Chapter Three

Interacting Population Models

Interacting population models are relevant where two or more populations depend on each other. We study, in detail, five examples of interacting populations:

1) Epidemic model,
2) Predator-prey interaction,
3) Competing species interaction,
4) Battle between two opposing groups.
5) Mutualism or symbiosis.

In this chapter, we concentrate on formulating the differential equation model governed by two simultaneous first-order differential equations.

Ecological systems may be extraordinarily complex- an inter-related system of plants and animals, predators, prey, flowering plants, insects, parasites, pollinators, seed-dispersing, etc. In each system there is a constant stream of arrivals and departures involving time periods of millions of years. New species evolve or arrive; others decline to extinction or migrate. Human interference has impacted hugely on most of the world's ecosystems, particularly over the past 200 years, with one seemingly insignificant species extinction able to spark a cascade of effects throughout the trophic levels.

Definition: Many processes are described by more than one differential equation. When these equations need to be satisfied simultaneously, the set of equations is known as a system of differential equations.

Definition: The system of equations is known as a dynamical system if it allows prediction of future states given present and/or past states.

Definition: The systems of equations may be coupled, which implies that their solutions are interdependent.

For example, in the case of two equations $x'(t) = F(x, y, t)$ and $y'(t) = G(x, y, t)$, if the solution of x' depends on the value of y and the solution of y' depends on x, then the equations are coupled. Otherwise, this system is said to be uncoupled.

1. $\dfrac{dx}{dt} = -k_1 x$

   $\dfrac{dy}{dt} = k_1 x - k_2 y$ is uncoupled.

2. $\dfrac{dx}{dt} = -k_1 x$

   $\dfrac{dy}{dt} = \alpha xy + \beta y$ is uncoupled.

Incubation period, Latent period and Generation time.

A specific characteristic of infectious disease epidemiology is the definition the different stages of infection according to time.

The starting point is the moment when a pathogen enters the host: this moment is often referred to as **'exposure moment'**. Immediately after this moment, the pathogen usually will move to the preferred tissue or target organ. This will be the place within the host where the pathogen can effectively multiply. Different pathogens may have different target organs. Hepatitis virus will target the liver for multiplication, for example, while Legionella will target the lungs.

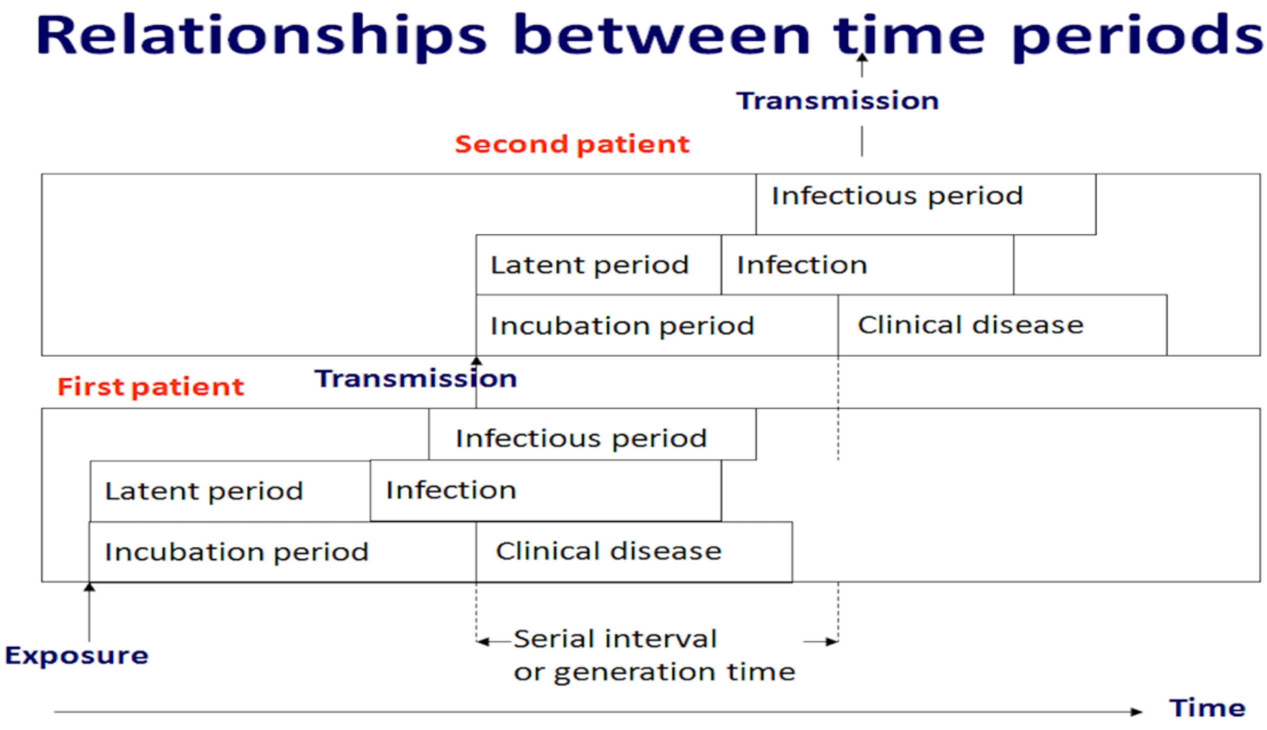
In the next stage, the pathogen will multiply and the host immune system will start a response. This is the start of the infectious process, where cellular and humoral host defences will be activated. Though this process may not yet be visible through clinical symptoms, there will be signs that can be observed through laboratory diagnostics (such as increased sedimentation rate, shift in the distribution of white blood cells). At this stage we may speak of '**an infection**' (which may be symptomatic or asymptomatic).

The period between exposure and infection is called **'latent period'**, since the pathogen is present in a 'latent' stage, without clinical symptoms or signs of infection in the host.

The period between exposure and onset of clinical symptoms is called **'incubation period'.**

The host may become infectious (i.e. able to transmit the pathogen to other hosts) at any moment of the infection. This moment will vary per pathogen.

The following schematic figure demonstrates these different time periods:



Model for an influenza outbreak

We develop a model to describe the spread of a disease in a population and use it to describe the spread of influenza in a boarding school. To do so, the population is divided into three groups: those susceptible to catching the disease, those infected with the disease and capable of spreading it, and those who have recovered and are immune from the disease. Modelling these interacting groups leads to a system of two coupled differential equations.

Model assumptions

When considering a disease, the population can be divided into distinct groups: susceptible $S(t)$ and contagious infective $I(t)$, where t denotes time. There are also those who have recovered from the disease and are no longer susceptible, who form a further separate group.

- We assume that the populations of susceptible and contagious infectives are large so that random differences between individuals can be neglected.

- We ignore births and deaths in this model and assume the disease is spread by contact.
- We neglect the latent period for the disease, setting it equal to zero.
- We assume all those who recover from the disease are then immune.

Formulating the Differential Equations

$$\begin{Bmatrix}\text{rate of change}\\ \text{in no.}\\ \text{susceptibles}\end{Bmatrix} = -\begin{Bmatrix}\text{rate}\\ \text{susceptibles}\\ \text{infected}\end{Bmatrix}$$

$$\begin{Bmatrix}\text{rate of}\\ \text{change in no.}\\ \text{infectives}\end{Bmatrix} = \begin{Bmatrix}\text{rate}\\ \text{susceptibles}\\ \text{infected}\end{Bmatrix} - \begin{Bmatrix}\text{rate}\\ \text{infectives}\\ \text{have recovered}\end{Bmatrix} \qquad \ldots(1)$$

$$\begin{Bmatrix}\text{rate of}\\ \text{change no.}\\ \text{recovered}\end{Bmatrix} = \begin{Bmatrix}\text{rate}\\ \text{infectives}\\ \text{have recovered}\end{Bmatrix}$$

- We assume that the rate infectives recovered is directly proportional to the number of invectives and write:

$$\begin{Bmatrix}\text{rate}\\ \text{infectives}\\ \text{recovered}\end{Bmatrix} = \gamma I(t), \qquad \ldots(2)$$

where γ is a positive constant of proportionality, called the **recovery rate**, or removal rate (is the rate at which people stop being infected) defined as 1/recovery period *T*, where the recovery period (mean infectious period) is how long it takes to recovery denoted γ^{-1}

- The rate susceptible are infected is $\lambda(t)S(t)$.

$$\begin{Bmatrix}\text{rate}\\ \text{susceptibles}\\ \text{infected}\end{Bmatrix} = \lambda(t)S(t) \qquad \ldots(3)$$

where $\lambda(t)$ is called the **force of infection**.

Putting together the assumptions for rate of new infections and rate of recoveries gives the system of differential equations

$$\frac{dS}{dt} = -\lambda(t)S,$$
$$\frac{dI}{dt} = \lambda(t)S - \gamma I, \qquad \text{... (4)}$$
$$\frac{dR}{dt} = \gamma I.$$

One suitable model for the force of infection is

$$\lambda(t) = \beta I(t), \qquad \text{... (5)}$$

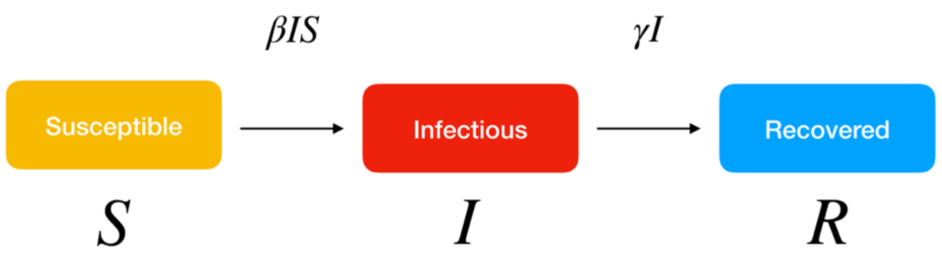
where β is the **effective contact rate**, calculate as multiply a **contact rate** (number of contacts per person per time) by the **risk of infection** (probability of virus transmission in the contact between a susceptible and an infectious)..

Our model for the spread of influenza now become

$$\frac{dS}{dt} = -\beta SI,$$
$$\frac{dI}{dt} = \beta SI - \gamma I, \qquad \text{... (6)}$$
$$\frac{dR}{dt} = \gamma I.$$

subject to the initial conditions $S(0) = s_0, I(0) = i_0$ and $R(0) = 0$.

Estimating parameters 1:



Estimating the value of parameters is often a difficult task. Without accurate parameter estimators, a model is less useful as a predictive tool. However, it may still be possible to infer the general behavior and therefore add insight into the possible processes underlying the model.

First:

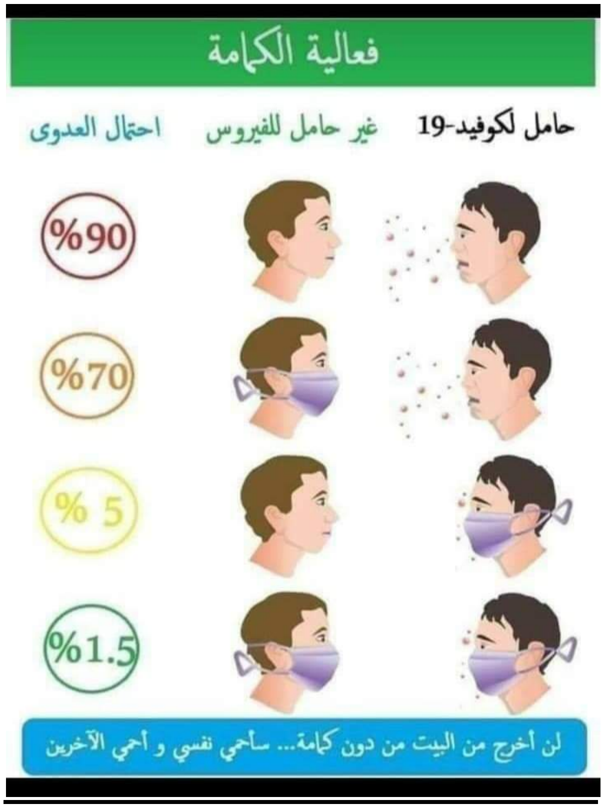
effective contact rate = contact rate* risk of infection

$$\beta = c * p$$

Example 1:

According to the picture, If the susceptible group contain 100 people and the infected person meet 20 people a day .

Find the number of infected next day.



Solution:

$$\beta_1 = 20 * \frac{90}{100} = 18$$

S(1)=100-18=82

I(1)=1+18=19

$$\beta_2 = 20 * \frac{70}{100} = 14$$

S(1)=100-14=86

I(1)=1+14=15

$$\beta_3 = 20 * \frac{5}{100} = 1$$

S(1)=100-1=99

I(1)=1+1=2

$$\beta_4 = 20 * \frac{1.5}{100} = 0.3$$

S(1)=100-0.3=100

I(1)=1+0.3=1

Second:

recovery rate = 1/recovery period

$$\gamma = \frac{1}{T}$$

Example 2:

If our recover period is 10 days and we have 200 sick people on day 10. How many recovers on day 11?

Solution:

since recover period γ^{-1}=10 days,

then the recovery rate $\gamma = 1/10$,

the recovers in 11th day = 200*(1/10)=20.

On 11th day, we have 20 people move from infectious group to Recovered group.

Example 3:

If the recover period is 3 days and we have 1200 sick people on day 3. How many recovers on day 5?

Solution:

Step 1

since recover period γ^{-1}=3 days,

then the recovery rate $\gamma = 1/3$,

the recovers in 4th day = 1200*(1/3)=400.

On 4th day, we have 400 people move from infectious group to Recovered group.

I(4)=1200-400=800.

R(4)=400.

Step 2

The recovers in 5th day= 800*(1/3)=267

I(5)=800-267=533

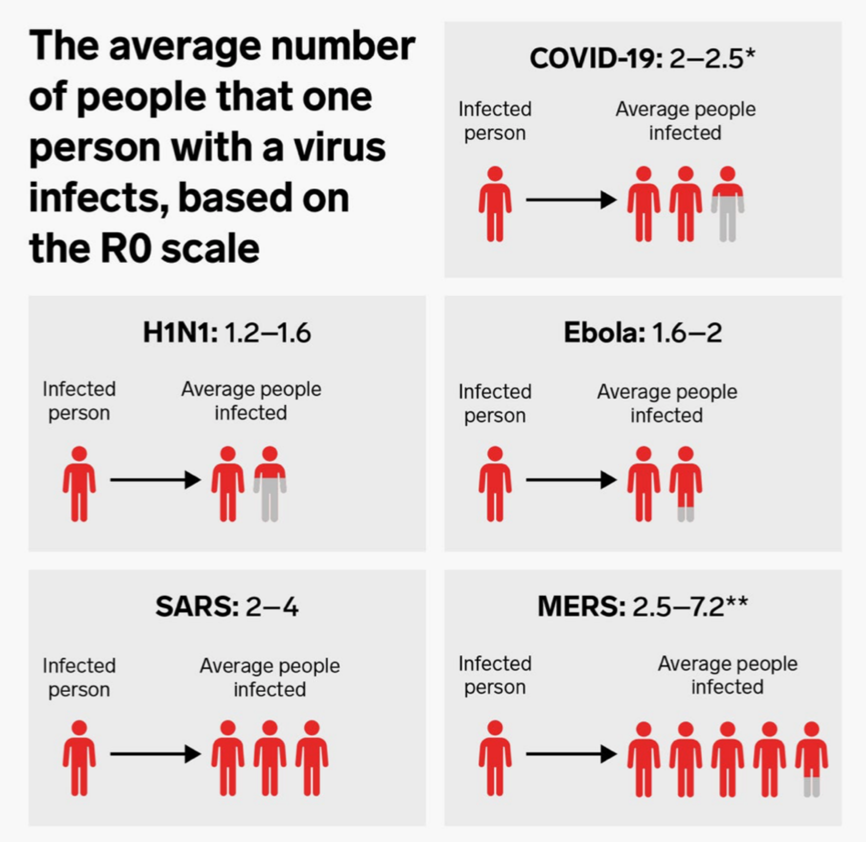
R(5)=400+267=667

Estimating parameters 2:

Estimating the parameter β is more difficult. We can use the definition of the basic reproducing number R_0, which defined as the expected number of cases directly generated by one case in a population where all individuals are susceptible to infection.

Logically, if the R_0 is less than 1, a disease outbreak should wane over time, and if it's greater than 1 case should continue to increase. Seasonal flu, for example, has an R_0 of around 1.5. The Spanish influenza of 1918-1919 had an R_0 as high as 2. Chickenpox, which is fairly infectious has an R0 of around 5.

Right away we need to notice something. The R_0 is clearly not the measure of how terrible a new infection will be. The Spanish Flu killed 50 Million people in 1918. I'll take chickenpox over Spanish flu any day of the week.



Furthermore R_0values are usually estimated from mathematical models, and the estimated values are dependent on the model used and values of other parameters. Suppose that infectious individuals make an average of β effective contact rate, with a mean infectious period of γ^{-1}. Then the basic reproduction number is:

$$R_0 = \frac{\beta}{\gamma} \quad \ldots(7)$$

this leads to

$$\beta = \gamma \cdot R_0 \ldots.(8)$$

During an epidemic, typically the number of diagnosed infected $I(t)$ over time t is known. In the early stages of an epidemic, growth is exponential, with a logarithmic growth rate

$$K = \frac{d \ln [\, I(t)]}{dt} \ldots(9)$$

The second Equation in system (6), $\left[\frac{dI}{dt} = \frac{\beta SI}{N} - \gamma I\right]$, could be write as an initial value problem

$\frac{dI}{dt} = (\beta S/N - \gamma)I$ with $I(0) = I_0$,

which has the analytic solution

$$I(t) = I_0 e^{\left(\frac{\beta S_0}{N} - \gamma\right)t} \ldots.(10)$$

To find doubling time T_d, substituting $I(T_d) = 2I_0$ into Eq. (10), we obtain

$2I_0 = I_0 e^{\left(\frac{\beta S_0}{N} - \gamma\right)T_d} \quad \Longrightarrow \quad 2 = e^{\frac{\beta S_0}{N} - \gamma T_d}$,

by assuming K$=\frac{\beta S_0}{N} - \gamma$, and take the ln for the both sides lead to,

$$K = \frac{\ln 2}{T_d} \ldots.(11)$$

If an individual after getting infected, infects exactly R_0 new individuals only after exactly a time γ^{-1} has passed, the number of infectious individuals over time grows as

$I(t) = I_0 \, R_0^{t\gamma}$,

$\ln[I(t)] = \ln[I_0] + t\gamma \ln[R_0]$.

The underlying matching differential equation is

$$\frac{dI(t)}{dt} = I(t)\,\gamma\,\ln[R_0]\,,$$

or

$$\frac{d\ln[I(t)]}{dt} = \ln[R_0]\ \gamma \ldots.(12)$$

Substituting Eq. (9) in Eq. (12) leads to

K= $\gamma\ \ln[R_0]$ or

$$R_0 = e^{\frac{K}{\gamma}} \ldots(13)$$

In conclusion to summarize the steps to estimate the value of $\boldsymbol{\beta}$ effective contact rate,

1- From the table of cases, calculate the doubling time T_d.

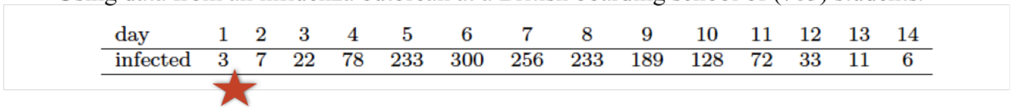
2- From Eq. (11) , calculate the logarithmic growth rate $K = \frac{\ln 2}{T_d}$.

3- Using Eq. (13) to find the basic reproducing number $R_0 = e^{\frac{K}{\gamma}}$.

4- Eq. (8) helps us to estimate the value of the effective contact rate $\beta = \gamma \cdot R_0$.

Example

Using data from an influenza outbreak at a British boarding school of (763) students.



day	1	2	3	4	5	6	7	8	9	10	11	12	13	14
infected	3	7	22	78	233	300	256	233	189	128	72	33	11	6

Based on knowledge of influenza we know that it has an infectious period of 1–3 days, D is the time an mean infected individual is infectious →

D=[(1+3)/2]=2 →

The recovery rate = 1/D
so we can take $\gamma = 1/2$ as our estimate.
There were three new infections →

R0 =3 in the first two days
we can use the definition of the basic reproduction number $R_0 = \beta/\gamma$
so this would give $\beta \simeq 3 * 1/2 = 1.5$
In large population $\beta=\beta/N$ → $\beta=1.5/763$

For initial conditions we assume the outbreak was started by a single infective at $t = 0$ so $I(0) = 1$ and $S(0) = 762$.

$$\frac{dS}{dt} = -\beta SI,$$

$$\frac{dI}{dt} = \beta SI - \gamma I,$$

$$\frac{dR}{dt} = \gamma I.$$

With initial conditions

$$S(0) = 762,\ I(0) = 1,\ \ R(0) = 0$$

To check the value of N: $762 + 1 + 0 = 763.$

If we substitute the values of $\gamma = 0.5 \text{ day}^{-1}$, $\beta = 2.18 \times 10^{-3} \text{ day}^{-1}$ in the above system, we get

$$\frac{dS}{dt} = -0.00218\, S\, I = f(S, I, R)$$

$$\frac{dI}{dt} = 0.00218\, S\, I - 0.5\, I = g(S, I, R)$$

$$\frac{dR}{dt} = 0.5\, I = h(S, I, R)$$

the Euler formulas become

$$S(k+1) = S(k) + \Delta t * \ f(S_k, I_k, R_k)$$

$$I(k+1) = I(k) + \Delta t * \ g(S_k, I_k, R_k)$$

$$R(k+1) = R(k) + \Delta t * \ h(S_k, I_k, R_k)$$

$$S(k+1) = S(k) + \Delta t * [\, -0.00218\, S(k) I(k)]$$

$$I(k+1) = I(k) + \Delta t * [\, 0.00218\, S(k) I(k) - 0.5\, I(k)]$$

$$R(k+1) = R(k) + \Delta t * \ [0.5\, I(k)]$$

Take k=0, $\Delta t = 1$

$$S(1) = S(0) \ - 0.00218\, S(0)\, I(0)$$

$$I(1) = I(0) + \ 0.00218\, S(0)\, I(0) - 0.5\, I(0)$$

$$R(1) = R(0) + \ 0.5\, I(0)$$

$$S(1) = 762 \ - 0.00218 * 762 * \ 1 = 760$$

$$I(1) = 1 + \ 0.00218 * \ 762 * 1 - 0.5 * 1 = 2$$

$$R(1) = 0 + \ 0.5 * 1 = 1$$

To check the value of N: $760 + 2 + 1 = 763$

Take k=1

$$S(2) = 760 \ - 0.00218 * 760 * \ 2 = 756$$

$$I(2) = 1 + 0.00218 * 760 * 2 - 0.5 * 2 = 4$$

$$R(2) = 0 + 0.5 * 1 = 3$$

To check the value of N: $756 + 4 + 3 = 763,$

we can continue with the steps until the susceptible group vanish and recovery group become the maximum.

Another method to solve the initial value problem with system of differential equation, we could use the MATLAB code or Mable code to find the approximation solution as :

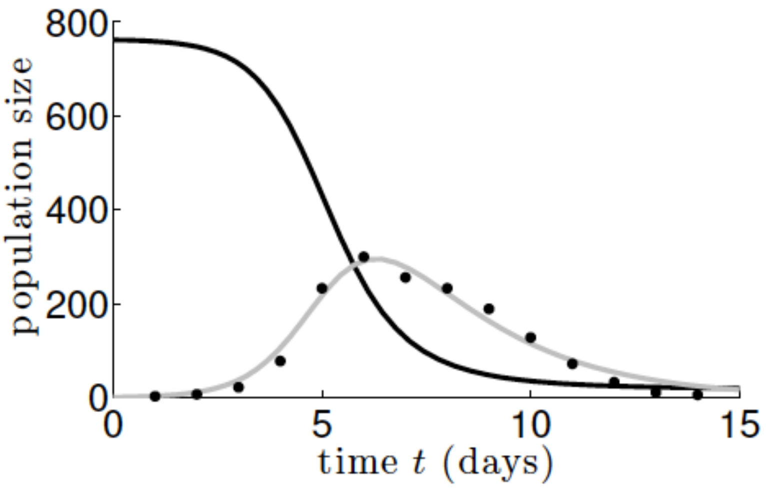
Listing 5.2: MATLAB code: c_pe_epidemic.m

```
function c_pe_epidemic
global beta gamma N;

tend = 15; %set the end time to run the simulation
u0 = [762; 1]; %set initial conditions as a column vector
beta=2.18*10^(-3); gamma=0.44;
[tsol, usol] = ode45(@rhs, [0, tend], u0);
Ssol = usol(:, 1); Isol = usol(:, 2);
plot(tsol, Ssol, ’r’); hold on; plot(tsol, Isol, ’b’);

function udash = rhs(t, u)
global betaf gamma N;
S=u(1); I=u(2);
lambda = beta*I; %force of infection
Sdash = -lambda*S;
Idash = lambda*S - gamma*I;
udash = [Sdash; Idash];
```

or

Listing 5.1: Maple code: c_pe_epidemic.mpl

```
restart:with(plots):with(DEtools):
unprotect(gamma); gamma:=’gamma’:
interface(imaginaryunit=i);

beta:=2.18*10^(-3): gamma:=0.44:
de1 := diff(S(t),t)=-beta*S(t)*I(t);
de2 := diff(I(t),t)=beta*S(t)*I(t)-gamma*I(t);
inits:=[S(0)=762,I(0)=1]:
myopts:=stepsize=0.1,arrows=NONE:
plot1:=DEplot([de1,de2],[S,I],t=0..30,[inits],scene=[t,S],linecolour=black,myopts):
plot2:=DEplot([de1,de2],[S,I],t=0..30,[inits],scene=[t,I],linecolour=red,myopts):
display(plot1,plot2);
```



2- Predator and Prey Model (Lotka-Volterra Model)

There are several types of predator-prey interactions: that of herbivores, which eat plant species, that of carnivores, which eat animal species, that of parasites, which live on or in another species (the host), and that of cannibals, which eat their own species and which is often an interaction between the adults and young.

One interesting example of a predator-prey interaction occurred in the late nineteenth century when the American citrus industry was almost destroyed by the accidental introduction from Australia of the cottony cushion scale insect. To combat this pest, its natural predator, the Australian ladybird beetle, was also imported, but this did not solve the problem and finally DDT was used to kill both predator and prey in a bid to eradicate the pest. Surprisingly, application of DDT to the orchards led to an increase in the scale insects, the original pest, suggesting that the use of pesticide is advantageous to the pest!

Model Assumptions

- Initially we assume the populations are large, sufficiently large to neglect random differences between individuals.
- We assume there are only two populations, the predator and the prey, that affect the ecosystem.
- We assume that the prey population grows exponentially in the absence of a predator.
- We ignore the effect of DDT initially, but modify the model later to incorporate its impact on the system.

Compartmental model

Determine a compartment diagram and appropriate word equation for each of the two populations, the predator and the prey.

Solution:

The only inputs for each population are births and the only outputs are deaths. However, the prey deaths occur due to the predators capturing and eating them. This is illustrated in the input-output compartmental diagram of the Figure below:

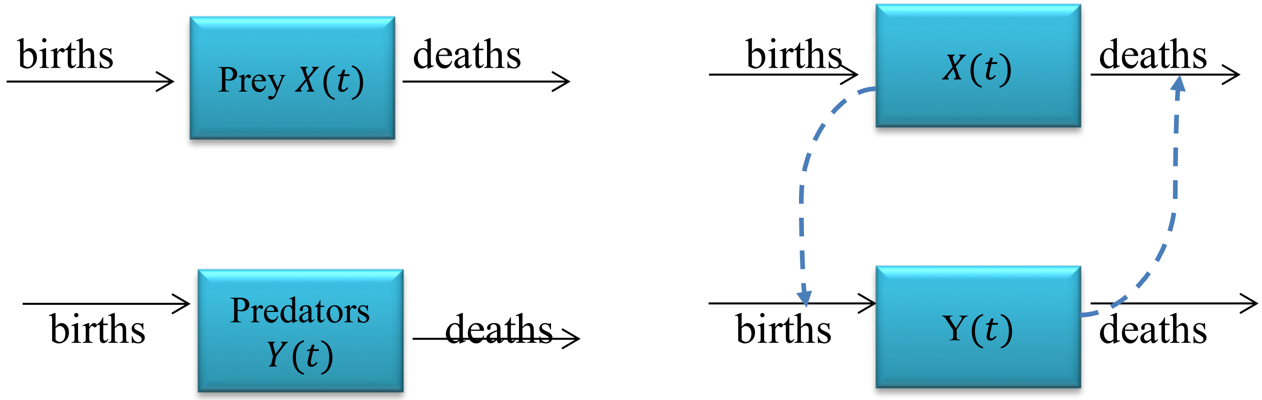


Figure : Input-output diagram for the 2-species predator-prey model. The additional diagram on the right includes dashed arrows illustrating how the different compartments influence the input and output rates.

Here we further distinguish between natural prey deaths and prey deaths due to predators. We also distinguish between natural predator births, occurring in the absence of prey, and the additional births that would occur due to the predators having more food from eating prey. The appropriate word equations are:

$$\left\{\begin{matrix}\text{rate of}\\ \text{change of}\\ \text{prey}\end{matrix}\right\} = \left\{\begin{matrix}\text{rate of}\\ \text{natural prey}\\ \text{births}\end{matrix}\right\} - \left\{\begin{matrix}\text{rate of}\\ \text{natural prey}\\ \text{deaths}\end{matrix}\right\} - \left\{\begin{matrix}\text{rate of}\\ \text{prey killed}\\ \text{by predators}\end{matrix}\right\},$$

$$\left\{\begin{matrix}\text{rate of}\\ \text{change of}\\ \text{predators}\end{matrix}\right\} = \left\{\begin{matrix}\text{rate of}\\ \text{natural}\\ \text{predators}\\ \text{births}\end{matrix}\right\} - \left\{\begin{matrix}\text{rate of}\\ \text{natural predators}\\ \text{deaths}\end{matrix}\right\} + \left\{\begin{matrix}\text{additianl}\\ \text{rate of}\\ \text{predators}\\ \text{births}\end{matrix}\right\} \qquad \dots (7)$$

Governing Equations

Let $X(t)$ denote the number of prey per unit area and $Y(t)$ the number of predators per unit area. Using the above assumptions and the word equations (7), formulate differential equations for the prey and predator densities.

$$\left\{\begin{matrix}\text{rate of}\\ \text{prey}\\ \text{births}\end{matrix}\right\} = b_1 X(t)$$

$$\dots (8)$$

$$\left\{\begin{matrix}\text{rate of}\\ \text{prey}\\ \text{natural deaths}\end{matrix}\right\} = a_1X(t)$$

$$\left\{\begin{matrix}\text{rate of}\\ \text{prey killed}\\ \text{by predators}\end{matrix}\right\} = c_1Y(t)X(t)$$

$$\left\{\begin{matrix}\text{natural}\\ \text{rate of}\\ \text{predators}\\ \text{births}\end{matrix}\right\} = b_2Y$$

$$\left\{\begin{matrix}\text{rate of}\\ \text{predators}\\ \text{natural deaths}\end{matrix}\right\} = a_2Y(t) \qquad \ldots(9)$$

$$\left\{\begin{matrix}\text{additianal}\\ \text{rate of}\\ \text{predators}\\ \text{births}\end{matrix}\right\} = c_2Y(t)X(t)$$

Now substitute equations (8) and (9) in (7). We obtain:

$$\therefore \frac{dX}{dt} = b_1X - a_1X - c_1XY, \qquad \frac{dY}{dt} = b_2Y - a_2Y + c_2XY$$

Let $\beta = b_1 - a_1$and $-\alpha = b_2 - a_2$ .Then

$$\frac{dX}{dt} = \beta X - c_1XY, \qquad \frac{dY}{dt} = -\alpha Y + c_2XY \qquad \ldots(10)$$

where we assume that β, α, c_1 and c_2 are all positive constants.

Example:

Check the Lotka–Volterra model in the limiting cases of prey with no predators, or predators with no prey.

Solution:

Suppose there are no predators $Y = 0$.

The equations then reduce to

$$\therefore \frac{dX}{dt} = \beta X,$$

which is the equation for exponential growth. The prey grows exponentially.

If there are no prey, then $X = 0$

$$\therefore \frac{dY}{dt} = -\alpha Y,$$

That is, exponential decay, which means that the predators population decreases exponentially and dies out.

Example:

With $\beta = 1,\ \alpha = 0.5,\ c_1 = 0.01$ and $c_2 = 0.005$

and initial conditions $X(0) = 200,\ Y(0) = 80.$

Solve the system of differential equation (10).n

Solution:

$\frac{dX}{dt} = X - 0.01\,XY$ and $\frac{dY}{dt} = -0.5\,Y + 0.005\,XY$

with initial conditions:

$X(0) = 200,\ Y(0) = 80$

$f(X,Y) = X - 0.01\,XY$ and

$g(X,Y) = -0.5\ Y + 0.005\,XY$

the Euler formulas become

$$X(k+1) = X(k) + \Delta t * \ f(X_k, Y_k)$$

$$Y(k+1) = Y(k) + \Delta t * \ g(X_k, Y_k)$$

$$X(k+1) = X(k) + \Delta t * [\,X_k - 0.01\,X_k Y_k]$$

$$Y(k+1) = Y(k) + \Delta t * [-0.5\,Y_k + 0.005\,X_k Y_k\,]$$

Take k=0, Δt =1, we get:

$$X(1) = X(0) + [X(0) - 0.01\,X(0)Y(0)]$$

$$Y(1) = Y(0) + [-0.5Y(0) + 0.005\,X(0)Y(0)\,]$$

substituting $X(0) = 200,\ Y(0) = 80$ into above equations, we get:

$$X(1) = 200 + [200 - 0.01 * 200 * 80]$$

$$X(1) = 200 + 40 = 240$$

$$Y(1) = 80 + [-0.5 * 80 + 0.005 * 200 * 80]$$

$$Y(1) = 80 + [-40 + 0.005 * 200 * 80]$$

$$Y(1) = 80 + [-40 + 80] = 120$$

Take k=1

$$X(2) = 240 + [240 - 0.01 * 240 * 120]$$

$$X(2) = 192$$

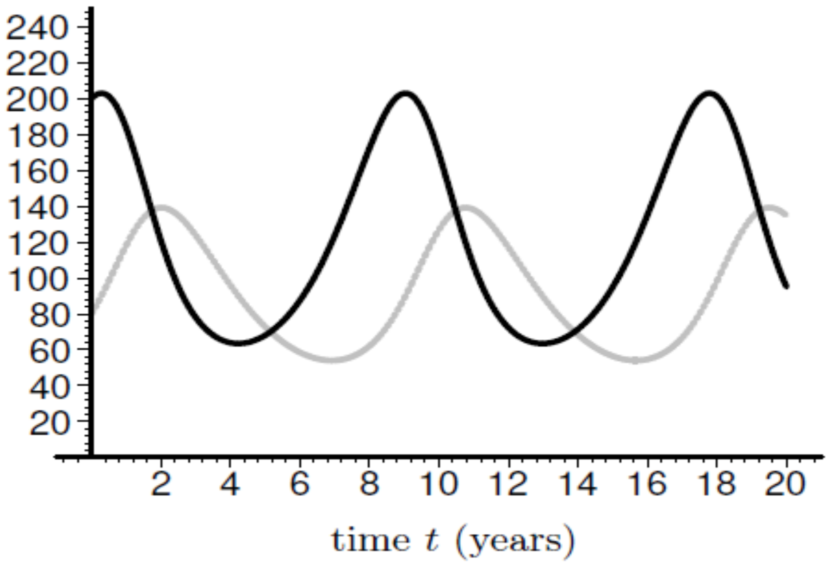
$$Y(2) = 120 + [-0.5 * 120 + 0.005 * 240 * 120]$$

$$Y(2) = 120 + 84$$

$$Y(2) = 204$$

Listing 5.4: MATLAB code: c_pe_predprey.m

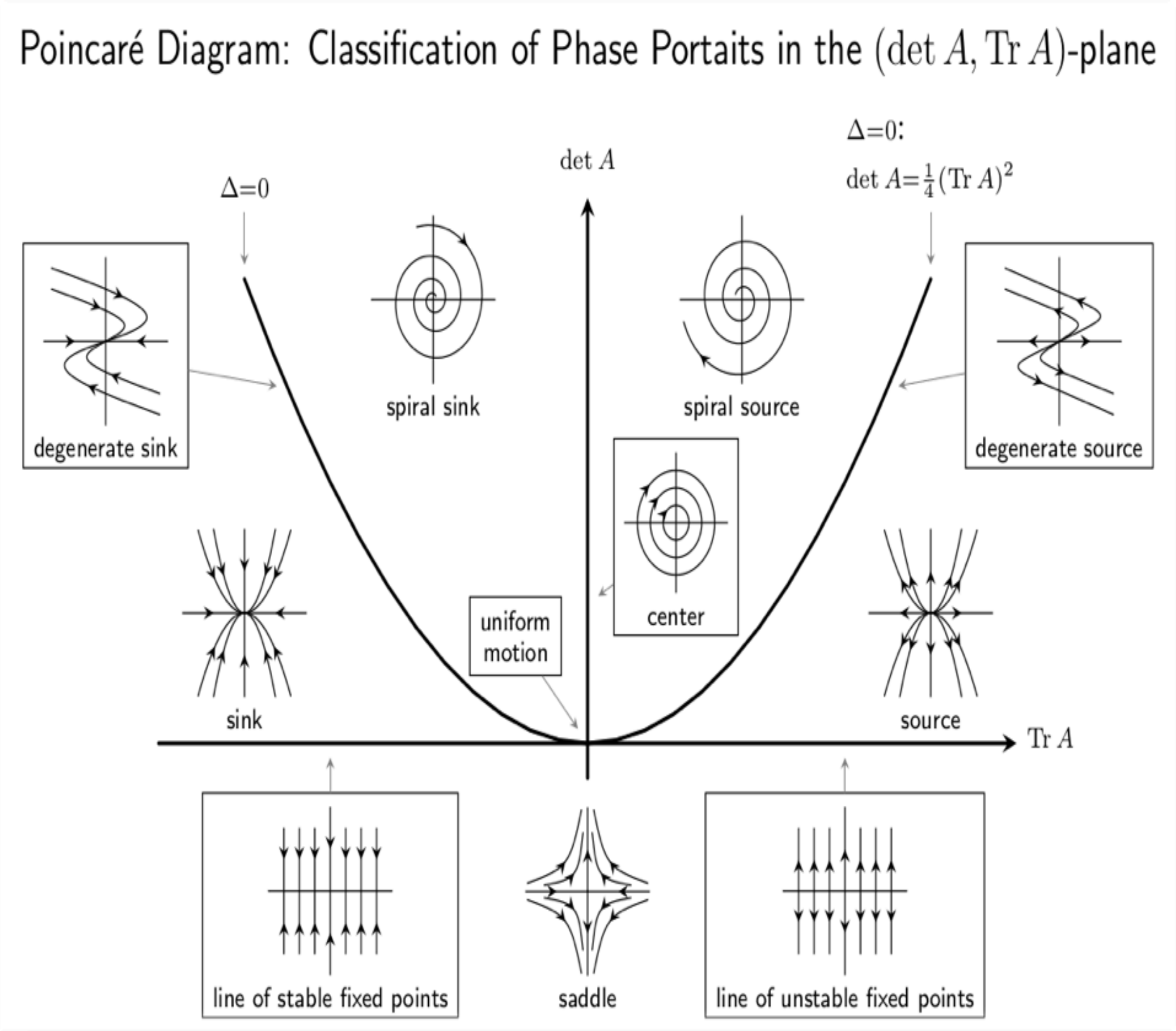
```
function c_cp_predprey
global beta1 alpha2 c1 c2;

beta1=1.0; alpha2=0.5; c1=0.01; c2=0.005;
tend = 20;     %set the end time to run the simulation
u0 = [200; 80]; %set initial conditions as column vector
[tsol, usol] = ode45(@rhs, [0, tend], u0);
Xsol = usol(:, 1); Ysol = usol(:, 2);
plot(tsol, Xsol, ’b’); hold on; plot(tsol, Ysol, ’r’);

function udot = rhs(t, u)
global beta1 alpha2 c1 c2;
X = u(1); Y=u(2);
Xdot = beta1*X - c1*X*Y;
Ydot = -alpha2*Y + c2*X*Y;
udot = [Xdot; Ydot];
```



Phase-Plane Analysis for Predator and Prey Model

Steps to find Phase plane for nonlinear system

1- Find the equilibrium points.
2- Find the Jacobian matrix.
3- linearize the system of nonlinear equations and derive the linearized system.
4- From the eigenvalues of the Jacobian matrices, classify any equilibrium point.
5- Sketch the trajectory behavior in the phase plane close to this point.



Poincaré Diagram: Classification of Phase Portaits in the $(\det A, \operatorname{Tr} A)$-plane

Example1 :

- Find the linearised for model with the prey population grows exponentially in the absence of a predator.

$$X' = \beta\, X - c_1XY$$
$$Y' = -\alpha\, Y + c_2XY$$

and hence classify all equilibrium points of the basic predator-prey model.

$$\beta X - c_1XY = 0 \longmapsto X(\beta - c_1Y) = 0$$

either $X = 0$ or $\beta - c_1Y = 0 \rightarrow Y = \frac{\beta}{c_1}$

$$-\alpha\, Y + c_2XY = 0 \longmapsto Y(-\alpha + c_2X)$$

either $Y = 0$ or $-\alpha + c_2X = 0 \rightarrow X = \frac{\alpha}{c_2}$

$\therefore$ (0,0) and $(\frac{\alpha}{c_2}, \frac{\beta}{c_1})$ are equilibrium points.

$$F(X,Y) = \beta\, X - c_1XY$$
$$\frac{\partial F}{\partial X} = \beta - c_1Y$$
$$\frac{\partial F}{\partial Y} = -c_1X$$

$$G(X,Y) = -\alpha\, Y + c_2XY$$
$$\frac{\partial G}{\partial X} = c_2Y$$
$$\frac{\partial G}{\partial Y} = -\alpha + c_2X$$

$*$ For $(X_e, Y_e) = (0,0)$

$$\mathrm{J} = \begin{bmatrix} \beta - c_1Y & -c_1X \\ c_2Y & -\alpha + c_2X \end{bmatrix}$$
$$= \begin{bmatrix} \beta & 0 \\ 0 & -\alpha \end{bmatrix}$$

with $det(A) = -\beta\alpha < 0 \quad \longmapsto \quad$ (0,0)is saddle point.

$*$ For $(X_e, Y_e) = (\frac{\alpha}{c_2}, \frac{\beta}{c_1})$

$$\mathrm{J} = \begin{bmatrix} \beta - c_1\dfrac{\beta}{c_1} & -c_1\dfrac{\alpha}{c_2} \\ c_2\dfrac{\beta}{c_1} & -\alpha + c_2\dfrac{\alpha}{c_2} \end{bmatrix}$$

$$= \begin{bmatrix} 0 & -\frac{c_1\alpha}{c_2} \\ \frac{\beta c_2}{c_1} & 0 \end{bmatrix}$$

$Tr(A) = 0$ and $det(A) = \frac{c_1\alpha}{c_2} . \frac{\beta c_2}{c_1} = \alpha\,\beta$

$$\therefore \left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\right) \quad \text{is center.}$$

Example2 :

- Find the linearised for model with the prey population grows logistically in the absence of a predator.

$$X' = \beta X\left(1-\frac{X}{K}\right) - c_1XY$$
$$Y' = -\alpha Y + c_2XY$$

and hence classify all equilibrium points of the basic predator-prey model.
From the first equation:

$$F(X,Y) = \beta X\left(1-\frac{X}{K}\right) - c_1XY = 0 \longmapsto X\left(\beta\left(1-\frac{X}{K}\right) - c_1Y\right) = 0$$

either $X = 0$ or $\left(\beta\left(1-\frac{X}{K}\right) - c_1Y\right) = 0$

If we substitute $X = 0$ in $= -\alpha Y + c_2XY$, we get: $Y = 0$.

From the second equation:

$$G(X,Y) = Y(-\alpha + c_2X) = 0$$

either $Y = 0$ or $-\alpha + c_2X = 0 \to X = \frac{\alpha}{c_2}$
If we substitute $X = \frac{\alpha}{c_2}$ in $\beta X\left(1-\frac{X}{K}\right) - c_1XY$, we get:

$$\beta\frac{\alpha}{c_2}\left(1-\frac{\frac{\alpha}{c_2}}{K}\right) - c_1\frac{\alpha}{c_2}Y = 0$$
$$\beta\left(1-\frac{\alpha}{c_2K}\right) - c_1Y = 0$$
$$Y = \frac{\beta}{c_1}\left(1-\frac{\alpha}{c_2K}\right)$$

$\therefore$ (0,0) and $\left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\left(1-\frac{\alpha}{c_2K}\right)\right)$ are equilibrium points.

$$F(X,Y) = \beta X\left(1-\frac{X}{K}\right) - c_1XY \qquad G(X,Y) = -\alpha Y + c_2XY$$
$$\frac{\partial F}{\partial X} = \beta - 2\frac{\beta X}{K} - c_1Y \qquad \frac{\partial G}{\partial X} = c_2Y$$
$$\frac{\partial F}{\partial Y} = -c_1X \qquad \frac{\partial G}{\partial Y} = -\alpha + c_2X$$

$*$ For $(X_e, Y_e) = (0,0)$

$$\mathrm{J} = \begin{bmatrix} \beta - 2\,\dfrac{\beta X}{K} - c_1 Y & -c_1 X \\ c_2 Y & -\alpha + c_2 X \end{bmatrix}$$

$$= \begin{bmatrix} \beta & 0 \\ 0 & -\alpha \end{bmatrix}$$

with $det(A) = -\beta\alpha < 0 \quad \longmapsto \quad$ (0,0)is saddle point.

$*$ For $(X_e, Y_e) = \left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\left(1 - \frac{\alpha}{c_2 K}\right)\right)$

$$= \begin{bmatrix} -\dfrac{\beta\alpha}{c_2 K} & -\dfrac{c_1\alpha}{c_2} \\ \dfrac{\beta c_2}{c_1}\left(1 - \dfrac{\alpha}{c_2 K}\right) & 0 \end{bmatrix}$$

$Tr(A) = -\dfrac{\beta\alpha}{c_2 K} < 0$ and $det(A) = \dfrac{c_1\alpha}{c_2} . \dfrac{\beta c_2}{c_1}\left(1 - \dfrac{\alpha}{c_2 K}\right) = \alpha\beta\left(1 - \dfrac{\alpha}{c_2 K}\right) > 0$

and according the values of the model paramete

$$\frac{Tr(A)^2}{4} < \Delta$$

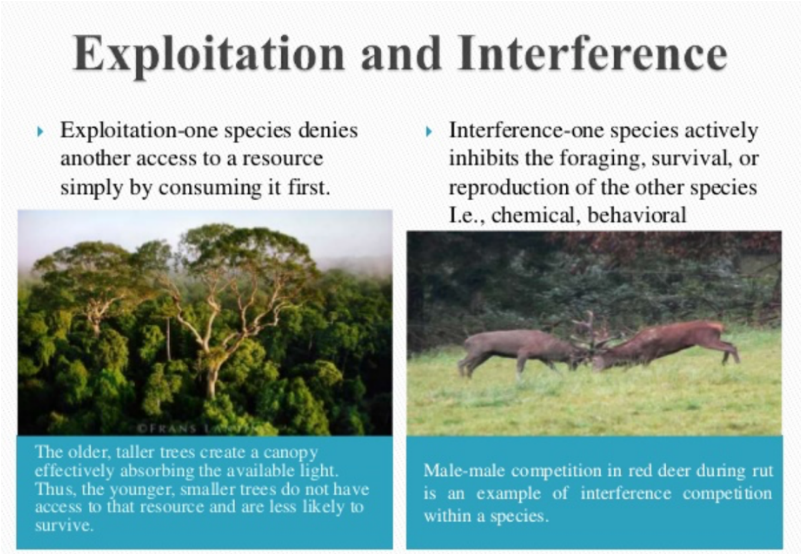
$\therefore \left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\left(1 - \frac{\alpha}{c_2 K}\right)\right)$ is stable spiral.

3-Competing Species Interaction (Lotka-Volterra Competition) Model

Another simple ecosystem to model is that of competing species, where two (or more) populations compete for limited resources such as food or territory. There are two aspects of competition: exploitation, when the competitor uses the resource itself and interference, where the population behaves in such a manner as to prevent the competitor from utilizing the resource. This system is very similar to the predator-prey model of the previous section; however, the terms describing the interaction between the species differ. As a result of competitions, either leads to competitive exclusion, local elimination of a competing species or coexistence of a single species or different species within a habitat but in different niches

Interspecific vs. Intraspecific Competition

- When competition is between individuals of:
  ---- same species (***intraspecific***)
  ---- different species (***interspecific***)



Exploitation and Interference

- Exploitation-one species denies another access to a resource simply by consuming it first.
- Interference-one species actively inhibits the foraging, survival, or reproduction of the other species I.e., chemical, behavioral

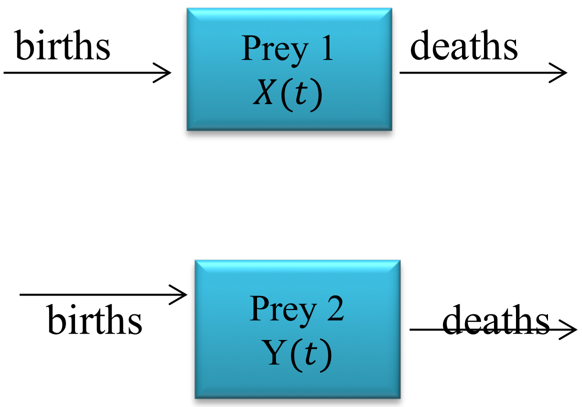
The older, taller trees create a canopy effectively absorbing the available light. Thus, the younger, smaller trees do not have access to that resource and are less likely to survive.

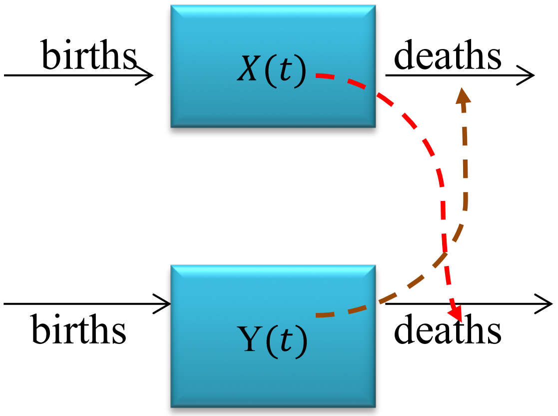
Male-male competition in red deer during rut is an example of interference competition within a species.

Model assumptions

- We assume the populations to be sufficiently large so that random fluctuations can be ignored without consequence.
- We assume that the two-species model reflects the ecosystem sufficiently accurately.
- We assume each population grows exponentially in the absence of the other competitor(s), although we later incorporate density-dependent growth for each.

General compartmental model





In words, we have for each population in the system

$$\left\{\begin{matrix}\text{rate of}\\ \text{change of}\\ \text{population}\end{matrix}\right\} = \left\{\begin{matrix}\text{rate of}\\ \text{population}\\ \text{births}\end{matrix}\right\} - \left\{\begin{matrix}\text{rate of}\\ \text{population}\\ \text{deaths}\end{matrix}\right\} \qquad \dots(11)$$

Formulating the differential equations

Since neither population is dependent on the other, we let the positive constants β_1 and β_2 describe the per-capita birth rates for species X and Y, respectively.

Since the two populations are competing for the same resource, the density of each population has a restraining effect, proportional to this density, on the other. So, the per-capita death rate for Y is proportional to X, and that for X is proportional to Y , which in symbols is

$$\left\{\begin{matrix}\text{rate of}\\ \text{species X}\\ \text{deaths}\end{matrix}\right\} = (c_1 Y)X, \qquad \left\{\begin{matrix}\text{rate of}\\ \text{species Y}\\ \text{deaths}\end{matrix}\right\} = (c_2 X)Y \qquad \dots(12)$$

Our model becomes

$$\frac{dX}{dt} = \beta_1 X - c_1 XY, \qquad \frac{dY}{dt} = \beta_2 Y - c_2 XY \qquad \ldots (13)$$

Example:

With the new competing system and

$$\beta_1 = 0.22, \qquad \beta_2 = 0.06$$

$$c_1 = 0.05 \qquad c_2 = 0.005$$

$$X(0) = 0.5 \qquad Y(0) = 1.5$$

Find the numerical solution.

Solution:

$\frac{dX}{dt} = 0.22\,X - 0.05\,XY, \qquad \frac{dY}{dt} = 0.06\,Y - 0.005\,XY$

with initial conditions $X(0) = 0.5$ and $Y(0) = 1.5$

$f(X,Y) = 0.22\,X - 0.05\,XY$ and

$g(X,Y) = 0.06\,Y - 0.005\,XY$

the Euler formulas become

$$X(k+1) = X(k) + \Delta t * f(X_k, Y_k)$$

$$Y(k+1) = Y(k) + \Delta t * g(X_k, Y_k)$$

$$X(k+1) = X(k) + \Delta t * [\,0.22X_k - 0.05\,X_k Y_k]$$

$$Y(k+1) = Y(k) + \Delta t * [0.06\,Y_k - 0.005\,X_k Y_k\,]$$

Take k=0, Δt =1, we get:

$$X(1) = X(0) + [0.22\,X(0) - 0.05\,X(0)Y(0)]$$

$$Y(1) = Y(0) + [0.06\,Y(0) - 0.005\,X(0)Y(0)\,]$$

substituting $X(0) = 0.5$, $Y(0) = 1.5$ into above equations, we get:

$$X(1) = 0.5 + [0.11 - 0.05 * 0.5 * 1.5]$$

$$X(1) = 0.5 + .073 = 0.573$$

$$Y(1) = 1.5 + [0.06 * 1.5 - 0.005 * 0.5 * 1.5]$$

$$Y(1) = 1.5 + [0.09 - 0.00375] = 1.586$$

Take k=1

$$X(2) = 0.573 + [0.126 - 0.05 * 0.573 * 1.586]$$

$$X(1) = 0.573 + [0.126 - 0.045] = 0.654$$

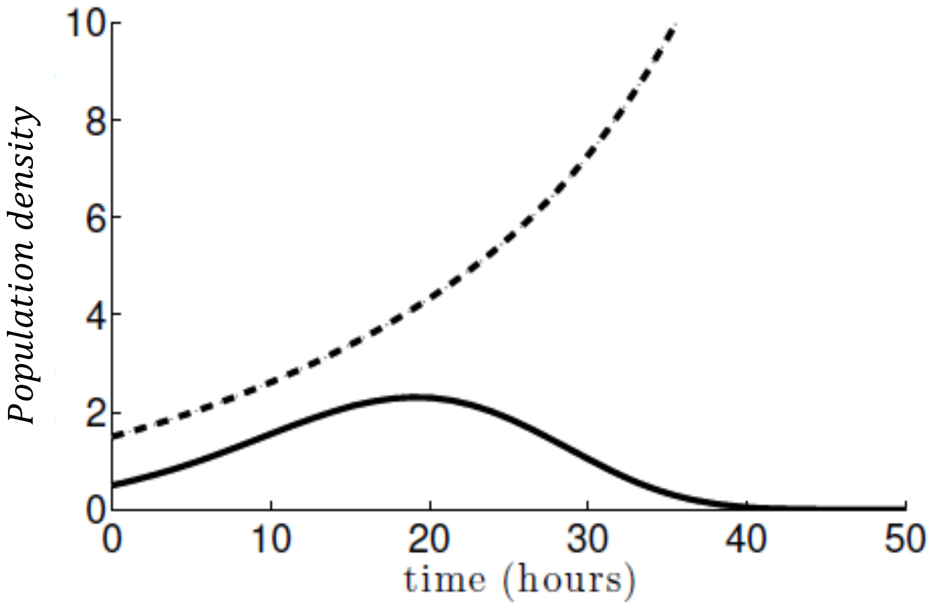
$$Y(2) = 1.586 + [0.06 * 1.586 - 0.005 * 0.654 * 1.586]$$

$$Y(2) = 1.586 + [0.095 - 0.005] = 1.676$$

…

Listing 5.5: MATLAB code: c_pe_compet.m

```
function c_pe_compet
global beta1 beta2 c1 c2;
beta1=0.22; beta2=0.06;
c1=0.053; c2=0.0046;
tend = 50; %the end time
u0 = [0.5; 1.5]; %set IC
[tsol, usol] = ode45(@rhs, [0, tend], u0);
Xsol = usol(:,1); Ysol = usol(:,2);
plot(tsol, Xsol, 'b'); hold on;
plot(tsol, Ysol, 'r:');
axis([0, tend, 0, 10]);

function udot = rhs(t, u)
global beta1 beta2 c1 c2;
X = u(1); Y=u(2);
Xdot = beta1*X - c1*X*Y;
Ydot = beta2*Y - c2*X*Y;
udot = [Xdot; Ydot];
```



Density-Dependent (Logistic) Growth

In 1932, the Russian microbiologist Gause described an experiment with two strains of yeast, Saccharomyces cervevisiae and Schizosaccharomyces kefir, hereafter called Species X and Species Y. These are described in Renshaw (1991). Gause found that, grown on their own, each species exhibited a logistic growth curve, but when grown together, the growth pattern changed with Species X dying out. We now extend the competition model to account for logistic growth in both species, in the absence of the other species. Let K_1 and K_2 be the carrying capacities for Species X and Y , respectively. Then including density-dependent growth in (13), we have

$$\frac{dX}{dt} = \beta_1 \, X\left(1 - \frac{X}{K_1}\right) - c_1XY, \qquad \frac{dY}{dt} = \beta_2 \, Y\left(1 - \frac{Y}{K_2}\right) - c_2XY \quad \text{... (14)}$$

With $d_1 = \frac{\beta_1}{K_1}$ and $d_2 = \frac{\beta_2}{K_2}$, system (14) becomes

$$\frac{dX}{dt} = \beta_1 \, X - d_1X^2 - c_1XY,$$

$$\frac{dY}{dt} = \beta_2 \, Y - d_2Y^2 - c_2XY \quad \text{... (15)}$$

Example:

With the new competing system logistic growth and

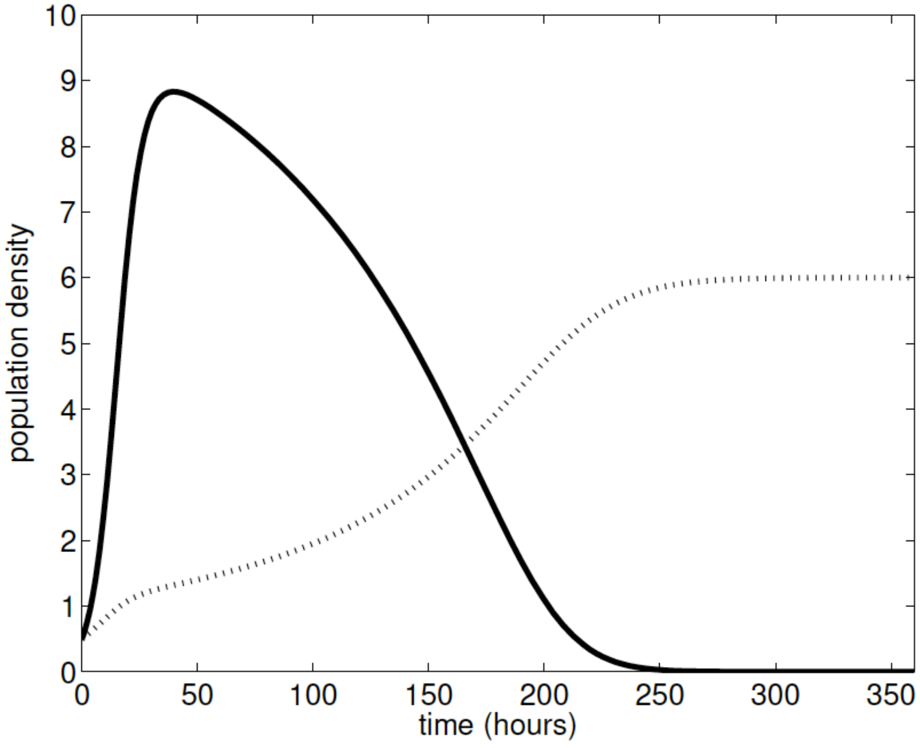
$$\beta_1 = 0.22, \qquad \beta_2 = 0.06$$
$$c_1 = 0.05 \qquad c_2 = 0.005$$
$$d_1 = 0.017 \qquad d_2 = 0.010$$
$$x(0) = 0.5 \qquad y(0) = 0.5$$

Find the numerical solution

Solution:

$$\frac{dX}{dt} = 0.22\,X - 0.017\,X^2 - 0.05\,XY, \qquad \frac{dY}{dt} = 0.06\,Y - 0.010Y^2 - 0.005XY$$

Note that these parameters correspond to the carrying capacities (in the absence of the other species) of $K_1 = \frac{\beta_1}{d_1} = 13.0$ and of $K_2 = \frac{\beta_2}{d_2} = 6.0$.



Phase-Plane Analysis for Competing Species Interaction

Example1 :

- Find the linearised for model with the prey population grows exponentially in the absence of a predator.

$$X' = \beta_1 X - c_1 XY$$
$$Y' = \beta_2 Y - c_2 XY$$

and hence classify all equilibrium points of the basic predator-prey model.

$$\beta_1 X - c_1 XY = 0 \longmapsto X(\beta_1 - c_1 Y) = 0$$

either $X = 0$ or $\beta_1 - c_1 Y = 0 \to Y = \frac{\beta_1}{c_1}$

$$\beta_2 Y + c_2 XY = 0 \longmapsto Y(\beta_2 + c_2 X)$$

either $Y = 0$ or $\beta_2 + c_2 X = 0 \to X = \frac{\beta_2}{c_2}$

$\therefore$ (0,0) and $(\frac{\beta_2}{c_2}, \frac{\beta_1}{c_1})$ are equilibrium points.

$$F(X,Y) = \beta_1 X - c_1 XY \qquad G(X,Y) = \beta_2 Y - c_2 XY$$
$$\frac{\partial F}{\partial X} = \beta_1 - c_1 Y \qquad \frac{\partial G}{\partial X} = -c_2 Y$$
$$\frac{\partial F}{\partial Y} = -c_1 X \qquad \frac{\partial G}{\partial Y} = \beta_2 - c_2 X$$

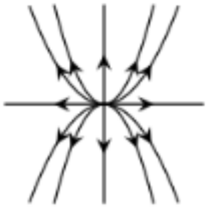
$*$ For $(X_e, Y_e) = (0,0)$

$$\begin{aligned} \mathrm{J} &= \begin{bmatrix} \beta_1 - c_1 Y & -c_2 Y \\ -c_1 X & \beta_2 - c_2 X \end{bmatrix} \\ &= \begin{bmatrix} \beta_1 & 0 \\ 0 & \beta_2 \end{bmatrix} \end{aligned}$$

with $det(A) = \beta_1 \beta_2 > 0$. the point $(X_e, Y_e) = (0,0)$ is not saddle point,

$Tr(A) = \beta_1 + \beta_2 > 0$ the point $(X_e, Y_e) = (0,0)$ is unstable,

$$\frac{Tr(A)^2}{4} = \frac{(\beta_1 + \beta_2)^2}{4} = \frac{(\beta_1)^2 + 2\beta_1\beta_2 + (\beta_2)^2}{4} > \beta_1\beta_2 = \det(A)$$



$\therefore$ (0,0) is unstable node (source)

$*$ For $(X_e, Y_e) = (\frac{\beta_2}{c_2}, \frac{\beta_1}{c_1})$

$$\mathrm{J} = \begin{bmatrix} \beta_1 - c_1 Y & -c_2 Y \\ -c_1 X & \beta_2 - c_2 X \end{bmatrix}$$

$$\mathrm{J} = \begin{bmatrix} \beta_1 - c_1 \dfrac{\beta_1}{c_1} & -c_2 \dfrac{\beta_1}{c_1} \\ -c_1 \dfrac{\beta_2}{c_2} & \beta_2 - c_2 \dfrac{\beta_2}{c_2} \end{bmatrix}$$

$$= \begin{bmatrix} 0 & -c_2 \dfrac{\beta_1}{c_1} \\ -c_1 \dfrac{\beta_2}{c_2} & 0 \end{bmatrix}$$

$Tr(A) = 0$ and $det(A) = c_1 \dfrac{\beta_2}{c_2} . c_2 \dfrac{\beta_1}{c_1} = \beta_1 . \beta_2 > 0$

$\therefore \left(\dfrac{\beta_2}{c_2}, \dfrac{\beta_1}{c_1}\right)$ is center.

Example2 :

- Find the linearised for model with the prey population grows logistically in the absence of a predator.

$$X' = \beta\, X\left(1 - \frac{X}{K}\right) - c_1XY$$
$$Y' = -\alpha\, Y + c_2XY$$

and hence classify all equilibrium points of the basic predator-prey model.
From the first equation:

$$F(X,Y) = \beta\, X\left(1 - \frac{X}{K}\right) - c_1XY = 0 \longmapsto X\left(\beta\left(1 - \frac{X}{K}\right) - c_1Y\right) = 0$$

either $X = 0$ or $\left(\beta\left(1 - \frac{X}{K}\right) - c_1Y\right) = 0$

If we substitute $X = 0$ in $= -\alpha\, Y + c_2XY$, we get: $Y = 0$.

From the second equation:

$$G(X,Y) = Y(-\alpha\ + c_2X) = 0$$

either $Y = 0$ or $-\alpha + c_2X = 0 \rightarrow X = \frac{\alpha}{c_2}$

If we substitute $X = \frac{\alpha}{c_2}$ in $\beta\, X\left(1 - \frac{X}{K}\right) - c_1XY$, we get:

$$\beta\,\frac{\alpha}{c_2}\left(1 - \frac{\frac{\alpha}{c_2}}{K}\right) - c_1\frac{\alpha}{c_2}Y = 0$$
$$\beta\,\left(1 - \frac{\alpha}{c_2K}\right) - c_1Y = 0$$
$$Y = \frac{\beta}{c_1}\left(1 - \frac{\alpha}{c_2K}\right)$$

$\therefore$ (0,0) and $\left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\left(1 - \frac{\alpha}{c_2K}\right)\right)$ are equilibrium points.

$$F(X,Y) = \beta\, X\left(1 - \frac{X}{K}\right) - c_1XY$$
$$\frac{\partial F}{\partial X} = \beta - 2\,\frac{\beta X}{K} - c_1Y$$
$$\frac{\partial F}{\partial Y} = -c_1X$$

$$G(X,Y) = -\alpha\, Y + c_2XY$$
$$\frac{\partial G}{\partial X} = c_2Y$$
$$\frac{\partial G}{\partial Y} = -\alpha + c_2X$$

$*$ For $(X_e, Y_e) = (0,0)$

$$\mathrm{J} = \begin{bmatrix} \beta - 2\,\frac{\beta X}{K} - c_1 Y & -c_1 X \\ c_2 Y & -\alpha + c_2 X \end{bmatrix}$$

$$= \begin{bmatrix} \beta & 0 \\ 0 & -\alpha \end{bmatrix}$$

with $det(A) = -\beta\alpha < 0 \quad \longmapsto \quad$ (0,0)is saddle point.

$*$ For $(X_e, Y_e) = \left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\left(1 - \frac{\alpha}{c_2 K}\right)\right)$

$$= \begin{bmatrix} -\frac{\beta\alpha}{c_2 K} & -\frac{c_1\alpha}{c_2} \\ \frac{\beta c_2}{c_1}\left(1 - \frac{\alpha}{c_2 K}\right) & 0 \end{bmatrix}$$

$Tr(A) = -\frac{\beta\alpha}{c_2 K} < 0$ and $det(A) = \frac{c_1\alpha}{c_2} . \frac{\beta c_2}{c_1}\left(1 - \frac{\alpha}{c_2 K}\right) = \alpha\beta\left(1 - \frac{\alpha}{c_2 K}\right) > 0$

and according the values of the model paramete

$$\frac{Tr(A)^2}{4} < \Delta$$

$$\therefore \left(\frac{\alpha}{c_2}, \frac{\beta}{c_1}\left(1 - \frac{\alpha}{c_2 K}\right)\right) \quad \text{is stable spiral.}$$

4-Model of a Battle

We now consider a novel type of population interaction: a destructive competition or battle between two opposing groups. These may be battles between two hostile insect groups, athletic teams, or human armies. While the models we derive here apply to the last case, the principles can be generalized and would apply to many other examples. The model we develop turns out to be a system of two coupled, linear differential equations.

Battles between armies have been fought since antiquity. In ancient times battles were primarily hand-to-hand combat. With the development of archery and then gunpowder, a crucial feature of battles has been aimed fire. Although many factors can affect the outcome of a battle, experience has shown that numerical superiority and superior military training are critical. The model we present was first developed in the 1920s by F. W. Lanchester who was also well known for his contributions to the theory of flight.

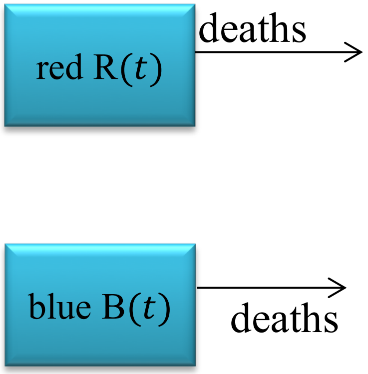
Our aim is to develop a simple model that predicts the number of soldiers in each army at any given time, provided we know the initial number of soldiers in each army (As with epidemics, we consider the number, rather than the density, of individuals.)

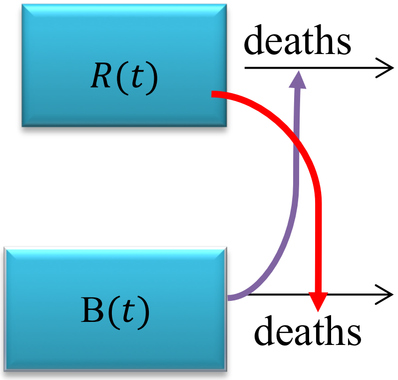
Model assumptions

- We assume the number of soldiers to be sufficiently large so that we can neglect random differences between them.
- We assume that there are no reinforcements and no operational losses (i.e., due to desertion or disease).
- Both armies use aimed fire

General compartmental model

The first step is to develop two-word equations that describe how the two populations change, based on the input-output principle of the balance law. Suppose the two opposing groups or populations are the red army and the blue army.





Example:

Determine the appropriate input-output diagram and associated word equations for the number of soldiers in both the red and blue armies. Since there are no reinforcements or operational losses, each population changes by the number of soldiers who are wounded by the other army. Thus, we can set up the input-output diagram as the previous Figure. and

$$\left\{\begin{matrix}\text{rate of}\\ \text{change of}\\ \text{red soldiers}\end{matrix}\right\} = -\left\{\begin{matrix}\text{rate red soldiers}\\ \text{wounded by}\\ \text{blue army}\end{matrix}\right\}$$

$$\left\{\begin{matrix}\text{rate of}\\ \text{change of}\\ \text{blue soldiers}\end{matrix}\right\} = -\left\{\begin{matrix}\text{rate blue soldiers}\\ \text{wounded by}\\ \text{red army}\end{matrix}\right\} \qquad \ldots (14)$$

In a real battle, there will be a mixture of shots: those fired directly at an enemy soldier and those fired into an area known to be occupied by an enemy, but where the enemy cannot be seen. Some battles may be dominated by one or the other firing method. We consider these two idealizations of shots fired as aimed fire and random fire. For the model, we assume only aimed fire for both armies.

In the aimed fire idealization, we assume all targets are visible to those firing at them. If the blue army uses aimed fire on the red army, then each time a blue soldier fires, he/she takes aim at an individual red soldier. The rate of loss of soldiers of the red army depends only on the number of blue soldiers firing at them and not on the number of red soldiers. We see later that this assumption is equivalent to assuming a constant probability of success (on average) for each bullet fired. For random fire, a soldier firing a gun cannot see his/her target but fires randomly into an area where enemy soldiers are known to be. The more enemy soldiers in that given area, the greater the rate of wounding. For random fire, we thus assume that the rate of enemy soldiers wounded is proportional to both the number firing and the number being fired at.

In summary, we make the following further assumptions:

- For aimed fire, the rate of soldiers wounded is proportional to the number of enemy's soldiers only.
- For random fire, the rate at which soldiers are wounded is proportional to both the number of soldiers.

Formulating the differential equations

Let $R(t)$ denote the number of soldiers of the red army and $B(t)$ the number of soldiers of the blue army. We assume aimed fire for both armies.

$$\left\{\begin{matrix}\text{rate red soldiers}\\ \text{wounded by}\\ \text{blue army}\end{matrix}\right\} = -a_1 B(t), \qquad \left\{\begin{matrix}\text{rate blue soldiers}\\ \text{wounded by}\\ \text{red army}\end{matrix}\right\} = -a_2 R(t) \qquad \dots(15)$$

where a_1 and a_2 are positive constants of proportionality. The constants a_1 and a_2 measure the effectiveness of the blue army and red army, respectively, and are called attrition coefficients.

We now substitute (15) into the basic word equation (14), where the rate of change in the number of red soldiers is $\frac{dR}{dt}$ and for the blue soldiers it is $\frac{dB}{dt}$. The two simultaneous differential equations are thus

$$\frac{dR}{dt} = -a_1 B, \qquad \frac{dB}{dt} = -a_2 R \qquad \dots(16)$$

Example:

During the Battle of Iwo Jima in the Pacific Ocean (1945), daily records were kept of all U.S. combat losses. These data are graphed and referenced in Braun (1979). The values of the attrition coefficients a_1 and a_2 have been estimated from the data

$a_1 = 0.0544$ and $a_2 = 0.0106$ and the initial numbers in the red and blue armies, respectively, were $r_0 = 66{,}454$ and $b_0 = 18{,}274$. Find the Numerical solution for the differential equations.

Solution:

$\frac{dR}{dt} = -0.0544\ B,$ $\qquad$ $\frac{dB}{dt} = -0.0106\ R$

with initial conditions $R(0) = 66454$ and $B(0) = 18274$
$f(R, B) = -0.0544\ B$ and

$g(R, B) = -0.0106\ R$

the Euler formulas become

$$R(k+1) = R(k) + \Delta t * \ f(R_k, B_k)$$

$$B(k+1) = B(k) + \Delta t * \ g(R_k, B_k)$$

$$R(k+1) = R(k) + \Delta t * [\,-0.05\ 44 * B(k)]$$

$$B(k+1) = B(k) + \Delta t * [-0.0106 * \ R(k)\,]$$

Take k=0, Δt =1, we get:

$$R(1) = R(0) + [-0.05\ 44 B(0)]$$

$$B(1) = B(0) + [-0.0106\ R(0)]$$

substituting $R(0) = 66454$, $B(0) = 18274$ into above equations, we get:

$$R(1) = 66454 + [-0.05\ 44 * 18274]$$

$$R(1) = 66454 - 994 = 65640$$

$$B(1) = 18274 + [-0.0106 * \ 66454]$$

$$B(1) = 18274 - 704 = 17570$$

Take k=1

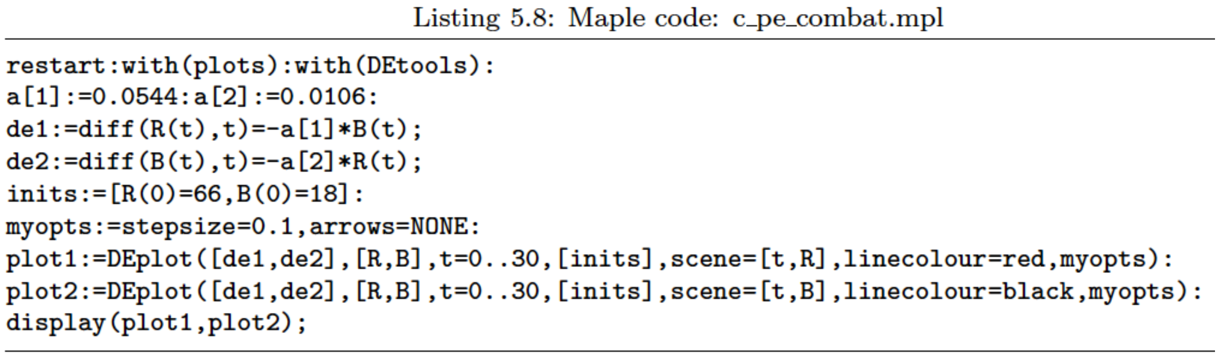
$$R(2) = 65640 + [-0.05\ 44 * 17570]$$

$$R(2) = 65640 - 956 = 64684$$

$$B(2) = 17570 + [-0.0106 * 65640]$$

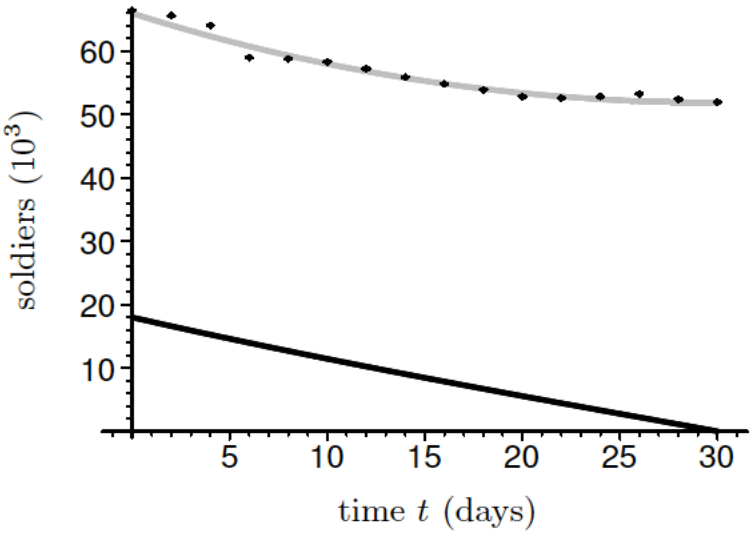
$$B(2) = 17570 - 696 = 16874$$

Solution by MATLAB:



Listing 5.8: Maple code: c_pe_combat.mpl

```
restart:with(plots):with(DEtools):
a[1]:=0.0544:a[2]:=0.0106:
de1:=diff(R(t),t)=-a[1]*B(t);
de2:=diff(B(t),t)=-a[2]*R(t);
inits:=[R(0)=66,B(0)=18]:
myopts:=stepsize=0.1,arrows=NONE:
plot1:=DEplot([de1,de2],[R,B],t=0..30,[inits],scene=[t,R],linecolour=red,myopts):
plot2:=DEplot([de1,de2],[R,B],t=0..30,[inits],scene=[t,B],linecolour=black,myopts):
display(plot1,plot2);
```



Limitations and extensions of the model

The model we have developed here was based on the assumption of aimed fire. More generally, battles occur where one army uses aimed fire and the other uses random fire (for example, guerrilla warfare) or where both armies use random fire (for example, long-range artillery). These models lead to the differential equations

$$\frac{dR}{dt} = -a_1 B, \qquad \frac{dB}{dt} = -c_2 RB \qquad \dots (17)$$

in the case of guerrilla warfare and

$$\frac{dR}{dt} = -c_1 RB, \qquad \frac{dB}{dt} = -c_2 RB \qquad \dots (18)$$

for long-range artillery or trench warfare.

Phase-Plane Analysis for Model of Battle

Example:

Classify the equilibrium points for the system

$$\frac{dR}{dt} = -a_1 B, \qquad \frac{dB}{dt} = -a_2 R$$

Solution:

the system can be written in matrix form

$$X' = AX \ , \quad A = \begin{bmatrix} 0 & -a_1 \\ -a_2 & 0 \end{bmatrix}$$

and

$$\left.\begin{matrix} -a_1 B = 0 \longmapsto B = 0 \\ -a_2 R = 0 \longmapsto R = 0 \end{matrix}\right\} \to (R_e, B_e) = (0,0)$$

The characterist equation is

$$\lambda^2 - tra(A) + det(A) = 0$$

$$\lambda^2 + (-a_1 a_2) = 0$$

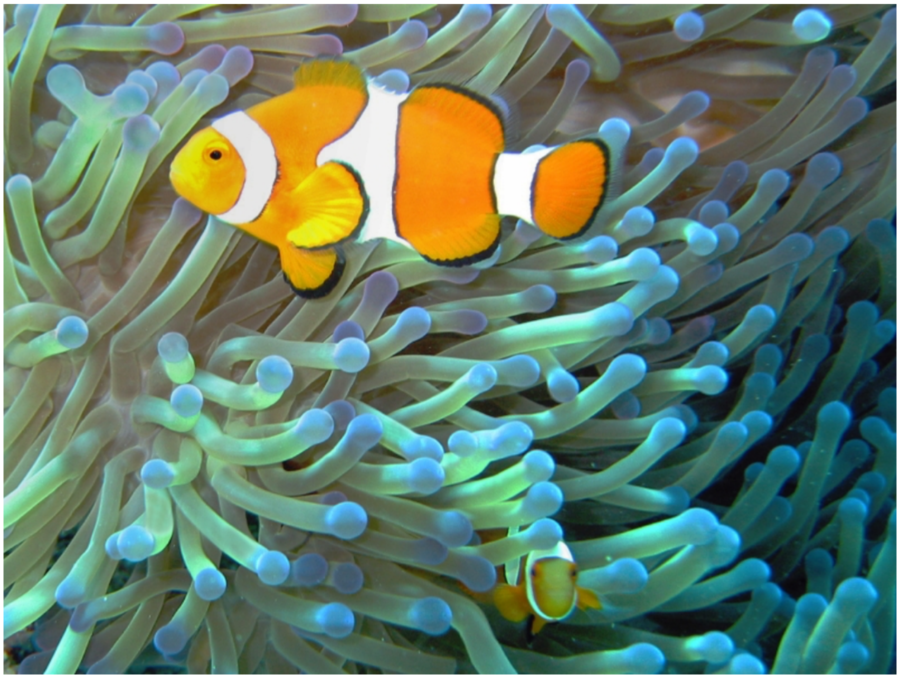
with $\det(A) = -a_1 a_2 < 0$

∴ The equilibrium point is a saddle point.

5-Mutualism Model

Mutualism is an ecological interaction between at least two species (=partners) where both partners benefit from the relationship.

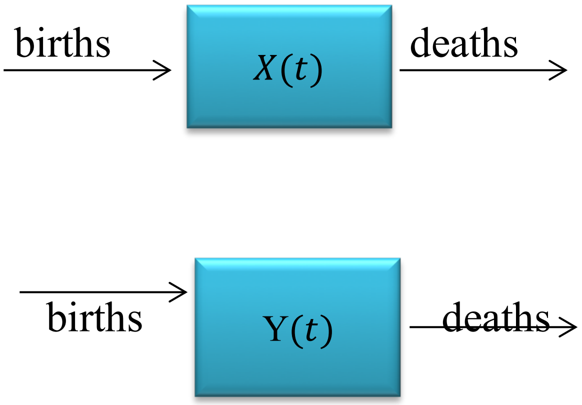
There are many examples where the interaction of two or more species is to the advantage of all mutualism or symbiosis often plays the crucial role in promoting such species: plant and dispersal of seed is one example. This area has not been as widely studied as the other even though its importance in comparable to that of predator-prey and competition interactions.

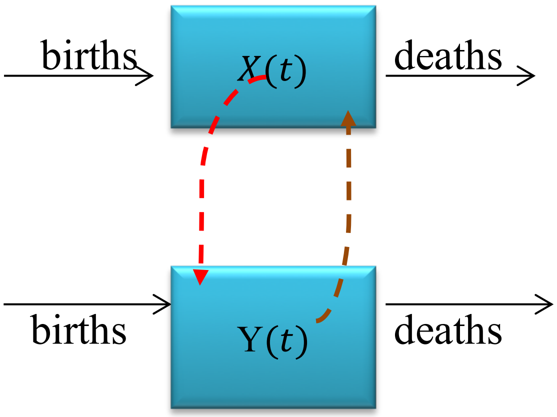


Model assumptions

- We assume the populations to be sufficiently large so that random fluctuations can be ignored without consequence.
- We assume that the two-species model reflects the ecosystem sufficiently accurately.
- We assume each population grows exponentially in the absence of the other partner(s), although we later incorporate density-dependent growth for each.

General compartmental model





In words, we have for each population in the system

$$\begin{Bmatrix}\text{rate of}\\ \text{change of}\\ \text{population}\end{Bmatrix} = \begin{Bmatrix}\text{rate of}\\ \text{population}\\ \text{births}\end{Bmatrix} - \begin{Bmatrix}\text{rate of}\\ \text{population}\\ \text{deaths}\end{Bmatrix} \qquad \dots(17)$$

Formulating the differential equations

We let the positive constants β_1 and β_2 describe the per-capita birth rates for species X and Y, respectively.

Since the two populations are mutualism where the interaction of two or more species is to the advantage. So, the per-capita birth rate for Y is proportional to X, and that for X is proportional to Y , which in symbols is

$$\begin{Bmatrix} \text{rate of} \\ \text{species } X \\ \text{births} \end{Bmatrix} = (c_1 Y)X, \qquad \begin{Bmatrix} \text{rate of} \\ \text{species } Y \\ \text{births} \end{Bmatrix} = (c_2 X)Y \qquad \dots(18)$$

Our model becomes

$$\frac{dX}{dt} = \beta_1 X + c_1 XY, \qquad \frac{dY}{dt} = \beta_2 Y + c_2 XY \qquad \dots(19)$$

where β_1, β_2, c_1 and c_2 are all positive constant.

Example:

Predict the number of two population live with mutualism with growth rates 0.4 and 0.2. The constants $c_1 = 0.002$ and $c_2 = 0.01$. The initial conditions are $X(0) = 25$ and $Y(0) = 10$.

Solutions:

By Euler numerical method, we could predict:

$$X(1) = X(0) + [0.4 * X(0) + 0.002 * X(0) * Y(0)]$$

$$X(1) = 25 + [0.4 * 25 + 0.002 * 25 * 10] = 36$$

$$Y(1) = Y(0) + [0.2 * Y(0) + 0.01 * X(0) * Y(0)]$$

$$Y(1) = 10 + [0.2 * 10 + 0.01 * 25 * 10] = 15$$

$$X(2) = 36 + [0.4 * 36 + 0.002 * 36 * 15] = 52$$

$$Y(2) = 15 + [0.2 * 15 + 0.01 * 36 * 15] = 23$$

and so on

Phase-Plane Analysis for Model of Mutualism

Remark: If we assume each population grows logistically in the absence of the other partner(s) system (19) become,

$$\frac{dX}{dt} = \beta_1 X\left(1 - \frac{X}{K_1}\right) + c_1XY, \qquad \frac{dY}{dt} = \beta_2 Y\left(1 - \frac{Y}{K_2}\right) + c_2XY \qquad \ldots(20)$$

where K_1 *and* K_2 are the carring capaciteies of the populations X and Y respectively

Example:

Find the linearised for model with the mutualism population grows logistically in the absence of a predator.

$$X' = X(1 - X) + 0.5\,XY$$
$$Y' = Y(2.5 - 1.5Y) + 0.25\,XY$$

and hence classify all equilibrium points of the mutualism model.

$\therefore$ (0,0), $\left(0, \frac{5}{3}\right)$, (1,0) and (2,2) are equilibrium points.

$$F(X,Y) = X(1 - X) + 0.5\,XY \qquad G(X,Y) = Y(2.5 - 1.5Y) + 0.25\,XY$$

$$\frac{\partial F}{\partial X} = 1 - 2\,X + 0.5\,Y \qquad \frac{\partial G}{\partial X} = 0.25\,Y$$

$$\frac{\partial F}{\partial Y} = 0.5\,X \qquad \frac{\partial G}{\partial Y} = 2.5 - 3Y + 0.25\,X$$

$*$ For $(X_e, Y_e) = (0,0)$

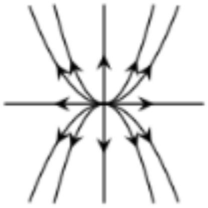
$$\mathrm{J} = \begin{bmatrix} 1 & 0 \\ 0 & 2.5 \end{bmatrix}$$

with $det(A) = 2.5 > 0$

$Tr(A) = 3.5 > 0$, the equilibrum point is unstable, and

$$\frac{Tr(A)^2}{4} > \Delta$$

$(X_e, Y_e) = (0,0)$ is an unstable node (source).



$* \text{ For } (X_e, Y_e) = \left(0, \frac{5}{3}\right)$

$$= \begin{bmatrix} 11/6 & 0 \\ 5/12 & -5/2 \end{bmatrix}$$

$$det(A) = -\frac{55}{12} < 0$$

$\therefore \left(0, \frac{5}{3}\right)$ is a saddle point.

$* \text{ For } (X_e, Y_e) = (1,0)$

$$= \begin{bmatrix} -1 & 1/2 \\ 0 & 11/4 \end{bmatrix}$$

$$det(A) = -\frac{11}{4} < 0$$

$\therefore$ (1,0) is a saddle point.

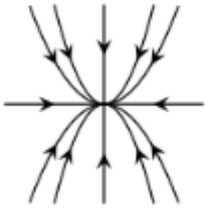
$* \text{ For } (X_e, Y_e) = (2,2)$

$$= \begin{bmatrix} -2 & 1 \\ -\frac{1}{2} & -3 \end{bmatrix}$$

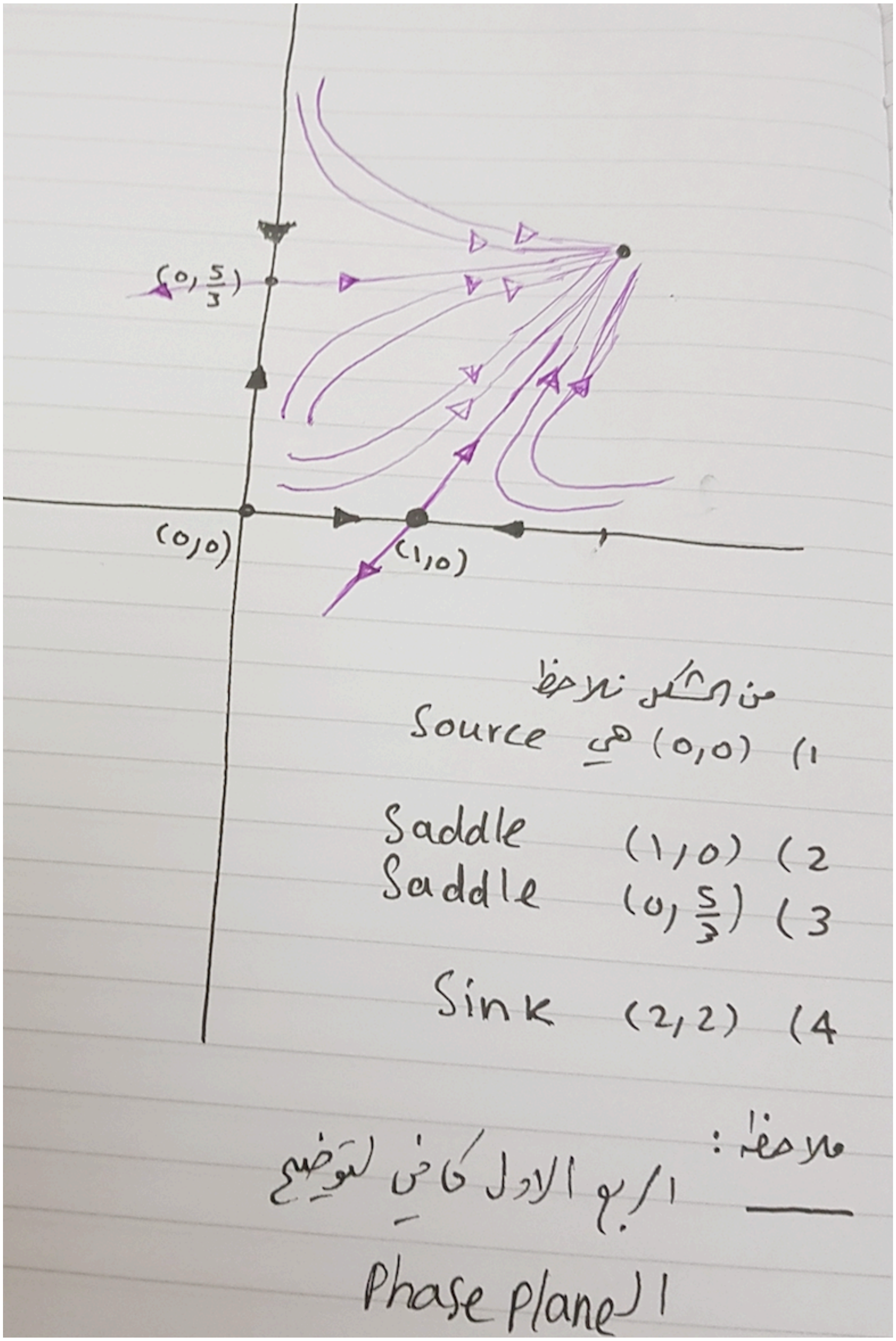
$$det(A) = 6 + \frac{1}{2} = 6.5 > 0$$

$Tr(A) = -5 < 0$, the equilibrum point is stable, and

$$\frac{(-5)^2}{4} < 6.5$$



$\therefore$ (2,2) is a stable node (sink).



من الشكل نلاحظ

1) (0,0) هي Source

2) (1,0) Saddle

3) $(0,\frac{5}{3})$ Saddle

4) (2,2) Sink

ملاحظة:

الرسم الاول كافي لتوضيح

ال Phase plane