Population Dynamics
Fundamentals of Mathematical Ecology/Biology

- 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, Bifurcations, interacting populations that include predation.
- Suitable for Post graduate students and beginning researchers in Mathematical Biology.
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Some useful results from ODE

A general first order initial value problem is given by

\[ y' = f(t, y), y(0) = y_0. \]

—a non-autonomous differential equation due to explicit involvement of the independent variable, \( t \), in the right hand side.

In the entire course we are going to deal with autonomous first order differential equations/systems.

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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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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 sometimes called as equilibrium points, critical points, stationery points, rest points or fixed points.
Example: $x' = x^2 - 3x + 2$

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

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

![Graph of the function $y = x^2 - 3x + 2$ with points at x=2 and x=1]
Therefore, 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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Thus, note that the equilibrium solutions are special constant solutions of the associated differential equation.
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 $\epsilon$) such that, for all initial conditions $N(t_0) = N_0$ satisfying $|N_0 - N^*| < \delta$, we have $|N(t) - N^*| < \epsilon$ for all $t > t_0$.

Alternatively, we say that an equilibrium solution is said to be stable if solutions starting close to equilibrium solution (in a $\delta$ neighborhood) remain in its $\epsilon$ neighborhood for all future times.
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Stability - Pictorial Representation

![Diagram illustrating stability and instability in population dynamics.](image)
**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 $\rho$ 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

![Diagram showing stable and unstable points](image-url)
Single Species Dynamics
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 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

- 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).
  - We will here study unstructured populations, but in reality structured populations arise and are important. Here "structure" means classes of age, size, sex...

  **Second:** we need to describe the time variation of the population. We will use (ordinary) derivatives for this purpose. Alternatively, we could also work with stochastic processes or discrete-time formulations...

  **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 time-changes of the population.
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Dynamics of a single species

- $N(t)$ represents total number or density of a population in an environment.
- $\frac{dN}{dt}$ 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.,

$$\frac{1}{N} \frac{dN}{dt} = b - d.$$
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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

\[ N(t) = N_0 e^{rt}. \]
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Thomas Robert Malthus (1766-1834)
Malthusian’s Model, \( \frac{dN}{dt} = rN, N(t_0) = N_0 \)

- 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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- 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.

- Before going into this, some examples:
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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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The modified model representing growth in a species is given by

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

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: \( f(N) = rN \left( 1 - \frac{N}{K} \right) \)

- Let us analyze the Logistic model in the light of the theorem done previously.
- We have

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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 $N_1 = 0, N_2 = K$

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

The trivial equilibrium, $N_1 = 0$ is unstable and $N_2 = K$ is asymptotically stable.
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**Analysis of Logistic Equation** \( \frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) \), \( N(t_0) = N_0 \)

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

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

- \( \frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) \).
- \( \left( \frac{1}{N} + \frac{1}{K-N} \right) dN = rdt. \)
- 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}.
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Logistic Model

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\begin{align*}
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Logistic Growth
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Simulation
Glory and Misery of Logistic Model

**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?**
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Further modification to the Logistic equation

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

\[
\frac{1}{N} \left( \frac{dN}{dt} \right)
\]
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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Allee Effect

Per-capita Growth With Allee Effect

\[ \frac{1}{N} \frac{dN}{dt} \]

\[ N \]

\[ K_0 \]

\[ K \]
Equation with Allee Effect

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

- \( N_1 = 0, N_2 = K_0, N_3 = K \) are the three equilibrium points.
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Interacting Populations
Till now we have discussed about the dynamics of a single species.

Present discussion is devoted to study the dynamics of two interacting population.

In particular Predator-Prey interactions.
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- In particular **Predator-Prey** interactions.
Predator-Prey Model development

- We assume coexistence of predators and prey in an environment.
- $N(t)$ - number or density of prey.
- $P(t)$ - number or density of predator.
- The food is abundant for the prey and they grow as per the equation $\frac{dN}{dt} = rN$ in the absence of the predator.
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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

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\frac{dN}{dt} = rN - cNP, \quad r, c > 0
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- In the absence of prey the predators die at an exponential rate.
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Lokta-Volterra Equations

Predator Prey dynamics: \( \frac{dN}{dt} = rN - cNP, \frac{dP}{dt} = bNP - mP. \)

- \( r \) is intrinsic growth rate of the prey population.
- \( c \) consumption rate of the predator per prey.
- \( b \) conversion factor
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- These equations are called Lotka - Volterra predator-prey equations.
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These equations are called **Lotka - Volterra predator-prey equations**.
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 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.
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.
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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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Isoclines

\[ G(x, y) = 0 \]

\[ F(x, y) = 0 \]
Equilibrium Points of Lotka-Volterra Equations

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

Prey isocline: \(N = 0,\quad r - cP = 0\).

Predator isocline: \(P = 0,\quad bN - m = 0\)

\(\Rightarrow (N_1, P_1) = (0, 0),\quad (N_2, P_2) = \left(\frac{m}{b}, \frac{r}{c}\right)\)
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Trivial Equilibrium Analysis

\[ N' = rN - cNP, \quad P' = bNP - mP: \text{ Analysis near (0, 0)} \]

- We study the stability/instability nature of these critical points.
- 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 \( (N_0 e^{rt}, P_0 e^{-mt}) \).
- Near (0, 0) the prey grows exponentially and the predators decrease exponentially.
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Nature of $(0, 0)$

- $(+, -)$
- $(-, +)$
- $(+, +)$
- $(-, -)$

- $(m/b, r/c)$

- N-isocline
- P-isocline
Interior Equilibrium Analysis

\[ N' = rN - cNP, \quad P' = bNP - mP: \text{Analysis near \( \left( \frac{m}{b}, \frac{r}{c} \right) \)}\]

- Define \( u = N - N_2, \quad v = P - P_2 \).
- This transforms the original system to
  \[ u' = -\frac{mc}{b} v - cuv, \quad v' = \frac{rb}{c} u + buv. \]
- 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
  \[ \frac{dv}{du} \approx -\frac{rb^2}{mc^2} \frac{u}{v} \]
- \( mc^2 v dv + rb^2 u du = 0 \)
- \( rb^2 u^2 + mc^2 v^2 = c^2 \Rightarrow rb^2 (N - N_2)^2 + mc^2 (P - P_2)^2 = C^2 \), represent ellipses around \((N_2, P_2)\).
N' = rN - cNP,  P' = bNP - mP: Analysis near \((\frac{m}{b}, \frac{r}{c})\)

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  \[\frac{dv}{du} \approx -\frac{rb^2}{mc^2} \frac{u}{v}\]

- \(mc^2vdv + rb^2udu = 0\)

- \(rb^2u^2 + mc^2v^2 = c^2 \Rightarrow rb^2(N - N_2)^2 + mc^2(P - P_2)^2 = C^2,\)

represent ellipses around \((N_2, P_2)\).
Interior Equilibrium Analysis

\[ N' = rN - cNP, \quad P' = bNP - mP: \text{Analysis near} \left( \frac{m}{b}, \frac{r}{c} \right) \]

- Define \( u = N - N_2, \quad v = P - P_2. \)
- This transforms the original system to
  \[ u' = -\frac{mc}{b} v - cuv, \quad v' = \frac{rb}{c} u + buv. \]
- 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 \( \frac{dv}{du} \approx -\frac{rb^2}{mc^2} u \)
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$N' = rN \ - \ cNP, \ \ \ P' = bNP \ - \ mP$: Analysis near $(\frac{m}{b}, \frac{r}{c})$

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Nature of \((N_2, P_2)\)
Global behaviour of $N' = rN - cNP, \quad P' = bNP - mP$

- Eliminating $t$ and rearranging the system we obtain
  \[
  \frac{(r-cP)dP}{P} = \frac{(bN-m)dN}{N}.
  \]
- Upon integration, we obtain $P^r e^{-cP} = K N^{-m} e^{bN}$.
- Represents ovals about $(N_2, P_2)$ in anti clockwise direction.
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Thus the considered system admits periodic solutions.
Periodic Solutions

- Let $T$ be the period of a solutions.
- Consider the equation \( \frac{dN}{dt} = rN - cNP \)
- Separating the variables and integrating over a time period $T$ we obtain
  \[
  \int_{t_0}^{t_0+T} \frac{dN}{N} = \int_{t_0}^{t_0+T} (r - cP)dt
  \]
  \[
  \Rightarrow \ln \left[ \frac{N(t_0+T)}{N(t_0)} \right] = rT - c \int_{t_0}^{t_0+T} Pdt
  \]
- Thus $rT - c \int_{t_0}^{t_0+T} Pdt = 0$
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Species Average

\[ \frac{1}{T} \int_{t_0}^{t_0+T} P \, dt = \frac{r}{c} \]

- Note that the LHS is nothing but the average of the predator density over a cycle i.e., \( P_{\text{average}} = \frac{r}{c} \).
- Following similar lines we can show that \( N_{\text{average}} = \frac{m}{b} \).
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Simulation
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.

Misery

- As Lotka-Volterra model exhibits orbital stability, once you are on a certain orbit in the phase space, it has certain amplitude and period.
- If we perturb this orbit, the system will stay on a new orbit, with different amplitude and period.
- But the real systems are under perturbations all the time, they would jump between trajectories but may not always be periodic. Moreover, the periodicity if exits is not effectively periodic.
- In fact, real predator-prey oscillations better described by limit cycle behaviour.
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Glory and Misery of Lotka-Volterra Model

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Some References

- Ecology of Populations, E. Ranta, P. Lundberg, V. Kaitala (Cambridge Univ. Press, 2006).
THANK YOU