

Lecture 8

The Allee Effect

Some populations have obstacles in reproduction when their numbers are small, because of a lack of suitable mates.

A growth model that takes this fact into account is the following:

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

$a, K, r > 0$: positive constants

$0 < a < K$ by assumption

K ... the carrying capacity

a ... this constant is the threshold population size below which the recruitment rate is negative, meaning that the population will shrink and ultimately go to extinction.

What are the equilibria of this system?

We set $g(N) = rN(N-a)\left(1 - \frac{N}{K}\right)$.

$$g(N) = 0 \Leftrightarrow N_1 = a \quad \text{or} \quad N_2 = K \quad \text{or} \quad N_3 = 0$$

$\Rightarrow N_1, N_2$ and N_3 are the equilibria.

We can classify these equilibria according to stability:

$$g(N) = rN(N-a)\left(1 - \frac{N}{K}\right)$$

$$g'(N) = \underset{\substack{\uparrow \\ \text{product rule}}}{r(N-a)\left(1 - \frac{N}{K}\right)} + rN\left(1 - \frac{N}{K}\right) - \frac{rN}{K}(N-a)$$

$$\cdot g'(N_1) = g'(a) = \cancel{r(a-a)\left(1 - \frac{a}{K}\right)} + ra\left(1 - \frac{a}{K}\right)$$

$$- \cancel{\frac{ra}{K}(a-a)}$$

$$= ra \underbrace{\left(1 - \frac{a}{K}\right)}_{> 0} > 0,$$

because $r, a > 0$ and $a < K$.

$\Rightarrow N_1 = a$ is stable

$$\cdot g'(N_2) = g'(K) = \cancel{r(K-a)\left(1 - \frac{K}{K}\right)} + rK \underbrace{\left(1 - \frac{K}{K}\right)}_{=0} - \frac{rK}{K}(K-a)$$

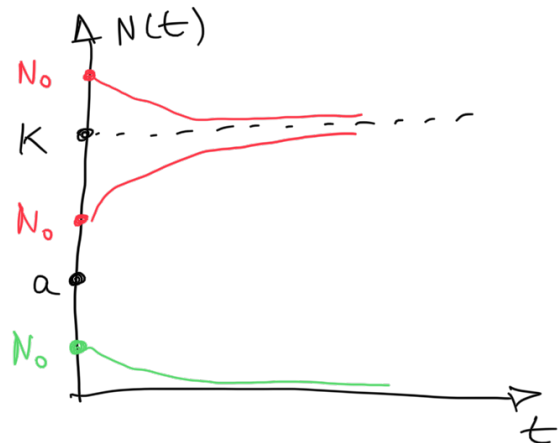
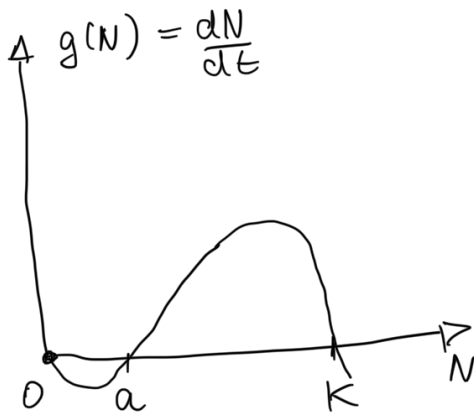
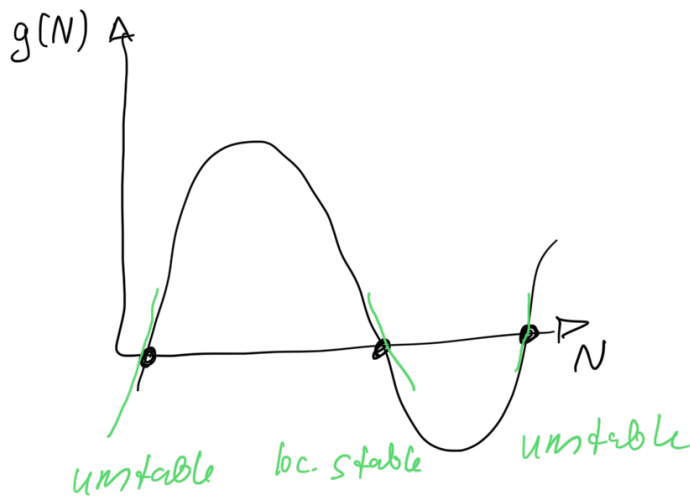
$$= -r(K-a) < 0, \text{ as } K > a, \\ a, r > 0.$$

$\Rightarrow N_2 = K$ is locally stable

$$\cdot g'(N_3) = g'(0) = r(0-a)\left(1 - \frac{0}{K}\right) + r \cdot 0 \cdot \left(1 - \frac{0}{K}\right) - \frac{r \cdot 0}{K}(0-a)$$

$$= -r \cdot a < 0$$

$\Rightarrow N_3 = 0$ is locally stable.



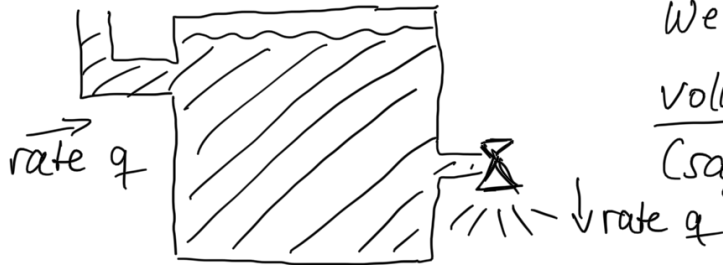
- $N_0 < a$: $N(t) \rightarrow 0$ for $t \rightarrow \infty$
- $N_0 > a$: $N(t) \rightarrow K$ for $t \rightarrow \infty$

In other words: If the initial population N_0 is too small ($N_0 < a$), then the population goes extinct. If the initial population is large enough (i.e., $N_0 > a$), then the population persists.

- parameter a is the threshold level.

⇒ the problem

Single Compartment Model



We have a constant
volume V of water
(say in a water tank)

The water contains a solute (eg. phosphorus).
The rate q by which the water enters is the
same by which it leaves (otherwise the
volume V would not be constant).

We want to study what happens to the
concentration $C(t)$ of the solution in the
compartment when the fluid which enters has
a different concentration.

By definition: $C = \frac{m}{V}$ (m : mass of
the solute)
(V : volume of
the compartment,

$C(t)$... concentration at time t

C_I ... concentration of the input

q ... rate of the input and output

$C_0 = C(0)$... concentration at time 0

E.g., if $C_I = 5 \text{ g/lt}$ and $q = 0.05 \text{ lt/sec}$,
then the rate of the input of mass in the
compartment is going to be

$$\frac{q \cdot C_I}{=} = 0.05 \text{ l/lsec} \cdot 5 \text{ g/l} \\ = 0.25 \text{ g/lsec}$$

What is the rate of output of mass?

We assume that the solution is "homogeneous", i.e. the concentration is the same in all areas of the compartment. Then the rate of output of mass is $q \cdot C(t)$.

In order to examine $C(t)$, we need to find a DE. We shall use the "Law of Conservation of Mass".

\Rightarrow The rate of change of mass in the compartment is equal to the rate of input of mass minus the rate of output of mass.

• mass in the compartment: $C(t) \cdot V$

• rate of change of this mass:

$$\frac{d}{dt} (C(t) \cdot V) = V \cdot \frac{dC}{dt}$$

• rate of input of mass: $q \cdot C_I$

• rate of output of mass: $q \cdot C(t)$

Hence: $V \cdot \frac{dC}{dt} = q \cdot C_I - q \cdot C(t)$

$$\Rightarrow \left[\frac{dC}{dt} = \frac{q}{V} (C_I - C(t)) \right]$$

$$\left[dt \quad v \quad \dots \right]$$

$$\Rightarrow \int \frac{1}{C_I - C} dC = \int \frac{q}{V} dt$$

$$\Rightarrow -\ln |C_I - C| = \frac{q}{V} t + K_1$$

(K_1 : constant)

We find the constant K_1 : When $t=0$,

$C(0) = C_0$, so

$$-\ln |C_I - C_0| = \frac{q}{V} \cdot 0 + K_1 = K_1$$

We substitute $K_1 = -\ln |C_I - C_0|$ back and obtain:

$$-\ln |C_I - C| = \frac{q}{V} t - \ln |C_I - C_0|$$

$$\Rightarrow \ln |C_I - C| = \ln |C_I - C_0| - \frac{q}{V} t$$

$$\Rightarrow \underline{|C_I - C|} = e^{\ln |C_I - C_0| - \frac{q}{V} t}$$

$$= \underline{|C_I - C_0|} \cdot e^{-\frac{q}{V} t}$$

The sign of $C_I - C(t)$ and $C_I - C_0$ is always the same for all t , because:

If $C_I > C_0$, then the concentration that enters the compartment will always be bigger than $C(t)$, ($C(t)$ can never exceed the

concentration that comes in).

If $C_I < C_0$, then C_I will always be smaller than $C(t)$ by the same argument.

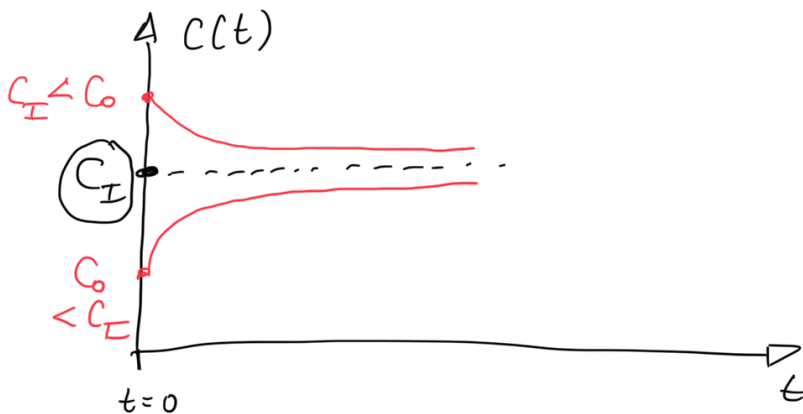
$$\Rightarrow C_I - C = (C_I - C_0) e^{-\frac{q}{V}t}$$

$$\Rightarrow -C = (C_I - C_0) e^{-\frac{q}{V}t} - C_I$$

$$\Rightarrow C(t) = C_I \left(1 - \left(1 - \frac{C_0}{C_I} \right) e^{-\frac{q}{V}t} \right)$$

The behaviour of the function $C(t)$ depends on $\frac{C_0}{C_I}$:

Solution curves:



Equilibria: $\frac{dC}{dt} = g(C) = \frac{q}{V} (C_I - C) \stackrel{!}{=} 0$

$$\Leftrightarrow C = C_I \text{ is the only equilibrium}$$

$$g'(C) = -\frac{q}{V} < 0 \Rightarrow \text{the equilibrium is locally stable.}$$

We can see that

$$\lim_{t \rightarrow \infty} C(t) = C_I$$

regardless of the initial condition.

$\Rightarrow C_I$ is even a globally stable equilibrium

This implies that no matter how much we perturb the equilibrium, the system will return to it.

Systems of Autonomous DEs

An Example from Epidemiology

All systems we have encountered so far involved a single DE. This is not always the case.

\rightarrow Example: Infectious disease:

At each time t , the population of fixed size N is divided into the following classes:

- $S(t)$: the number of susceptibles which can get infected.
- $I(t)$: the infected (who can transmit the disease)
- $R(t)$: the number of people who recovered (they have become immune)

The flow among these classes:



Assumptions:

I. The susceptibles become infected at a rate that is proportional to the number of the infected:

$$\frac{dS}{dt} = -b \cdot S(t) \cdot I(t).$$

II. The infected ones recover at a constant rate:

$$\frac{dR}{dt} = a \cdot I(t).$$

The total population is constant:

$$N(t) = N \Rightarrow \frac{dN}{dt} = 0$$

$$\Rightarrow \frac{dS}{dt} + \frac{dI}{dt} + \frac{dR}{dt} = 0$$

(because $S + I + R = N$)

$$\Leftrightarrow \frac{dI}{dt} = -\frac{dS}{dt} - \frac{dR}{dt}$$

$$= b S(t) I(t) - a I(t).$$

\Rightarrow So we have the system of DEs:

$$\frac{dS}{dt} = -bSI$$

$$\frac{dI}{dt} = bSI - aI$$

$$\frac{dR}{dt} = aI$$

Assumption: At $t=0$, we have

$$S(0) > 0, I(0) > 0, R(0) = 0.$$

The infection spreads if $I(t) > I(0)$ at some $t > 0$.

Will the infection spread?

→ Answer: As long as $\left. \frac{dI}{dt} \right|_{t=0} > 0$, the infection will spread.

$$\Rightarrow \left. \frac{dI}{dt} \right|_{t=0} = \underline{bS(0)I(0) - aI(0)}$$

$$\begin{aligned} \Rightarrow \left. \frac{dI}{dt} \right|_{t=0} > 0 &\Leftrightarrow bS(0) > a \\ &\Leftrightarrow \boxed{\frac{b}{a} S(0)} > 1 \end{aligned}$$

The number $\frac{b}{a} S(0) =: R_0$ is the basic reproductive rate of the infection.

Problems: (i.) Prove that $S(t)$ is decreasing.

Problem ...

(ii) Prove that not everyone will get infected.

Answer: (i) The derivative of S w.r.t. R is:

$$\frac{dS}{dR} = \frac{\frac{dS}{dt}}{\frac{dR}{dt}} = \frac{-bS \cancel{I}}{a \cancel{I}} = -\frac{b}{a} S$$

$$\int \frac{dS}{S} = \int \left(-\frac{b}{a}\right) dR$$

$$\Rightarrow \ln |S| = -\frac{b}{a} R + C$$

In order to find C , we use $R(0) = 0$:

$$\ln S(0) = -\frac{b}{a} \underbrace{R(0)}_{=0} + C \Rightarrow C = \ln S(0)$$

$$\Rightarrow \ln S = -\frac{b}{a} R + \ln S(0)$$

$$\Rightarrow S = e^{-\frac{b}{a} R(t)} \cdot e^{\ln S(0)}$$

$$= e^{-\frac{b}{a} R(t)} \cdot S(0), \quad t \geq 0$$

Since the function $R(t)$ is increasing,
 $S(t)$ is decreasing.

$$(ii) S(t) = S(0) \cdot e^{-\frac{b}{a} R(t)}, \quad t \geq 0$$

... $t \geq 0$:

for any $t \geq 0$.

$$R(t) \leq N \Rightarrow -\frac{b}{a} R(t) \geq -\frac{b}{a} N$$

$$\Rightarrow S(t) = S(0) \cdot e^{-\frac{b}{a} R(t)} \geq S(0) e^{-\frac{b}{a} N} > 0$$

$\Rightarrow S(t) > 0$ for all $t \geq 0$, and so,
not everyone will get infected.