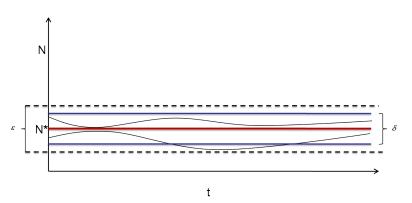
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Stability - Pictorial Representation



Definition (Asymptotical Stability)

An equilibrium solution N^* is said to be asymptotically stable if

- it is stable
- if there exists a $\rho > 0$ such that for all N_0 such that $|N_0 N^*| < \rho \Rightarrow \lim_{t \to \infty} |N(t) N^*| = 0$.

Alternatively, an equilibrium solution is said to be asymptotically stable if it is stable and in addition all solutions initiating in a ρ neighborhood of the equilibrium solution approach the equilibrium solution eventually.

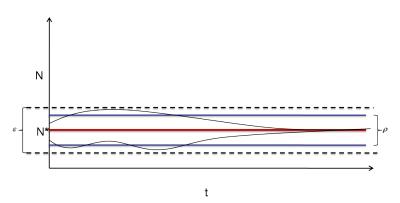
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Asymptotical Stability - Pictorial Representation



Definition (Unstable Solution)

A solution of the system

$$\frac{dN}{dt}=f(N).$$

is said to be unstable if it is not stable.

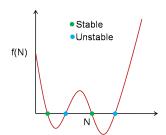
Theorem (A Useful Theorem in One-dimensional Space)

Suppose that N^* is an equilibrium point of the differential equation N' = f(N), where f(N) is assumed to be a continuously differentiable function with $f'(N^*) \neq 0$. Then the equilibrium point N^* is asymptotically stable if $f'(N^*) < 0$, and unstable if $f'(N^*) > 0$.

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Example



Stability, Instability

Introduction

Single Species Dynamics

- 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 and populations reproduce.
 - Note: we will study populations and not the individuals.
- ▶ Populations change in size, they grow or decrease due to birth, death, migration.

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The Basic Framework

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
- First: a population is described by its number of individuals (in some cases, however, by the biomass).
- Second: we need to describe the time variation of the population. We will use (ordinary) derivatives for this purpose. Alternatively, we could
- ▶ Three: we need to know what causes these time variations. Which biological processes. Then we have to translate this into (convenient) mathematical language how these biological processes affect the

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Malthusian Model

- N(t) represents total number or density of a population in an environment.
- $ightharpoonup \frac{dN}{dt}$ stands for rate of change in the entire population.
- ▶ $\frac{1}{N} \frac{dN}{dt}$ represents per capita rate of change in the entire population. (Change in the total population due to an individual.)
- To start with, we assume that the population changes due to births and deaths only.
- ▶ If b, d represent per capita birth and death rates then their difference represents per capita rate of change, i.e.,

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Dynamics of a single species: $\frac{1}{N} \frac{dN}{dt} = b - d$.

► Thus the governing dynamic equation for the population is

$$\frac{dN}{dt} = rN$$

where r = b - d called as *intrinsic growth rate*. This model is called *exponential model* or *Malthusian model*.

▶ If the initial population at time t_0 , $N(t_0) = N_0$, the solution of this differential equation is given by

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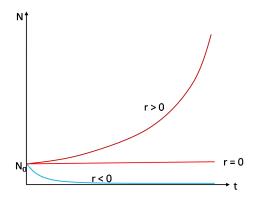
Thomas Robert Malthus (1766-1834)

- ▶ Per capita growth rate, $\frac{1}{N} \frac{dN}{dt}$, is always constant (b d).
- The growth rate of the population is always increasing (decreasing) if r > 0 (r < 0).
- ▶ The population grows (decays) exponentially from the initial value N_0 since $N(t) = N_0 e^{rt}$. The population will remain constant only when births and deaths balance each other, i.e., b = d or r = 0.

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Malthusian's Model,
$$\frac{dN}{dt} = rN$$
, $N(t_0) = N_0$



- From the model we observe that the population either blows up to infinity or decays to zero exponentially which is not realistic.
- This calls for a modification in the model. The present model assumes that the per capita growth rate is independent of the population.
- It is more realistic to assume that the per capita growth rate to be a function of total population in view of the fact that the population always has to share the limited food resources which naturally limits their growth.
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Exponential Growth

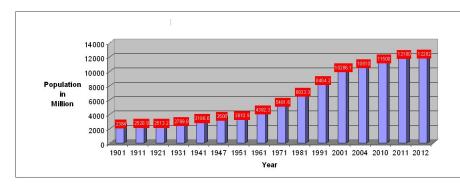


Figure: The population of India. Until 1951-1961, the growth is well approximated by an exponential curve.



Exponential Growth

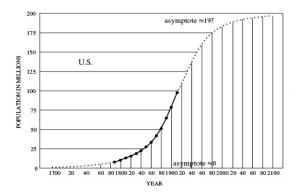


Figure: The population of USA. Until 1920, the growth is well approximated by an exponential curve.



Modified Model

 Hence we assume that the per capita growth rate of the population is linearly decreasing function of the total population, given by

$$\frac{1}{N}\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)$$

where K is called carrying capacity which represents the total population the environment can support.

▶ Observe that the per capita growth rate continuously reduces from r as the population N increases from zero and it becomes zero when the population reaches K. This seems reasonable as resources are always limited and the population are controlled by these resources.

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Logistic Model

The modified model representing growth in a species is given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), N(t_0) = N_0$$

which is called as Logistic Model or Verhulst Model.

Logistic Model



Figure: P-F. Verhulst, first introduced the logistic equation in 1838. On the right side, Raymond Pearl, who "rediscovered" Verhulst's work.

Parabolic Population Growth: $f(N) = rN (1 - \frac{N}{K})$

- Let us analyze the Logistic model in the light of the theorem done previously.
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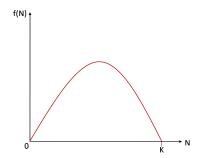
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Analysis of Logistic Equation $\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right), N(t_0) = N_0$

$$f(N) = 0 \Rightarrow N = 0 \text{ or } K$$
.

Logistic equation admits two equilibrium points given by $N_1 = 0, N_2 = K$

$$f'(N) = r\left(1 - \frac{2N}{K}\right), \quad f'(N_1) = r > 0, \quad f'(N_2) = -r < 0$$

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- Thus the solution behaves as per $\frac{dN}{dt} \approx rN$ leaving the neighborhood of 0. This illustrates the instability of zero equilibrium solution.

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$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), N(t_0) = N_0$$

- Let us study the nature of the equilibrium N = K. Let us define x = N K and substitute in Logistic equation.
- ▶ We obtain $\frac{dx}{dt} = -rx \frac{rx^2}{K}$. If N_0 is closer to K then x^2 will be smaller and can be neglected. Hence $\frac{dx}{dt} \approx -rx$
- ► Thus x(t) = N(t) K decays to zero exponentially. This illustrates asymptotic stability of K.

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Logistic Model

Solution of Logistic equation: $\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right), N(0) = N_0$

- integrating either side and using the initial condition $N(0) = N_0$ we obtain

$$ln\left(\frac{N}{K-N}\frac{K-N_0}{N_0}\right) = rt \Rightarrow \frac{N}{K-N} = \frac{N_0}{K-N_0}e^{rt}.$$

 $N(t) = \frac{RN_0 S^2}{2} = \frac{RN_0}{2}$

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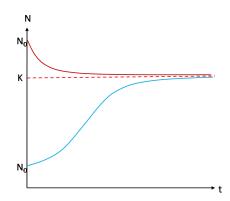
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Introduction

OOO

Logistic Model

Logistic Growth



Simulation

Introduction

Logistic Growth Simulation

Glory

- Simple and its solvable.
- Allows us to introduce the concept of carrying capacity.
- A good approximation in several cases.

Misery

- Too simple.
- Does not model more complex biological facts.

Why one should like the logistic equation?

 Minimal model using which we can build more complex/sonhisticated ones.



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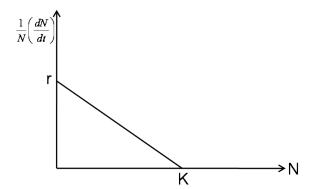
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Further modification to the Logistic equation

Logistic equation assumes that Per capita growth large when the population is small.



Further modification to the Logistic equation ...

- If the population is small there may not be any interaction at all among the population.
- Hence it is reasonable to assume that an environment requires a minimum number of population to enable growth in them.
- Per-capita growth rate of the population requires modification

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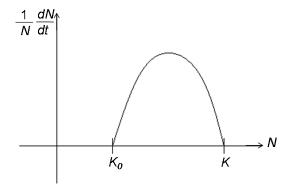
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Per-capita Growth With Allee Effect



Equation with Allee Effect

$$\frac{dN}{dt} = rN\left(\frac{N}{K_0} - 1\right)\left(1 - \frac{N}{K}\right)$$

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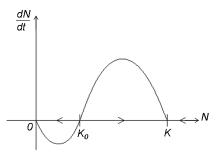
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Simulation

Introduction

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Interacting Populations

Single Species Dynamics

Predator-Prey Models

- ➤ Till now we have discussed about the dynamics of a single species with and without harvesting.
- Applied bifurcation analysis to derive conclusions on maximum sustainable yield.
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- We assume coexistence of predators and prey in an environment.
- \triangleright N(t) number or density of prey.
- P(t) number or density of predator.
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Predator-Prey Models

Prey Equation

- There are encounters between prey and predator.
- They result in consumption of prey by the predator.
- Number of encounters is proportional their densities.
- In presence of predators the prey dynamic equation gets modified to

$$\frac{dN}{dt} = rN - cNP, \quad r, c > 0$$

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Lotka-Volterra

Equilibria, Stability



Vito Volterra (1860 - 1940)

Vito Volterra (1860-1940), an Italian mathematician, proposed the equation now known as the Lotka-Volterra one to understand a problem proposed by his future 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 James Lotka (1880 - 1949)

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". His results are independent from the work of Volterra

Introduction

Lotka - Volterra equations: N' = rN - cNP, P' = bNP - mp.

- We wish to study this nonlinear two dimensional coupled differential system.
- Find if there are any equilibrium points for the system and investigate their nature.
- ▶ Obtain information about the qualitative behaviour of its solutions (N(t), P(t)).

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A few definitions

Consider an autonomous system

$$x' = F(x, y), \quad y' = G(x, y)$$

- Equilibrium points of this system are the points satisfying F(x, y) = 0 = G(x, y).
- ► F(x, y) = 0 is called x isocline and G(x, y) = 0 is called y isocline.
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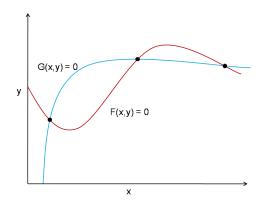
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Isoclines



Equilibrium Solutions

Equilibrium Points of Lotka-Volterra Equations

Isoclines:
$$(r - cP)N = 0$$
, $(bN - m)P = 0$

Prey isocline: N = 0, r - cP = 0.

Predator isocline: P = 0, bN - m = 0

$$\Rightarrow (N_1, P_1) = (0, 0), (N_2, P_2) = (\frac{m}{b}, \frac{r}{c})$$

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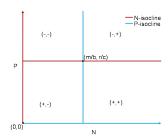
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Isocline Figure



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- In the vicinity of (0,0) we can neglect the terms involving NP.
- ▶ Hence we have $\frac{dN}{dt} \approx rN$, $\frac{dP}{dt} \approx -mP$.
- ▶ If the initial population is (N_0, P_0) , the solution is (N_0e^{rt}, P_0e^{-mt}) .
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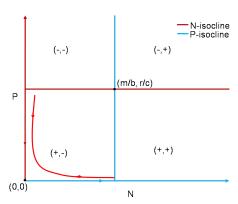
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Nature of (0,0)



$$N' = rN - cNP$$
, $P' = bNP - mP$: Analysis near $(\frac{m}{b}, \frac{r}{c})$

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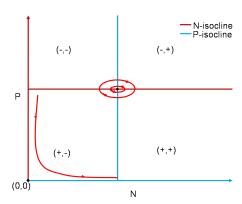
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- This transforms the original system to $u' = -\frac{mc}{b}v cuv$, $v' = \frac{rb}{c}u + buv$.
- Let (N_0, P_0) be in the vicinity of (N_2, P_2) .
- Since u, v are small we can neglect their product terms and hence we obtain $\frac{dv}{du} \approx -\frac{rb^2}{mc^2} \frac{u}{v}$
- $mc^2 vdv + rb^2 udu = 0$
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$$N' = rN - cNP$$
, $P' = bNP - mP$: Analysis near $(\frac{m}{b}, \frac{r}{c})$

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Introduction

Nature of (N_2, P_2)



Global behaviour of N' = rN - cNP, P' = bNP - mP

- Eliminating t and rearranging the system we obtain $\frac{(r-cP)dP}{P} = \frac{(bN-m)dN}{N}.$
- ▶ Upon integration, we obtain $P^r e^{-cP} = KN^{-m}e^{bN}$
- represents ovals about (N_2, P_2) in anti clockwise direction

Global Dynamics

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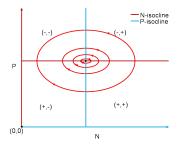
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Thus the considered system admits periodic solutions.

- Let *T* be the period of a solutions.
- ► Consider the equation $\frac{dN}{dt} = rN cNP$
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OOO

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Simulation

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Glory

Although it is an oversimplified model for predator-prey system, it captures an important feature that this kind of systems exhibits oscillations — which are inherent to dynamics.

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Some References

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THANK YOU