Discrete Mathematical Models in Life Sciences

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Syllabus

- A brief Introduction to MAPLE
- One Dimensional Models
  - Lab 1, Lab 2
- Linear Systems, Leslie Models and life cycles, determinant-trace stability analysis, and Age-Structured Models
- Nonlinear two-dimensional Models: Stability and Bifurcation
- Competition Models
  - Lab 3
- Predator-Prey and Host-parasite Models
  - Lab 4
- Genetics and the Hardy-Weinberg principle

Mathematical Modeling:

Objectives:

- **Developing Mathematical Models**
- **Graphical Analysis of the Models: Time Series and Cob-Web Diagrams**
- **Conducting Laboratory Experiments**
- **Plotting the raw data and parameter estimation**
- **Comparing the data from the laboratory and the data obtained from the mathematical models**
- **Modifying the Models**

One-dimensional Models

The main focus here is on populations which are a basic unit in ecology. A population is defined as a group of individuals of the same species within a limited area. Mathematical Models are used to predict the size or density (population size per unit area) of a population at any time in the future.

Most plants, insects, mammals and organisms reproduce seasonally or they reproduce only once (semelparous species) (multiple reproductions: Iteroparity species). In these situations, we measure the size of a population at periodic intervals of time, or from one generation to the next.

Let:

N_t =the size (density) of a population at time t,

N_{t+1} =the size (density) of a population at time $t+1$.

Then our model can be written in the form $N_{t+1} = F(N_t)$

This equation will be written in a more convenient form.

$$N_{t+1} = N_t f(N_t)$$

Where

N_{t+1} / N_t is called the **fitness function** of the population or the **rate of population growth**, or the **net reproduction rate**.

Equation (1) or (2) is called a difference equation, where $t \in Z^+$, the set of nonnegative integers.

- **Two types of Models**

I. Density independent (Linear) Models

A population model is said to be **"density dependent"** (i.e. linear) if its fitness (rate of population growth) function $f(N)$ is independent of its size (density).

That is, if $f(N) =$ constant = R. Thus

$$N_{t+1} = R\,N_t$$

By iteration, we obtain the solution

$$N_t = R^t N_o$$

In this case, either $N_t \to o$ as t $\to \infty$ if $|R| > 1$.

- For a **continuous model**, we would have $\frac{dN}{dt} = rN$, whose solution is $N(t) = N_o e^{rt}$. Thus $R = e^r \approx 1 + r$

II. Density dependent (Nonlinear Models)

In these models, we assume that the fitness function $f(N)$ depends on the size (density) of the population. The central question now is "how to find the appropriate fitness function."

- **A unified approach for discrete models**

Biological Assumptions

1. When the population size is very small $(N = 0)$, the population grows geometrically, i.e., the fitness function $f(N) = R > 1$ (as in the linear case)
2. As the population size N increases, its fitness $f(N)$ decreases.
3. The fitness decreases to the value 1, when the population reaches a threshold size, called the carrying capacity K. This is the sustainable population size and it is the equilibrium point of the difference equation (the fixed point of the map F).

Under these assumptions, one may develop a plethora of models including all the known ones.

(i) The discrete logistic model (logistic map)

Here we assume that the fitness function $f(N)=\dfrac{N_{t+1}}{N_t}$ decreases linearly.

- The equation of the line passing through the points (0,R) and (K,1) is given by:

$$\frac{N_{t+1}}{N_t}=f(N_t)=-\left(\frac{R-1}{K}\right)N_t+R=\frac{RK-(R-1)N_t}{K}$$

$$N_{t+1}=N_t\left[R-\left(\frac{R-1}{K}\right)N_t\right]$$

If we switch to “r”, r =R-1, we get

$$\boxed{N_{t+1}=N_t\left[1+r\left(1-\frac{N_t}{K}\right)\right]}$$

***For dynamists, if we let $\frac{R-1}{RK}N = x$, we get the popular logistic map**

F(x) =Rx (1-x)

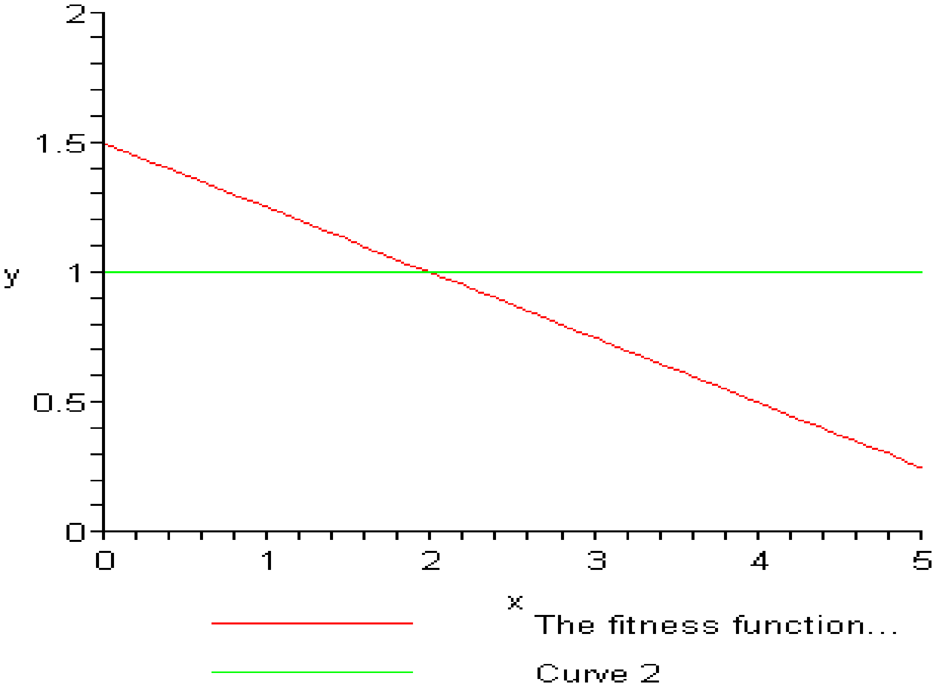


Figure 1: The fitness function of the discrete logistic model

(ii) The Ricker Model

Here we assume that the fitness function $f(N)$ decreases exponentially,

$$f(N) = \mathbf{e}^{\mathbf{(r\text{-}sN)}}$$

To find r and s, we utilize the assumptions:

$$f(0) = R = e^{r} = r = \ln R \ (R \approx 1 + r)$$

$$f(K) = 1 = e^{r-SK} \Rightarrow \ r\text{-}sk = 0 \Rightarrow s = \frac{r}{K}$$

Hence: $\dfrac{N_{t+1}}{Nt} = e^{r - \frac{r}{k}N_t}$

And now we have the **Ricker model**

$$\boxed{N_{t+1} = N_t e^{r\left(1 - \frac{N_t}{K}\right)}}$$

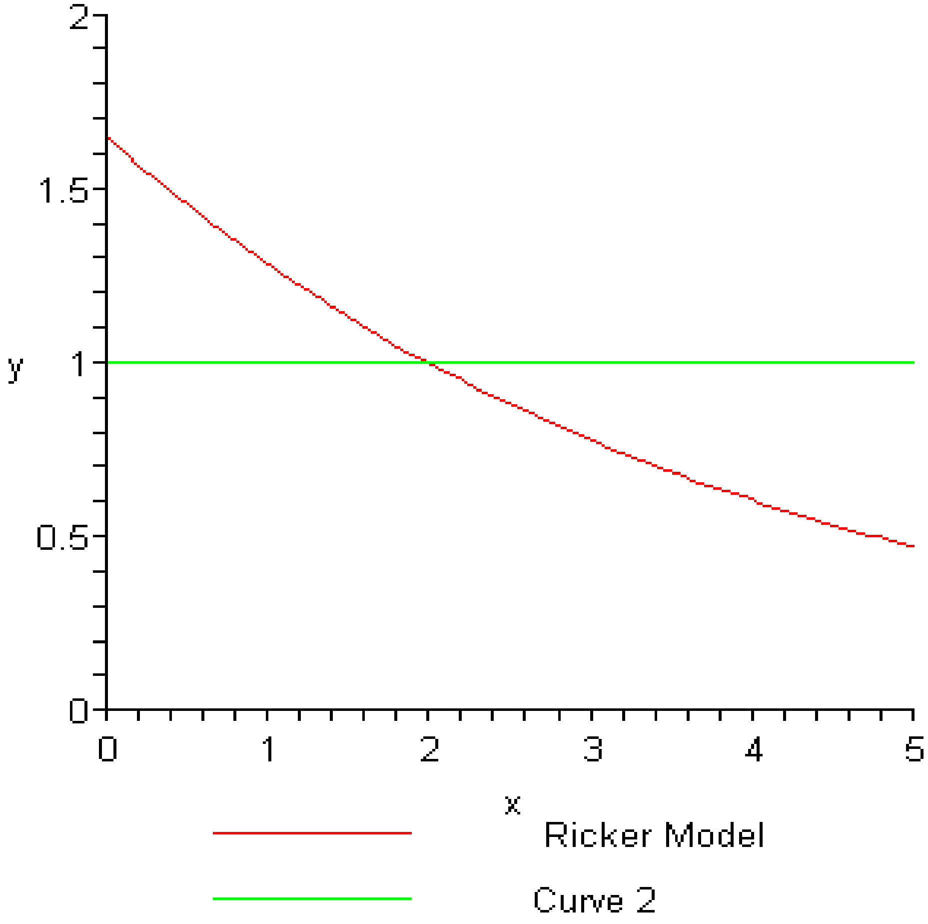


Figure 2: The fitness function of the Ricker model

(iii) The Beverton-Holt Model

Here we assume that the fitness function $f(N)$ decreased as a rational function.

$$f(N) = \frac{a}{1+bN}$$

Now $f(0) = R = a$

$$f(K) = 1 = \frac{R}{1+bK} \Rightarrow b = \frac{R-1}{K}$$

$$\frac{N_{t+1}}{N_t} = \frac{R}{1+\left(\frac{R-1}{K}\right)N_t}$$

$$\boxed{N_{t+1} = \frac{RKN_t}{K+(R-1)N_t}}$$

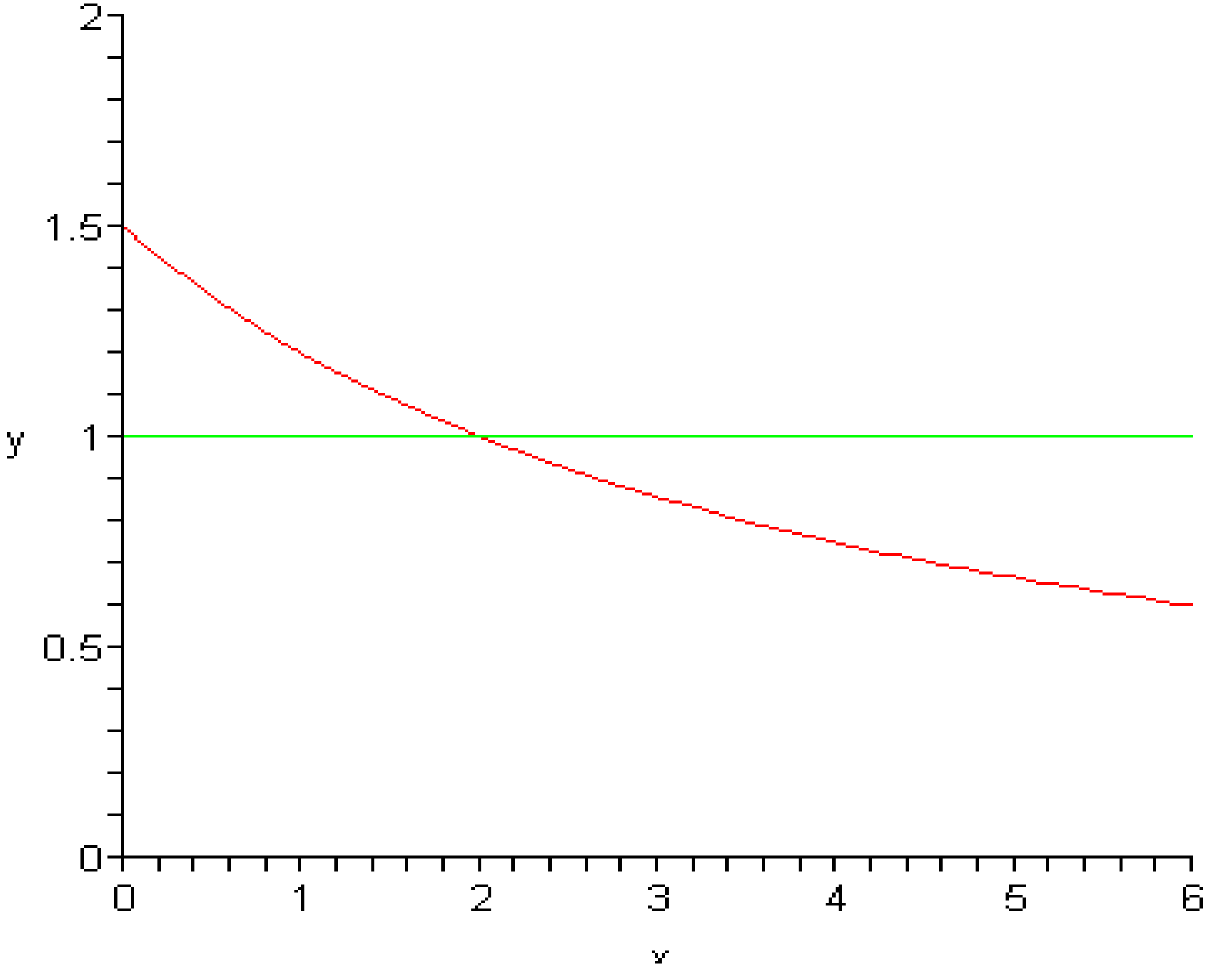


Figure 3: The fitness function of the Beverton-Holt model

The Moral of the above story

It is now evident that based on our biological assumptions, one may construct infinitely many models that satisfy those assumptions. There are two points worth mentioning here.

1. **Though all the models are mathematically correct, one may verify in the lab that some models are better fit to the obtained data than others. For instance, in the data obtained in the lab on the density of E. Coli and paramecium, both the Beverton-Holt and the Ricker models were better fit than the discrete logistic model.**
2. **The second point to make is that some models possess richer dynamics than others and are thus potentially more useful in describing complicated behavior. For example, the Beverton-Holt model is too simplistic to account for cyclic behavior such as bust and boom in population density, while both the Ricker and logistic models may exhibit cyclic behavior and even chaos.**

Parameter Estimation

1. Logistic Model

$$\frac{N_{t+1}}{N_t} = R - \left(\frac{R-1}{K}\right) N_t$$

$$Y = mx+b \qquad b=R,\ m = \frac{1-R}{K} \Rightarrow K = \frac{1-R}{m}$$

2. Ricker Model

$$\frac{N_{t+1}}{N_t} = e^{r\left(1-\frac{N_t}{K}\right)} \Rightarrow \ln\left(\frac{N_{t+1}}{N_t}\right) = r - \frac{r}{K} N_t$$

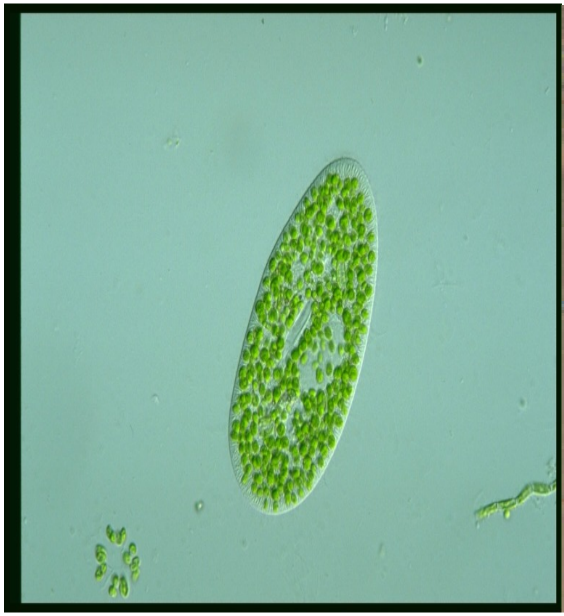
$$y = mx+b, \qquad b = r \qquad and \qquad m = \frac{-r}{K} \Rightarrow K = \frac{-r}{m}$$

3. Beverton-Holt Model

$$\frac{N_t}{N_{t+1}} = \frac{K+(R-1)N_t}{KR} = \frac{1}{R} + \frac{R-1}{RK} N_t$$

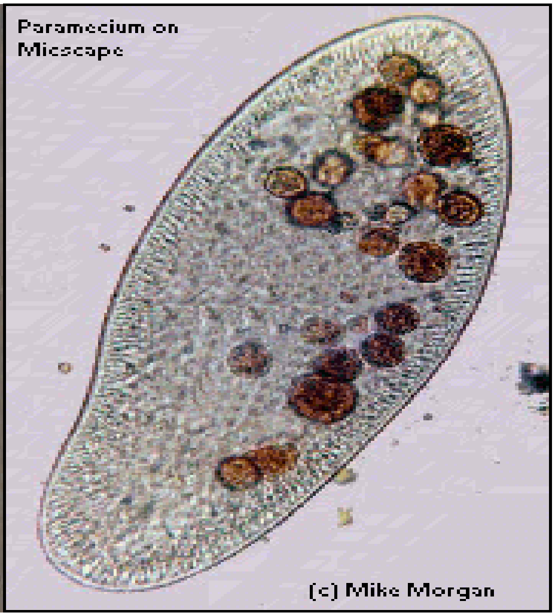
$$Y = mx+b \qquad B = \frac{1}{R} \Rightarrow R = \frac{1}{b} \qquad m = \frac{R-1}{RK} \Rightarrow K = \frac{R-1}{mR}$$

Paramecium



P. Caudatum

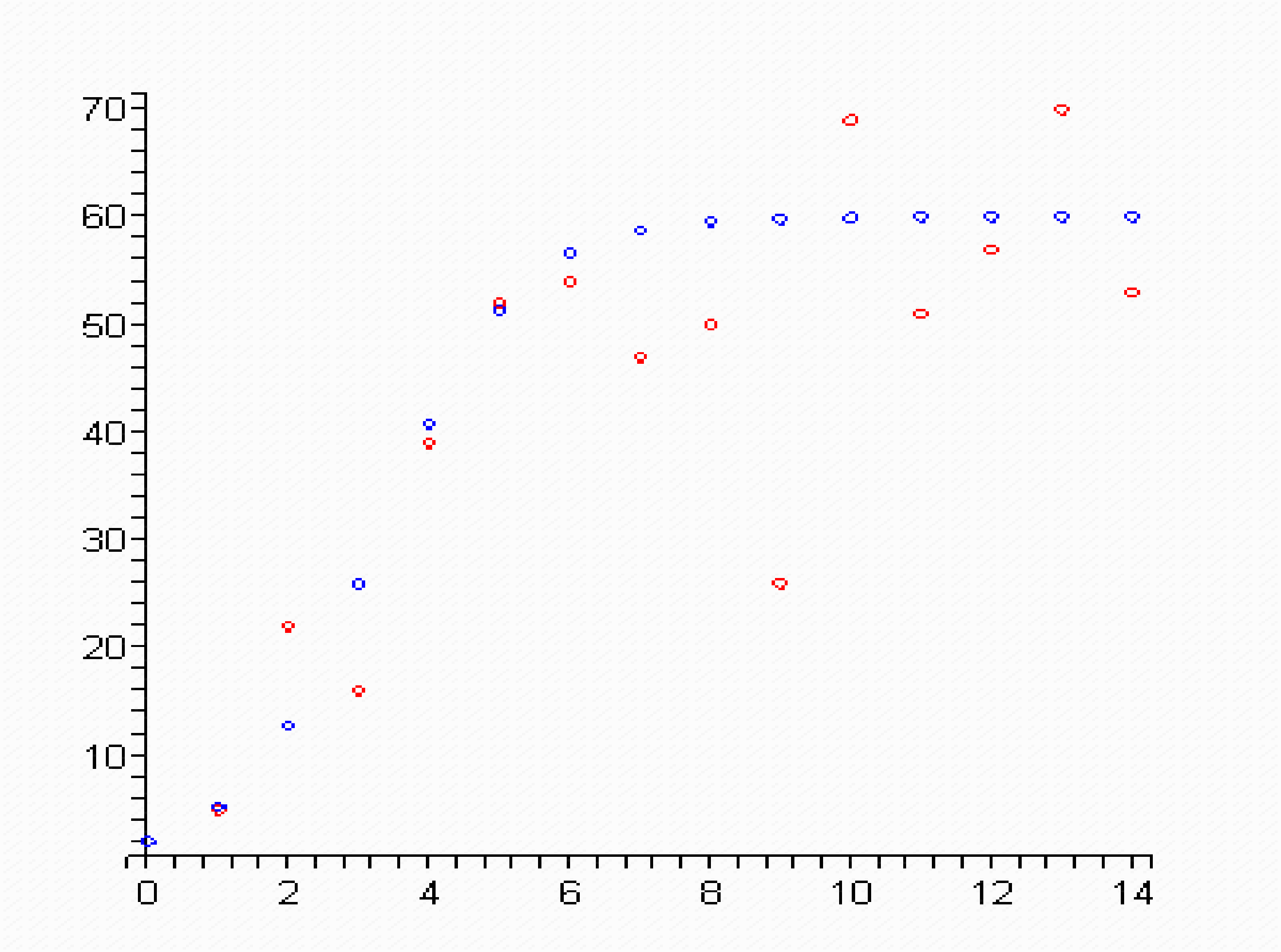
P. Aurelia



P. Caudatum

```
restart:with(plots):T:=[0,1,2,3,4,5,6,7,8,9,10,11,12,13,14,
15];
```

```
                    T := [0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15]

> S:=[2,5,22,16,39,52,54,47,50,26,69,51,57,70,53,59,57];
              S := [2, 5, 22, 16, 39, 52, 54, 47, 50, 26, 69, 51, 57, 70, 53, 59, 57]

> pts:=[seq([T[k],S[k]],k=1..15)];
      pts := [[0, 2], [1, 5], [2, 22], [3, 16], [4, 39], [5, 52], [6, 54], [7, 47], [8, 50], [9, 26], [10, 69], [11, 51], [12, 57],

             [13, 70], [14, 53]]

> p1:=plot(pts,style=point):
> F:=n->if n=0 then 2 else 2.8*60*F(n-1)/(60+1.8*F(n-1))
end if:
> pt:=[seq([T[k],F(T[k])],k=1..15)]:
> p2:=plot(pt,style=point,color=blue):
> display(p1,p2);
>
```



>

P. Caudatum: Blue=data from the Beverton-Holt model; Red= data from the lab

```
>
restart:with(plots):T:=[2,5,22,16,39,52,54,47,50,26,6
9,51,57,70,53,59,57];
```

$$T := [2, 5, 22, 16, 39, 52, 54, 47, 50, 26, 69, 51, 57, 70, 53, 59, 57]$$

```
>
S:=[2/5,5/22,22/16,16/39,39/52,52/54,54/47,47/50,50/2
6,26/69,69/51,51/57,57/70,70/53,53/59,59/57,1];
```

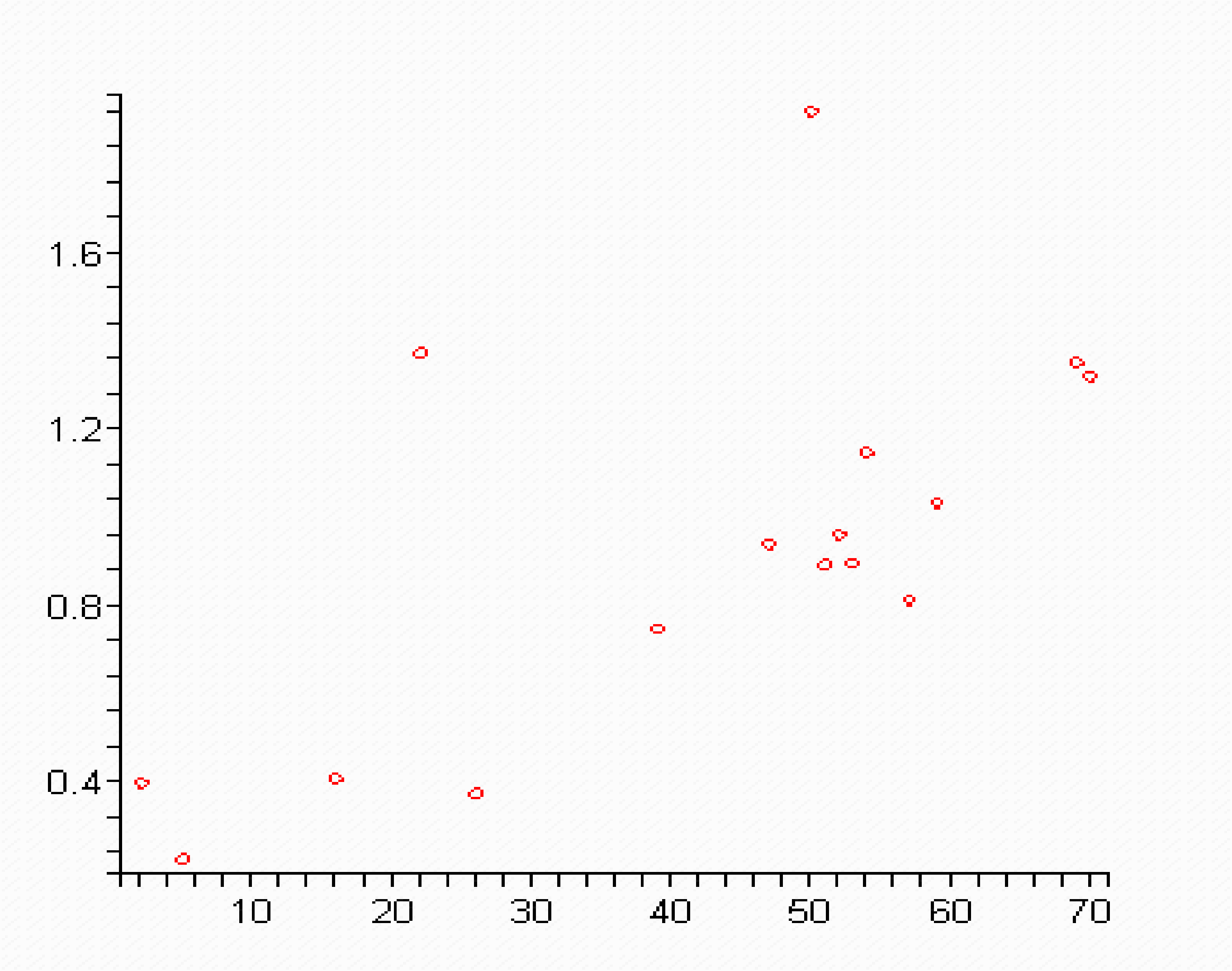
$$S := \left[\frac{2}{5}, \frac{5}{22}, \frac{11}{8}, \frac{16}{39}, \frac{3}{4}, \frac{26}{27}, \frac{54}{47}, \frac{47}{50}, \frac{25}{13}, \frac{26}{69}, \frac{23}{17}, \frac{17}{19}, \frac{57}{70}, \frac{70}{53}, \frac{53}{59}, \frac{59}{57}, 1\right]$$

```
> pts:=[seq([T[k],S[k]],k=1..16)];
```

$$pts := \left[\left[2, \frac{2}{5}\right], \left[5, \frac{5}{22}\right], \left[22, \frac{11}{8}\right], \left[16, \frac{16}{39}\right], \left[39, \frac{3}{4}\right], \left[52, \frac{26}{27}\right], \left[54, \frac{54}{47}\right], \left[47, \frac{47}{50}\right], \left[50, \frac{25}{13}\right],\right.$$

$$\left.\left[26, \frac{26}{69}\right], \left[69, \frac{23}{17}\right], \left[51, \frac{17}{19}\right], \left[57, \frac{57}{70}\right], \left[70, \frac{70}{53}\right], \left[53, \frac{53}{59}\right], \left[59, \frac{59}{57}\right]\right]$$

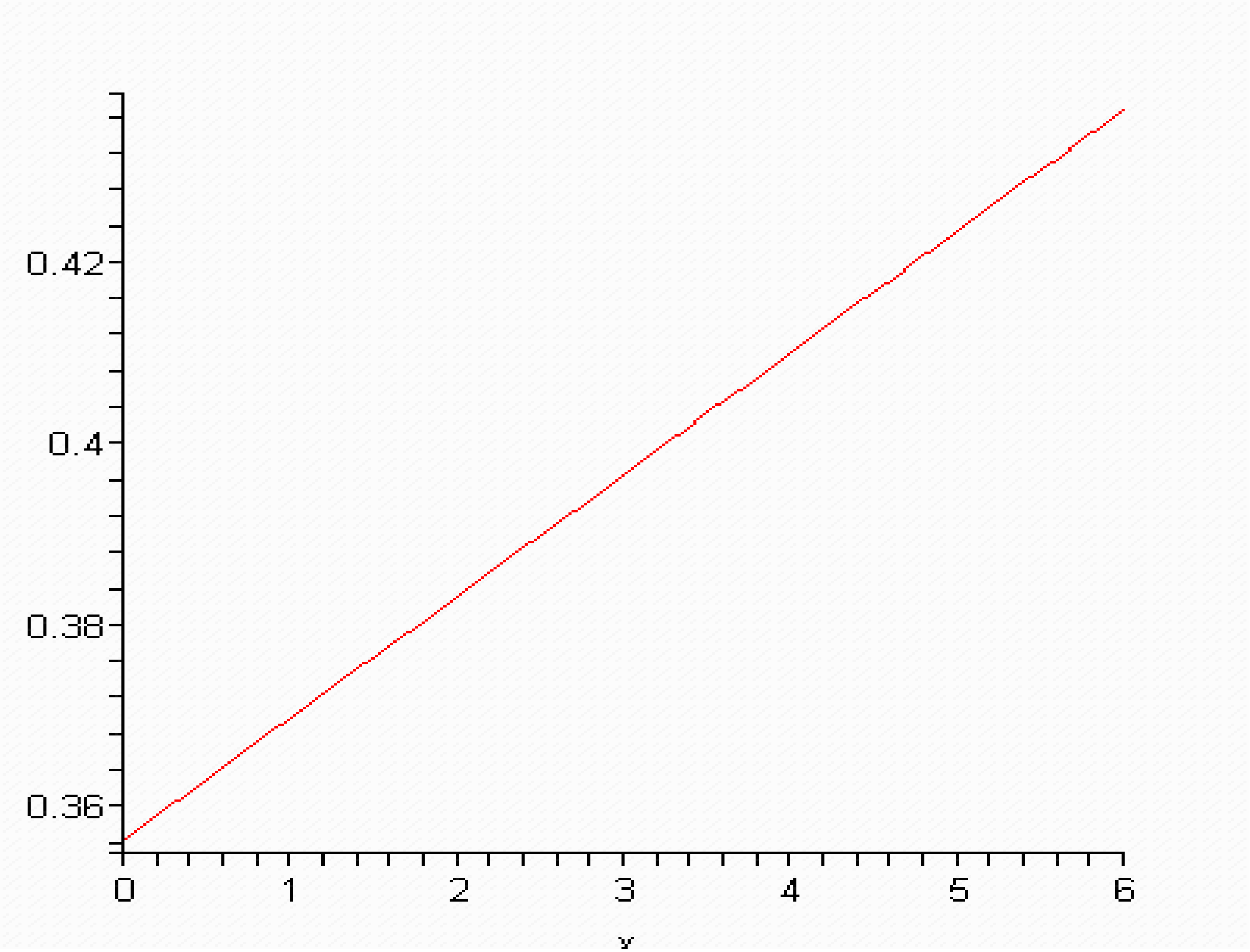
```
> p1:=plot(pts,style=point):
> display(p1);
```



Estimation of parameters of P. Caudatum

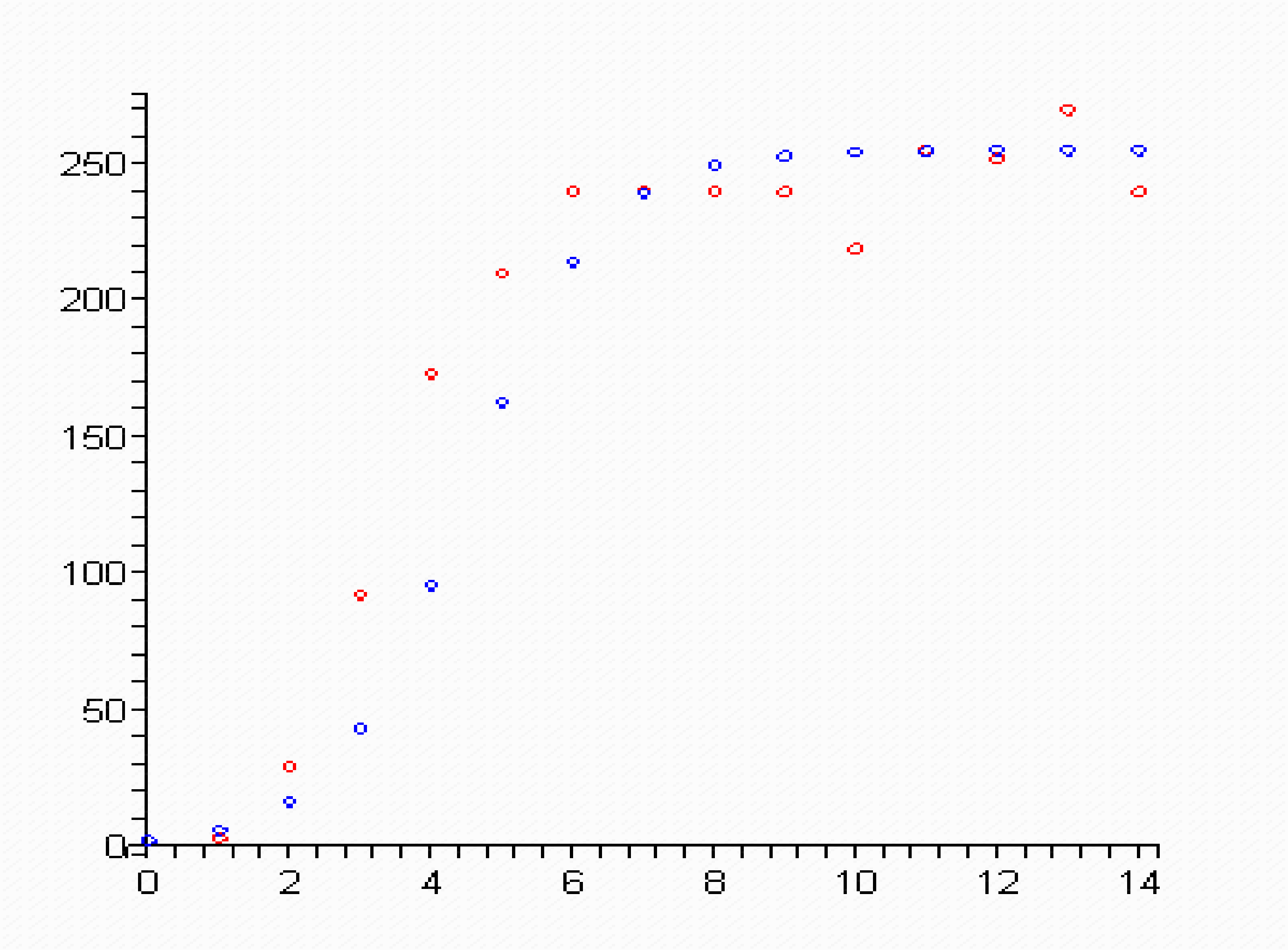
```
> with(CurveFitting):

LeastSquares([[2,2/5],[5,5/22],[22,22/16],[16,16/
39],[39,39/52],[52,52/54],[54,54/47],[47,47/50],[
50,50/26],[26,26/69],[69,69/51],[51,51/57],[57,57
/70],[70,70/53],[53,53/59],[59,59/57],[57,1]], x
);plot(253376505595052076707/71071745785060980960
0+190495500123181 3129/142143491570121961920*x,x=0
..6);
```

$$\frac{253376505595052076707}{710717457850609809600}+\frac{190495500123181 3129}{142143491570121961920}\,x$$



Estimation of parameters of P. Caudatum

```
> Parameciun: P. Aurelia
restart:with(plots):T:=[0,1,2,3,4,5,6,7,8,9,10,11,12,13,14,
15];
                T := [0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15]

>
S:=[2,3,29,92,173,210,240,240,240,240,219,255,252,270,240,2
49];
      S := [2, 3, 29, 92, 173, 210, 240, 240, 240, 240, 219, 255, 252, 270, 240, 249]

> pts:=[seq([T[k],S[k]],k=1..15)];
     pts := [[0, 2], [1, 3], [2, 29], [3, 92], [4, 173], [5, 210], [6, 240], [7, 240], [8, 240], [9, 240], [10, 219], [11, 255],
             [12, 252], [13, 270], [14, 240]]

> p1:=plot(pts,style=point):
> F:=n->if n=0 then 2 else 2.95*255*F(n-1)/(255+1.95*F(n-
1)) end if:
> pt:=[seq([T[k],F(T[k])],k=1..15)]:
> p2:=plot(pt,style=point,color=blue):
> display(p1,p2);
```



P. Aurelia: Blue: Data from the Beverton-Holt model; Red= Data from the Lab.

```
>
restart:with(plots):T:=[2,3,29,92,173,210,240,240,240,240,219,255,2
52,270,240,249];
```

$$T := [2, 3, 29, 92, 173, 210, 240, 240, 240, 240, 219, 255, 252, 270, 240, 249]$$

```
>
S:=[2/3,3/29,29/92,92/173,173/210,210/240,1,1,1,240/249,219/255,255
/252,252/270,270/240,240/249,1];
```

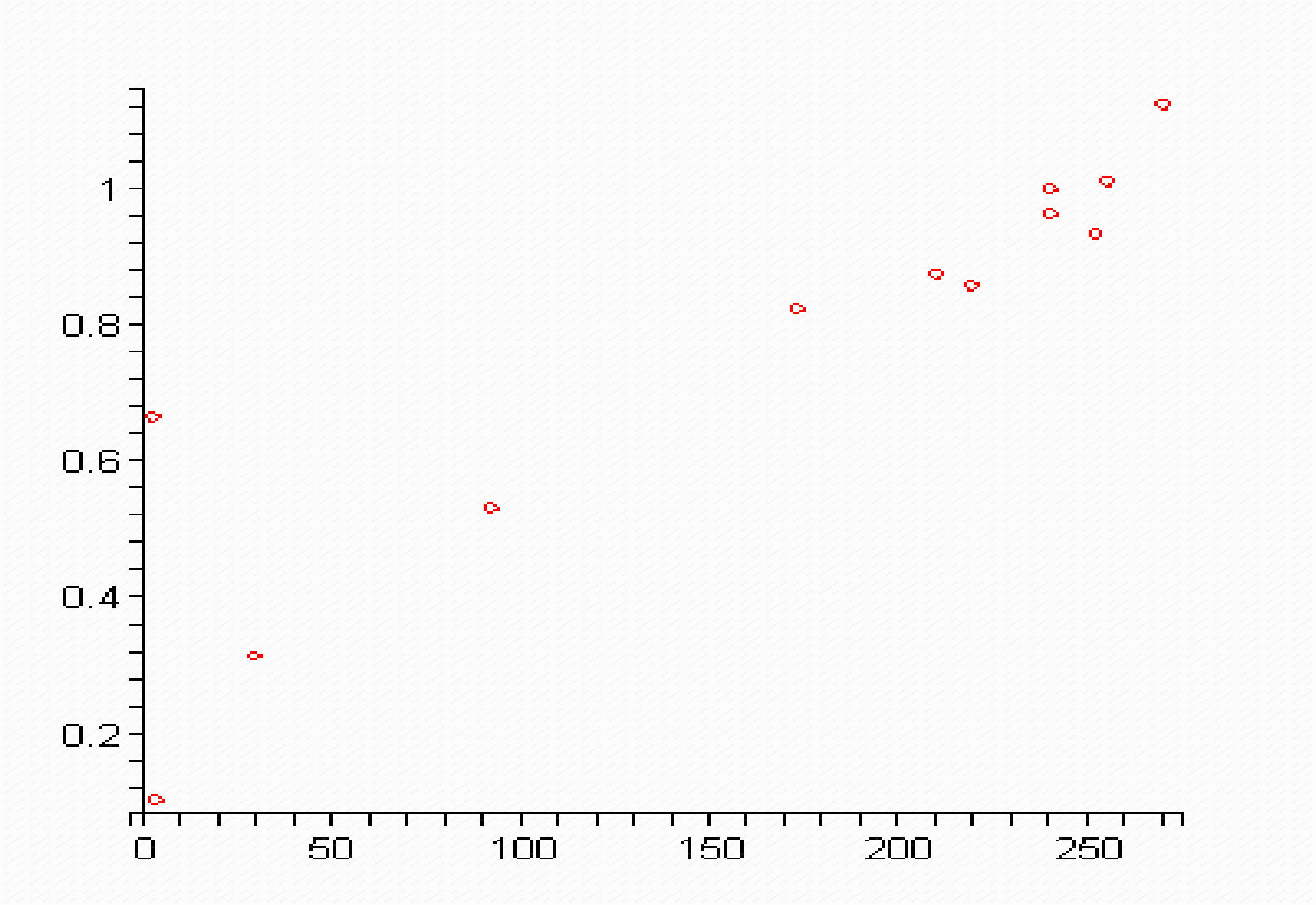
$$S := \left[\frac{2}{3}, \frac{3}{29}, \frac{29}{92}, \frac{92}{173}, \frac{173}{210}, \frac{7}{8}, 1, 1, 1, \frac{80}{83}, \frac{73}{85}, \frac{85}{84}, \frac{14}{15}, \frac{9}{8}, \frac{80}{83}, 1\right]$$

```
> pts:=[seq([T[k],S[k]],k=1..15)];
```

$$pts := \left[\left[2, \frac{2}{3}\right], \left[3, \frac{3}{29}\right], \left[29, \frac{29}{92}\right], \left[92, \frac{92}{173}\right], \left[173, \frac{173}{210}\right], \left[210, \frac{7}{8}\right], [240, 1], [240, 1], [240, 1],\right.$$

$$\left.\left[240, \frac{80}{83}\right], \left[219, \frac{73}{85}\right], \left[255, \frac{85}{84}\right], \left[252, \frac{14}{15}\right], \left[270, \frac{9}{8}\right], \left[240, \frac{80}{83}\right]\right]$$

```
> p1:=plot(pts,style=point):
> display(p1);
```



Estimation of parameters of P. Aurelia

```
> with(CurveFitting):
LeastSquares(
[[2,2/3],[3,3/29],[29,29/92],[173,173/210],[240,1],[241,1],[219,219
/255],[252,252/270],[240,240/249],[249,1]], x );
```

$$\frac{1821049645003}{5368659548280} + \frac{4640191449}{1789553182760}\, x$$

```
>restart:with(plots):T:=[0,1,2,3,4,5,6,7,8,9,10,11,12,13,14,15];
```

$$T := [0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15]$$

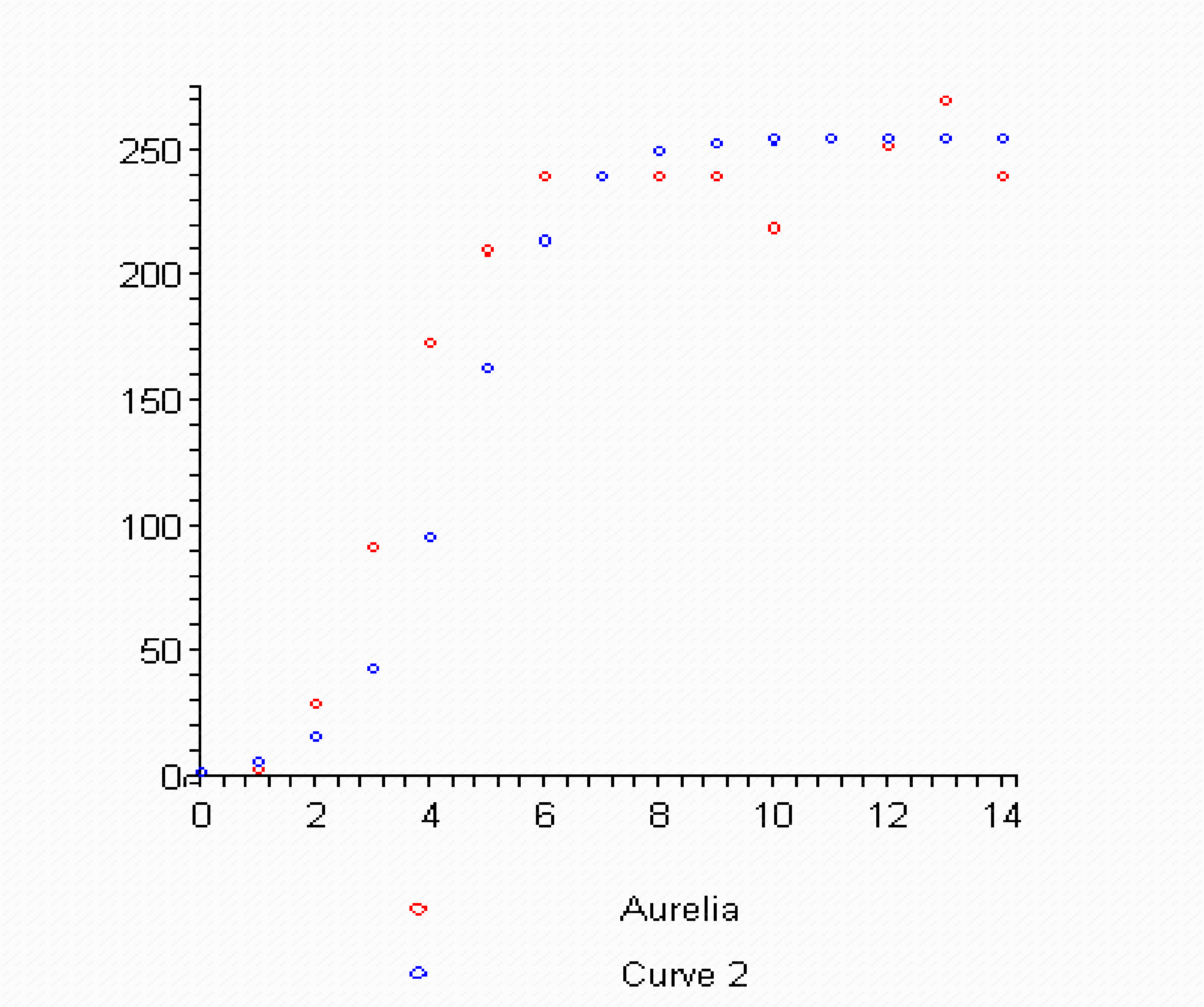
```
> S:=[2,3,29,92,173,210,240,240,240,240,219,255,252,270,240,249];
```

$$S := [2, 3, 29, 92, 173, 210, 240, 240, 240, 240, 219, 255, 252, 270, 240, 249]$$

```
> pts:=[seq([T[k],S[k]],k=1..15)];
```

$$pts := [[0, 2], [1, 3], [2, 29], [3, 92], [4, 173], [5, 210], [6, 240], [7, 240], [8, 240], [9, 240], [10, 219], [11, 255], [12, 252], [13, 270], [14, 240]]$$

```
> p1:=plot(pts,style=point):
> F:=n->if n=0 then 2 else 2.95*255*F(n-1)/(255+1.95*F(n-1)) end if:
> pt:=[seq([T[k],F(T[k])],k=1..15)]:
> p2:=plot(pt,style=point,color=blue):
> display(p1,p2);
```


250
200
150
100
50
0
0
2
4
6
8
10
12
14
Aurelia
Curve 2

Stability Analysis

Fixed (equilibrium) points, $F(N^*) = N^*$

Periodic Points: $F^k(\overline{N}) = \overline{N}$

Orbit of a k-periodic point: $O(\overline{N}) = \{\overline{N}, F(\overline{N}), F^2(\overline{N}), \ldots, F^{k-1}(\overline{N})\}$.

If we let $\overline{N} = N_o$ and use the language of difference equations ($N_{t+1} = F(N_t)$), then $O(N_0) = \{N_0, N_1, \ldots, N_{k-1}\}$

Theorem (1) A fixed point N^* is

(i) Stable (asymptotically stable) if $|F'(N^*)| < 1$ (sink, attracting)

(ii) unstable if $|F'(N^*)| > 1$ (source, repelling)

(iii) "Neutral" if $|F'(N^*)| = 1$

Using the chain rule we have the following theorem.

Theorem (2) A *k*-periodic orbit is

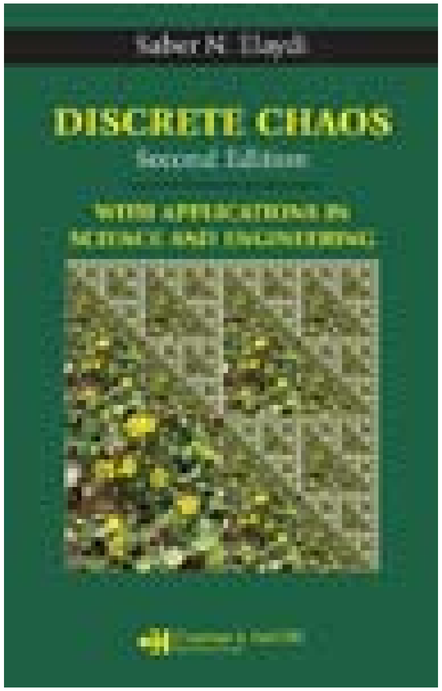
(i) Stable if $\left|F'(N_o)\times F'(N_1)\times\ldots\times F'(N_{k-1})\right|<1$

(ii) Unstable if $\left|F'(N_o)\times F'(N_1)\times\ldots\times F'(N_{k-1})\right|>1$

(iii) "Neutral" if $\left|F'(N_o)\times F'(N_1)\times\ldots\times F'(N_{k-1})\right|=1$

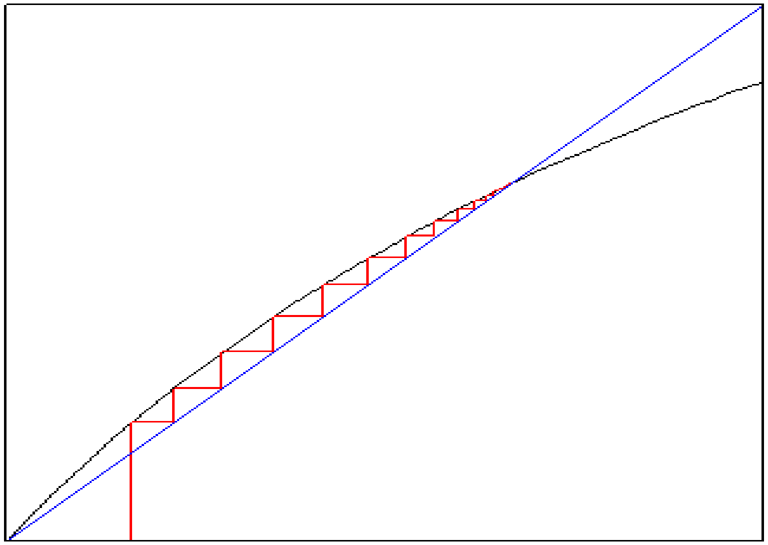
A complete analysis of the neutral case can be found in

"Elaydi, Discrete Chaos:2$^{\text{nd}}$ Edition, CRC/Chapman & Hall 2008."



Remarks:

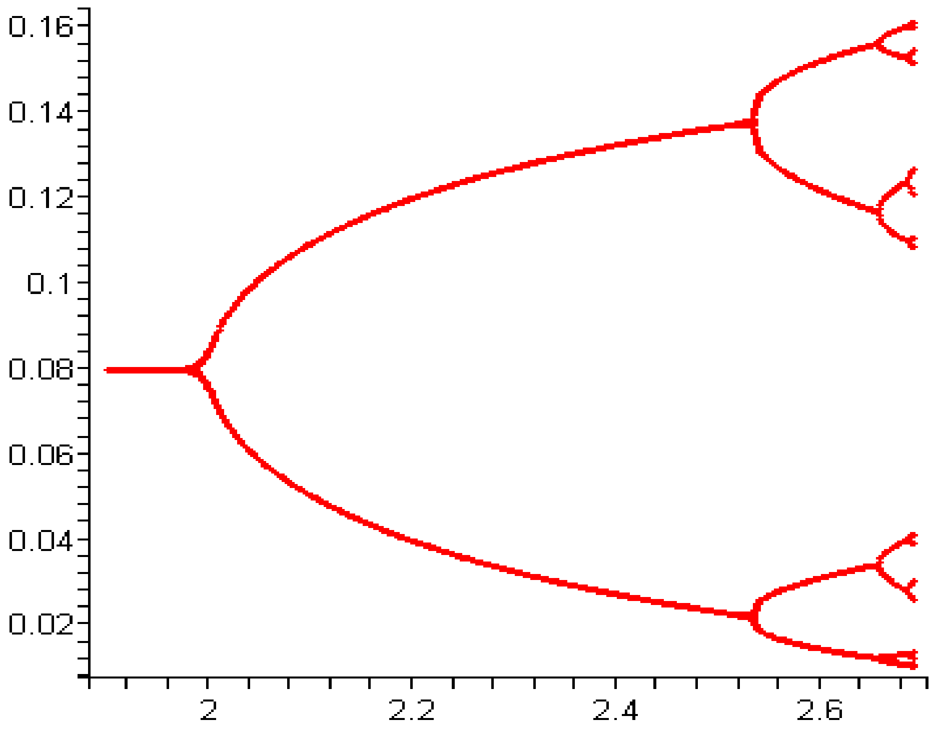
1. The dynamics of the Beverton-Holt Model is simple (and is similar to the dynamics of the logistic differential equation $\frac{dx}{dt} = rx(1-x)$.)



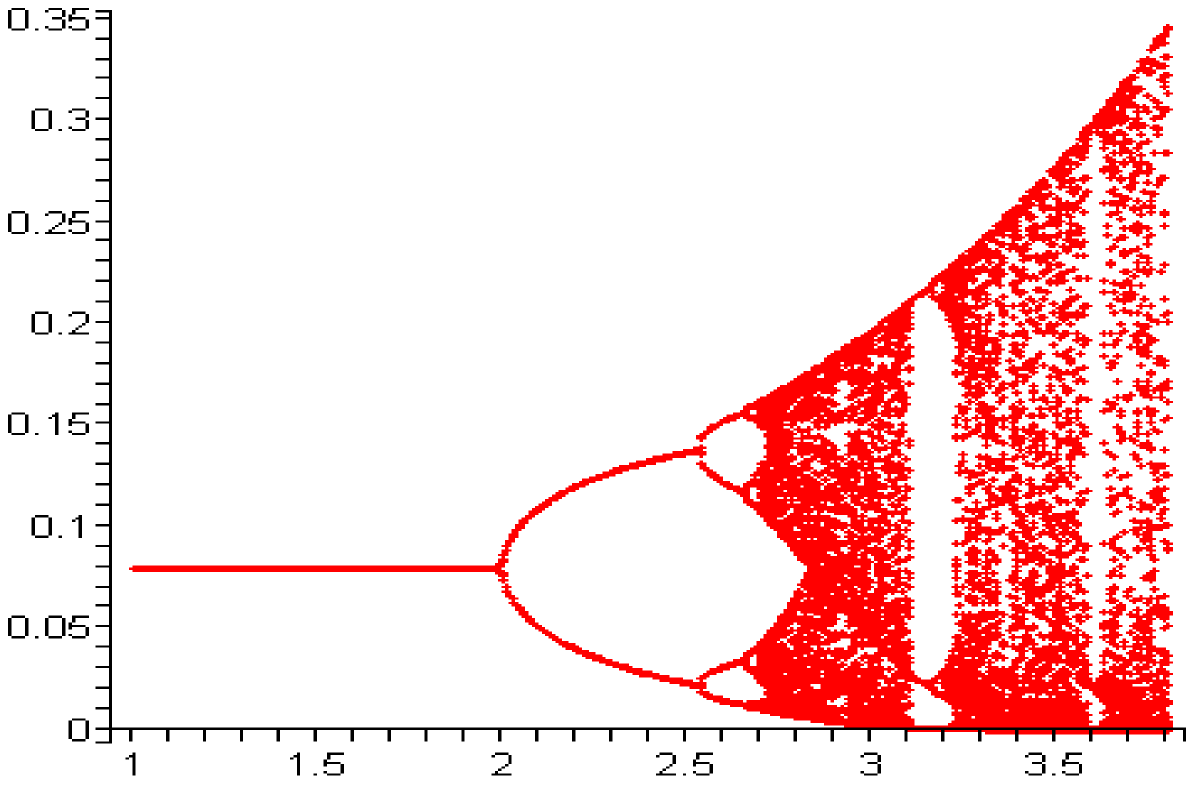
Cobweb (Stair-step) diagram of the Beverton-Holt map.

There are two fixed points $N_1^* = 0$, which is unstable, and $N_2^* = K$ which is globally stable on $(0, \infty)$.

2. The dynamics of both the discrete logistic and the Ricker Models is rather complicated: from period doubling bifurcation to chaotic dynamics



Bifurcation diagram of the Ricker model: Period Doubling



Bifurcation diagram for the Ricker model
Entering the chaotic region

Competition Models

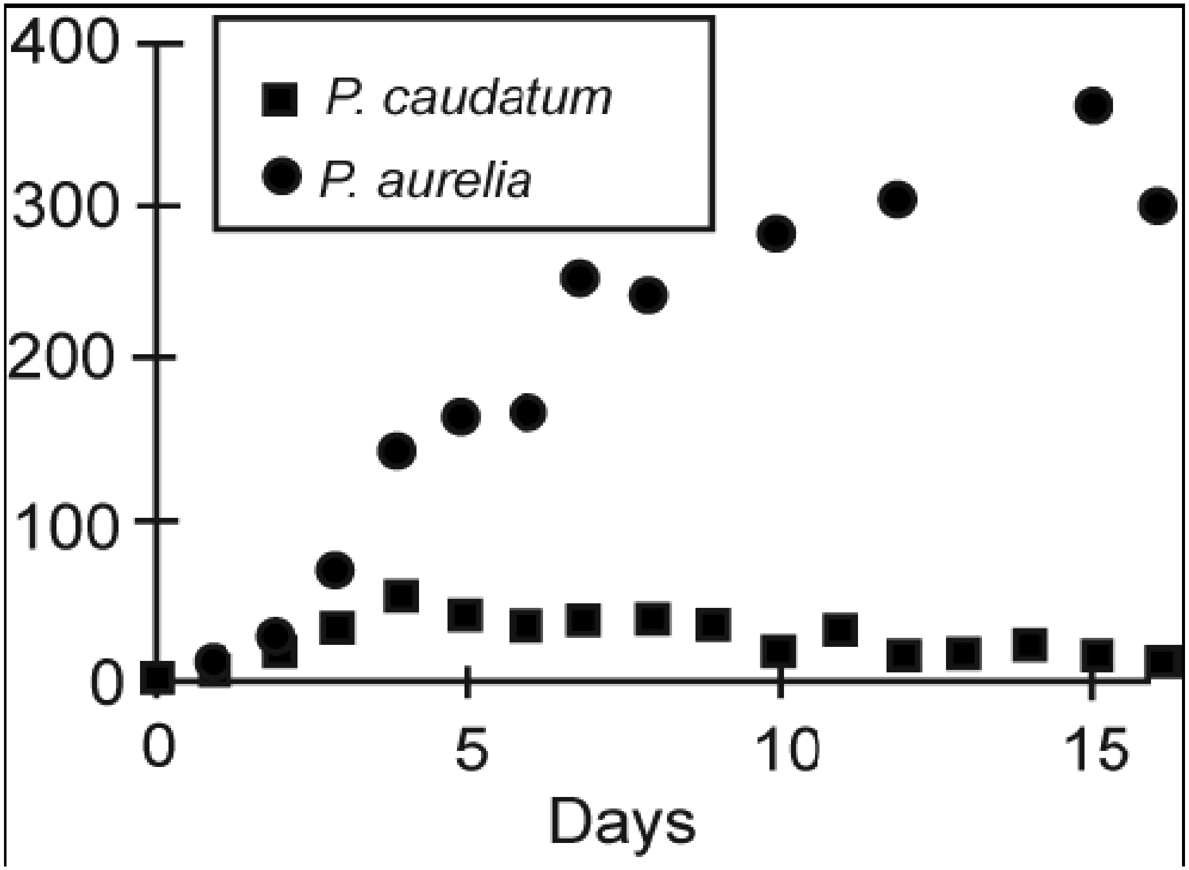
There are two types of competition, one occurs among individuals of the same species (intraspecific), and the other occurs among two (or more) species (interspecific competition).

*Intraspecific competition was accounted for in one dimensional models as we have already seen.

*Interspecific competition will be our focus here. G.F. Gause (1935) conducted an experiment on three different species of paramecium, P. Aurelia, P. Caudatum and P. Bursarua T. Park (1954) conducted a similar experiment on two species of the flour beetles, Tribolium (T) Castaneum and T. confusum.

Based on these experiments, the competition exclusion principle" was established:

If two species are very similar (such as sharing the same food ecological niche, etc.), they cannot coexist.



P. Aurelia out competes P. Caudatum

Leslie-Gower Competition Model

Let x_t, y_t be the population densities of species *x* and *y*.

Assumptions:

(i) In the absence of species *y*, species *x* grows according to the Beverton-Holt Model,

$$x_{t+1} = \frac{R_1 K_1 x_t}{K_1 + (R_1 - 1)x_t}$$

(ii) In the absence of species x, species y grows according to the Beverton-Holt Model,

$$y_{t+1} = \frac{R_2 K_2 y_t}{K_2 + (R_2 - 1)y_t}$$

If species x and y are competing, then their fitness f will be adversely affected:

$$f(x_t) = \frac{R_1 K_1}{K_1 + (R_1 - 1)x_t + c_2 y_t}$$

$$f(y_t) = \frac{R_2 K_2}{K_2 + (R_2 - 1)y_t + c_1 x_2(t)}$$

Where c_2 measures the competition efficiency of species y and c_1 measure the competition efficiency of species x. Hence we have the Leslie-Gower Model.

$$x_{t+1} = \frac{R_1 K_1 x_t}{K_1 + (R_1 - 1)x_t + c_2 y_t}$$

$$y_{t+1} = \frac{R_2 K_2 y_t}{K_2 + (R_2 - 1)y_t + c_1 x_t}$$

I. The Ricker Competition Model

$$x_{t+1} = x_t \exp[r_1(1 - \frac{x_t}{K_1}) - c_2 y_t]$$

$$y_{t+1} = y_t \exp[r_2(1 - \frac{y_t}{K_1}) - c_1 x_t]$$

II. The Discrete Logistic Competition Model

$$x_{t+1} = x_t[1 + r_1(1 - \frac{x_t}{K_1}) - c_2 y_t$$

$$y_{t+1} = y_t[1 + r_2(1 - \frac{y_t}{K_2}) - c_1 x_t$$

Estimation of parameters

Leslie-Gower Model (as an example)

Step 1. Find R_1, K_1, R_2, K_2 by growing species x and y separately as for single species.

Step 2. For t=I, $0 \le i \le n-1$, we have

$$x_{i+1} = \frac{R_1 K_1 x_i}{K_1 + (R_1 - 1)x_i + c_2^i y_i}$$

Hence
$$c_2^i = \frac{R_1 K_1 x_i - x_{i+1}(K_1 + (R_1 - 1)x_i)}{y_i x_{i+1}}$$

We estimate c_2 as the average of all c_2^i

$$c_2 = \frac{1}{n}\sum_{i=0}^{n-1} c_2^i$$

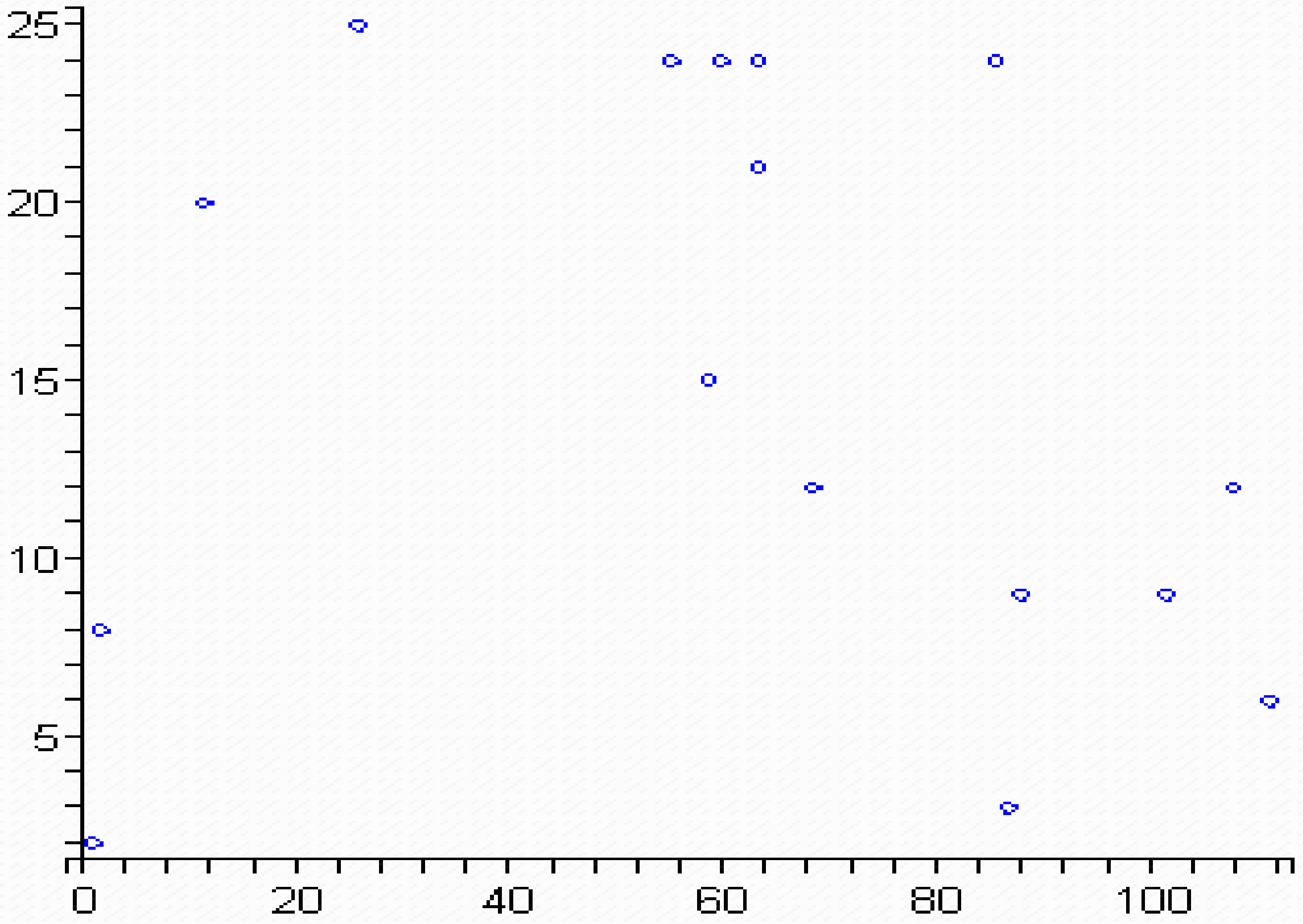
Comparative Data Analysis

Now we use the data obtained from the lab to plot the phase space of the two species of Paramecium, namely, P. Aurelia, and P. Caudatum.

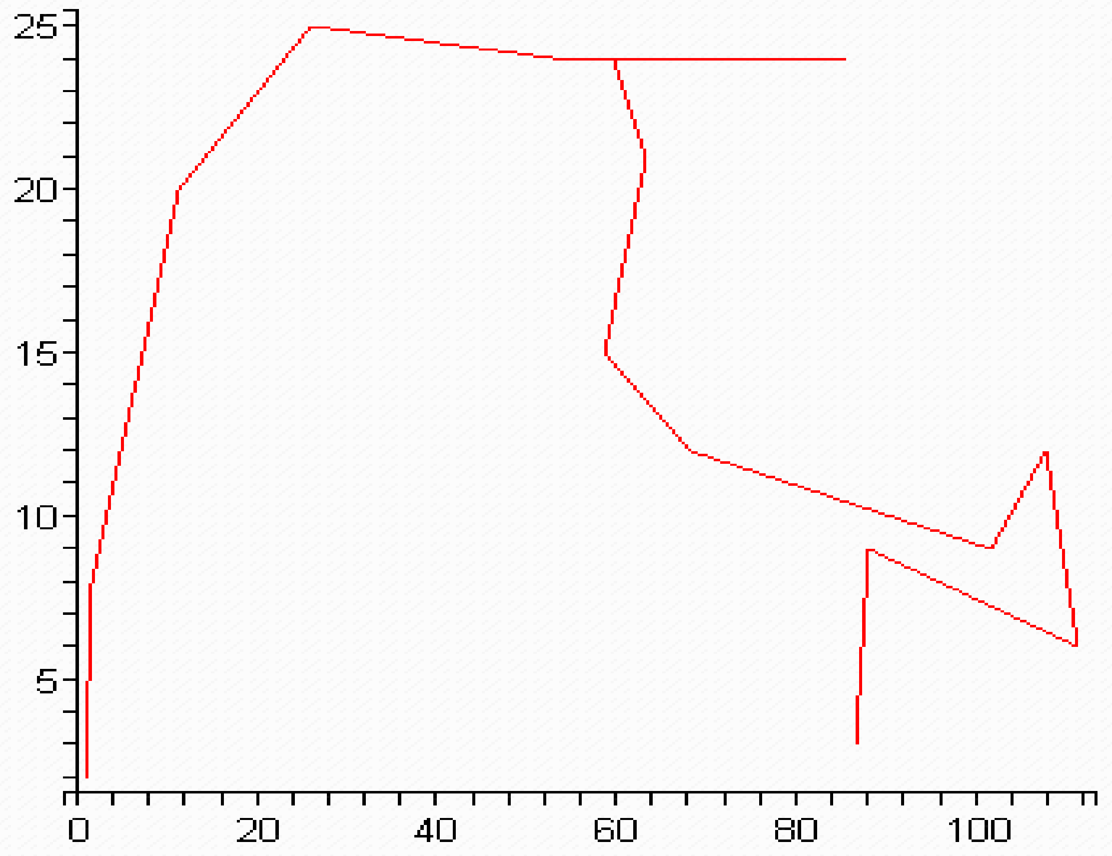
```
pts:=seq([T[k],S[k]],k=1..16);
```

```
    pts := [0.78, 2], [1.56, 8], [11.31, 20], [25.74, 25], [54.99, 24], [63.18, 24], [85.41, 24], [59.67, 24], [63.18, 21],
          [58.50, 15], [68.25, 12], [101.40, 9], [107.64, 12], [111.15, 6], [87.75, 9], [86.58, 3]
```

```
   > plot([pts],
   style=point,symbol=diamond,color=blue);
```

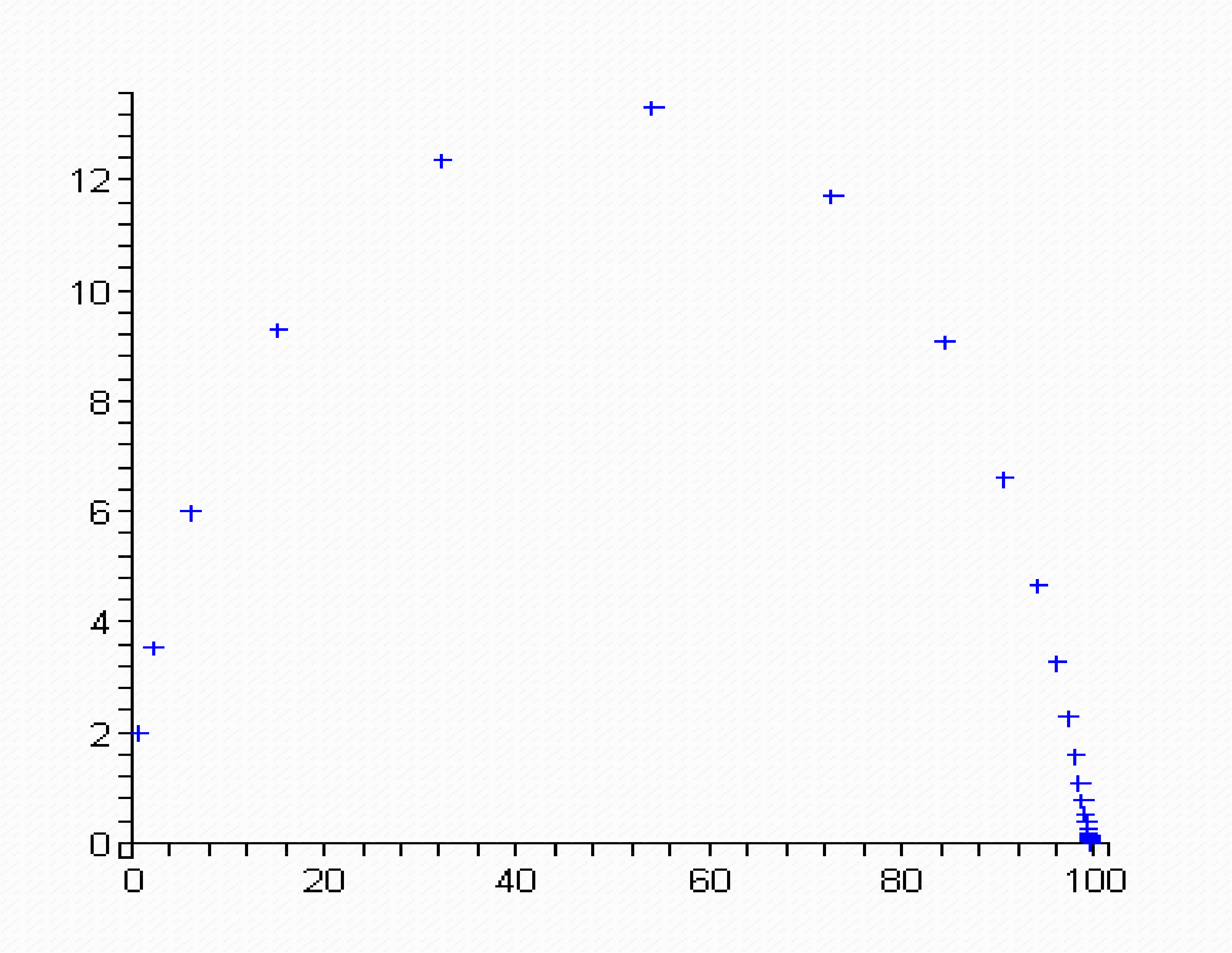


P. Aurelia out competes P. Caudatum: Phase space portrait



P. Aurelia out competes P. Caudatum: Phase space portrait

```
#Phase Space
> restart;
> x[0]:=2*0.39:y[0]:=2:N:=4000:
> for n from 0 to N do
 >
x[n+1]:=2.95*255*0.39*x[n]/(255*0.39+1.95*x[n]+y[
n]): y[n+1]:=1.84*60*y[n]/(60+0.84*y[n]+x[n]):
 > end do:
> pointlist:=seq([x[n],y[n]],n=0..N):
> plot([pointlist],
style=point,symbol=point,color=blue):
> plot([pointlist]);

> pointlist:=seq([x[n],y[n]],n=0..N):
> plot([pointlist],
style=point,symbol=cross,color=blue);
```



Phase space portrait of the Leslie-Gower model

Stability Analysis

(Leslie-Gower Model)

Equilibrium (fixed) points:

$$x_{t+1} = F(x_t, y_t)$$
$$y_{t+1} = G(x_t, y_t)$$

Solve: F(x,y) = x and G(x,y) = y

For Leslie-Gower we obtain four fixed points (0,0), (K_1,0), (0,K_2), (x^*, y^*), where

$$x^* = \frac{(R_2 - 1)[K_1(R_1 - 1) - c_2K_2}{(R_1 - 1)(R_2 - 1) - c_1c_2}$$
$$y^* = \frac{(R_1 - 1)[K_2(R_2 - 1) - c_1K_1}{(R_1 - 1)(R_2 - 1) - c_1c_2}$$

*Stability via linearization

We find the Jacobian matrix of system (1)

$$J = \begin{pmatrix} \dfrac{\partial F}{\partial x} & \dfrac{\partial F}{\partial y} \\ \dfrac{\partial G}{\partial x} & \dfrac{\partial G}{\partial y} \end{pmatrix}$$

The eigenvalues of J determine the stability of the equilibria of (1).

Determinant-Trace Analysis

Given a 2x2 matrix A= (aij), its characteristic equation is given by

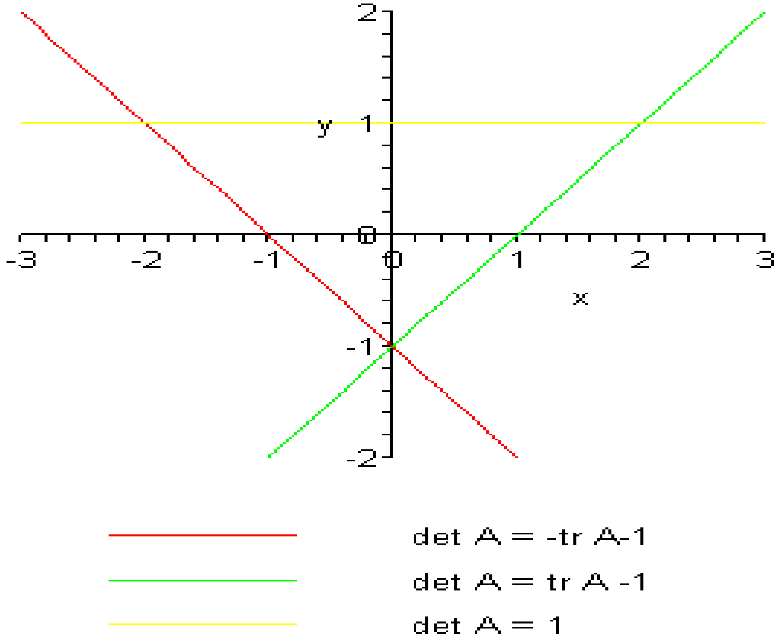
$$\lambda^2 - trA\lambda + \det A = 0$$

$$\lambda = \frac{trA}{2} \pm \frac{1}{2}\sqrt{(trA)^2 - 4\det A}$$

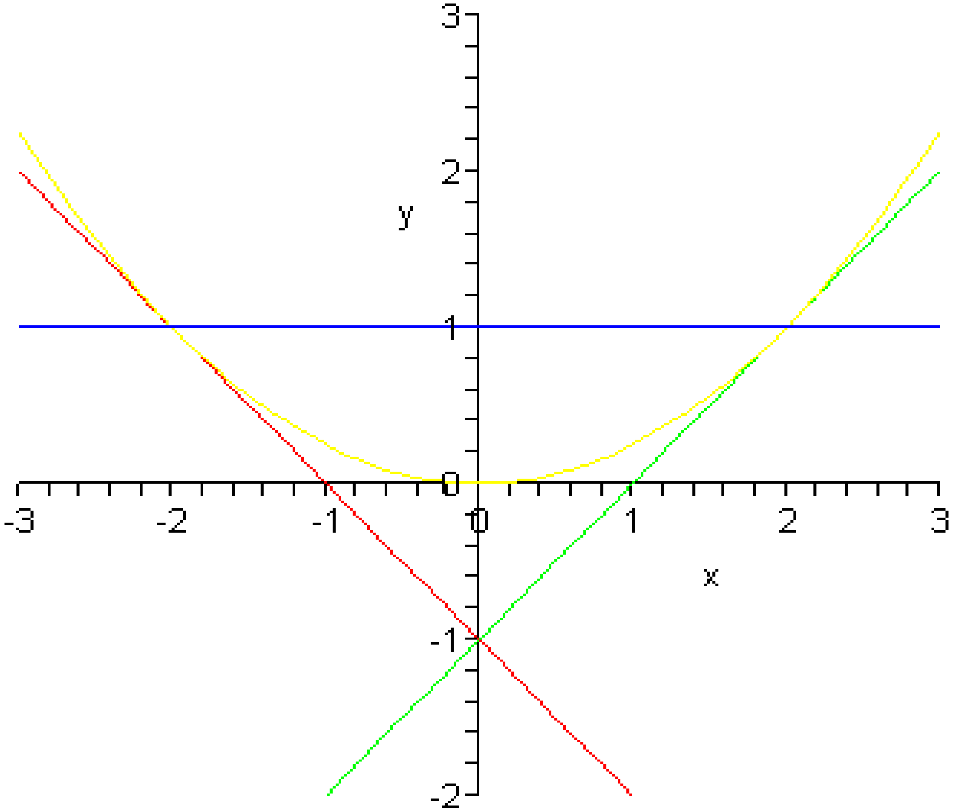
Theorem. The eigenvalues of A lie inside the unit desk if

$$\boxed{|tr\,A| < 1 + \det\ A < 2}$$

-1=tr A<det A, det A> - tr A-1, det A<1



Determinant-Trace Analysis I



Determinant-Trace Analysis II

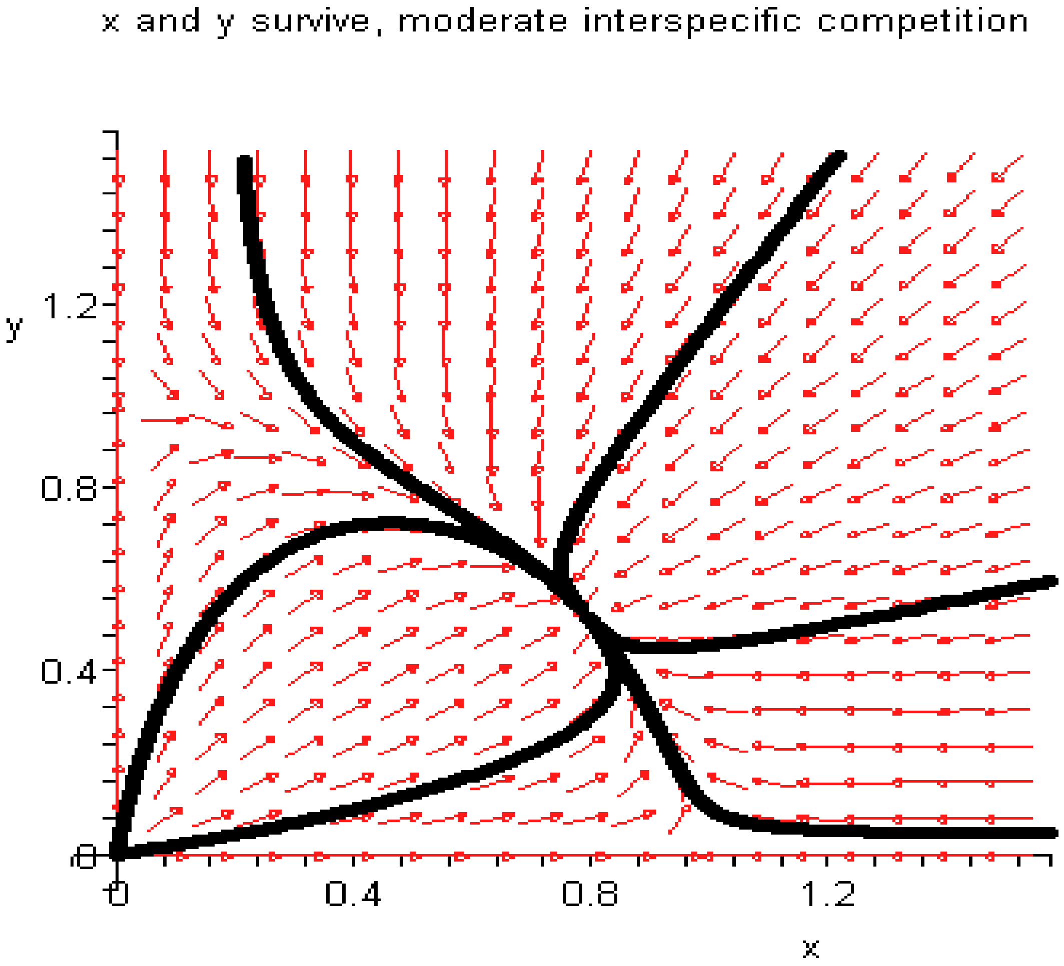
(From S. Elaydi, Discrete Chaos, 2008)

Let $M_2 = \frac{(R_2 - 1)}{K_2} \frac{(R_2 K_2 - 1)}{(R_1 K_1 - 1)}$ and $M_1 = \frac{(R_1 - 1)(R_1 K_1 - 1)}{K_1 (R_2 K_2 - 1)}$

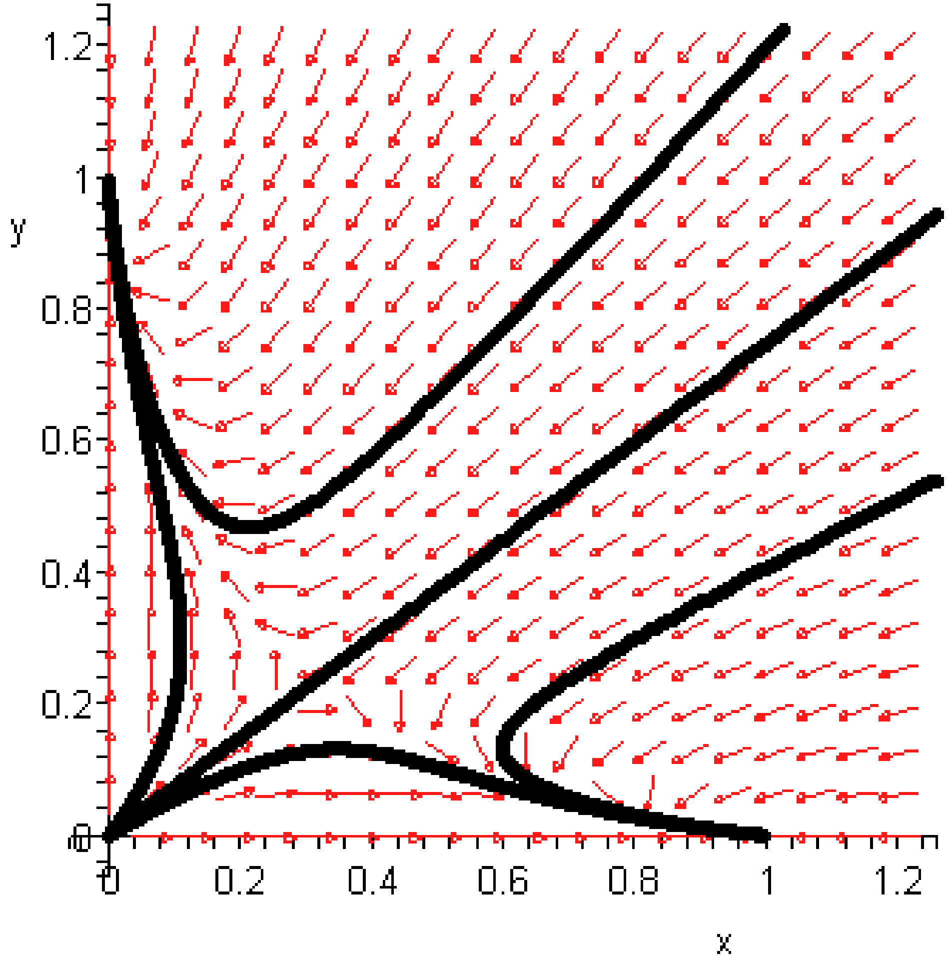
Theorem. The following statements hold for the Leslie-Gower Model

1. If $C_2 < M_2$ and $C_1 < M_1$, then (x^*, y^*) is “globally stable”
2. If $C_2 < M_2$ and $C_1 > M_1$, then $(K_1, 0)$ is “globally stable”
3. If $C_2 < M_2$ and $C_1 < M_1$, then $(0, K_2)$ is “globally stable”
4. If $C_2 < M_2$ and $C_1 > M_1$, then $(K_1, 0)$ and $(0, K_2)$ are “locally” stable, while (x^*, y^*) is a saddle.

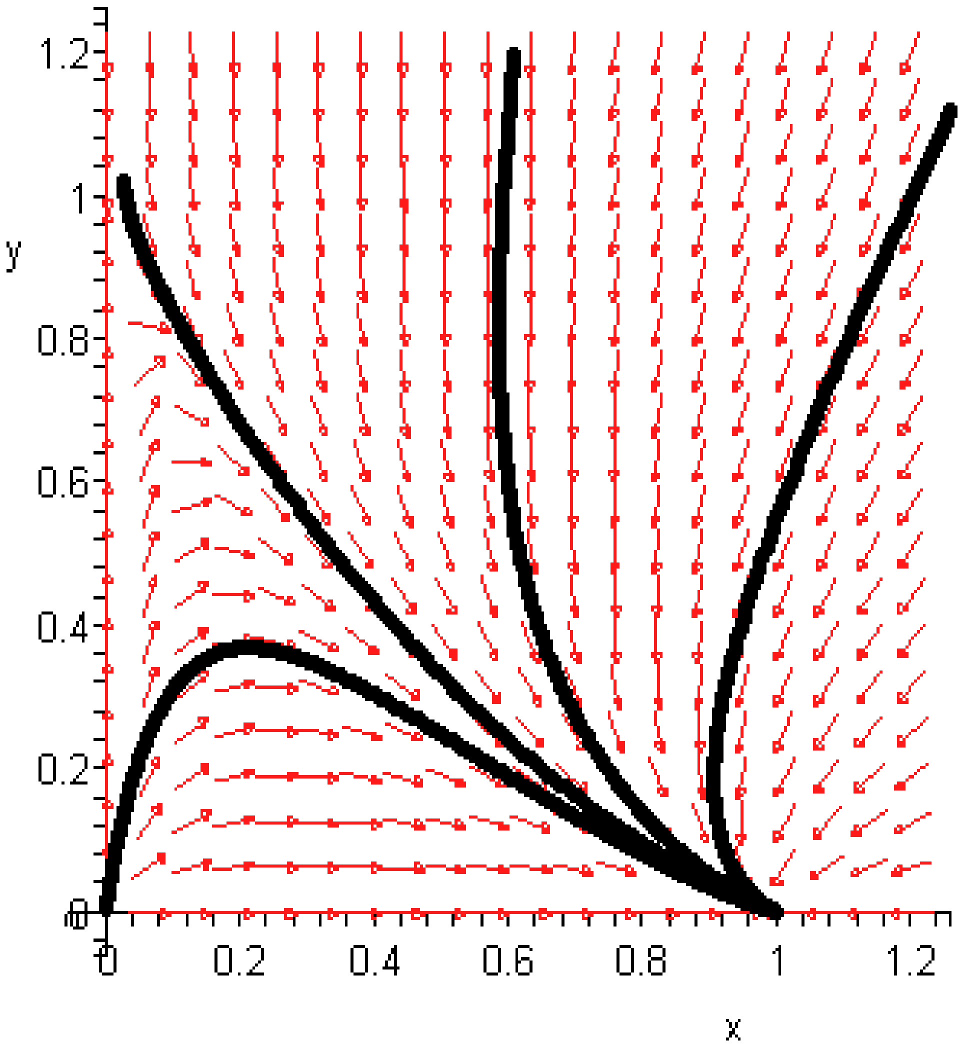
The four scenarios are depicted in the graphs below.

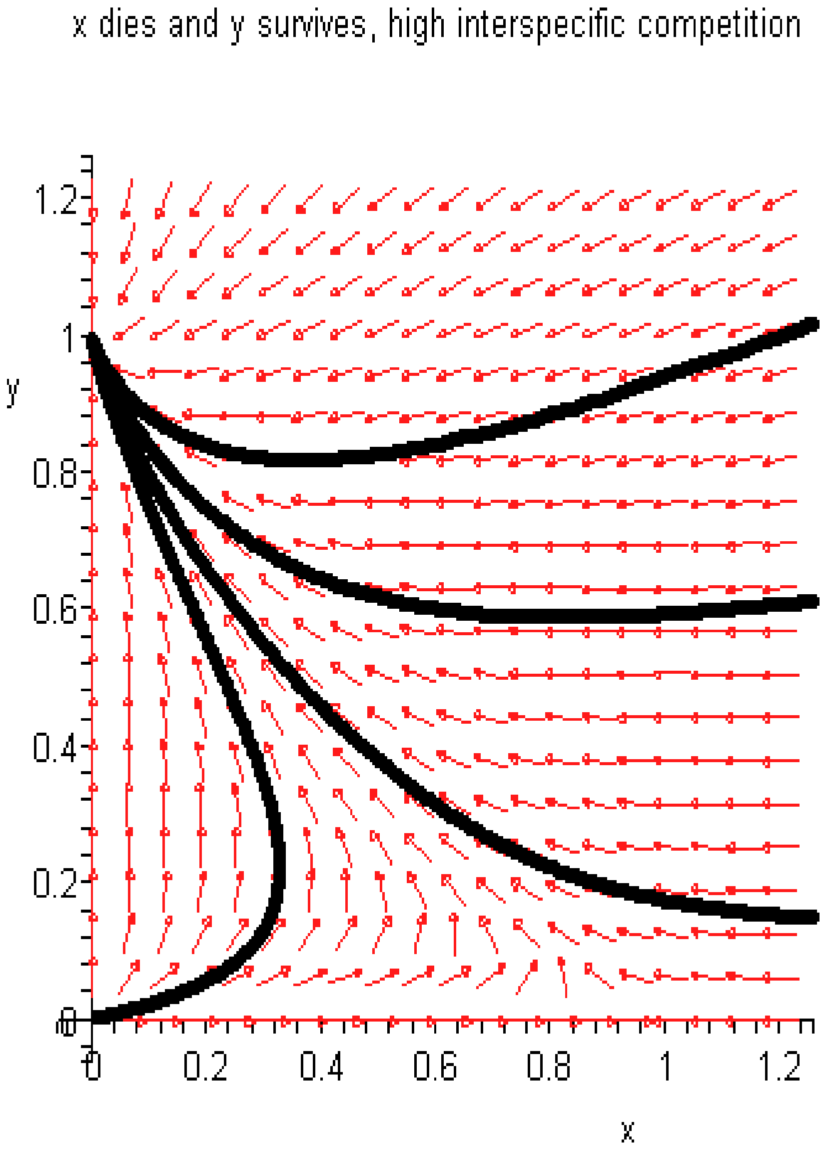


A saddle, high interspecific competition



y dies and x survives, high interspecific competition




x dies and y survives, high interspecific competition
1.2
1
0.8
0.6
0.4
0.2
0
y
0
0.2
0.4
0.6
0.8
1
1.2
x

Predator-Prey Models

In 1933 and later with Bailey in 1935, Nicholson made two assumptions for building his host-parasitoid model. Though the model deals mainly with parasites, it serves as a starting point for understanding and constructing predator-prey models.

Let N_t denote the population size of the prey (host) at the time period t, and P_t denote the population size of the predator (parasitoid) at time period t.

The Nicholson's assumptions on parasitoid searching behavior are:

(1) The total number of encounters of the parasitoids with hosts is given by

$$N_e = a N_t P_t \quad (4.1)$$

Where a is the probability that a given predator will encounter a given prey during its search lifetime.

(2) These N_e encounters are distributed randomly among the available hosts. Nicholson made use of the poison distribution for the occurrence of discrete random events, in this case the occurrence of encounters between a predator and its prey. The distribution is defined by the mean frequency of occurrence, namely, the average number of encounters with a given prey, i.e. N_e / N_t.

If we assume that a parasitoid lays as egg at each encounter, then the ratio N_e/N_t is the average number of eggs laid per host. On the other hand, for predators that consume their prey, the ratio N_e/N_t is the average number encounters with a particular "prey location". Thus the probability of a host (prey location) being encountered 0, 1, 2, …, n times is given respectively by

$$e^{-\bar{x}}, \bar{x}e^{-\bar{x}}, \frac{\bar{x}^2}{2!}e^{-\bar{x}}, \ldots, \frac{\bar{x}^n}{n!}e^{-\bar{x}}$$

Where $\bar{x} = N_e/N_t$. For our purpose, we only need the probability that the host or the prey not being detected (the zero term of the distribution, namely exp($-N_e/N_t$)

Consequently, the probability of actually being parasitized (attached) is given by

$$1\text{-exp}(-N_e/N_t)$$

Let

$$N_a = N_t\,[1-exp(-N_e/N_t)] \qquad (4.2)$$

Substituting from (4.1) into (4.2) yields

$$N_a = N_t\,[1-exp\,(-aP_t)] \qquad (4.3)$$

In the final step of creating the model we assume that each host parasitized leads to one adult parasitoid in the next generation, i.e.,

$$P_{t+1} = N_a.$$

Substituting in (4.3) we obtain

$$P_{t+1} = N_t[1-exp(-aP_t)]$$

Moreover, assuming that in the absence of the parasitoids (prey), the host (prey) grows geometrically with rate R, then we have

$$N_{t+1}=RN_t \exp(-a P_t).$$

The Nicholson-Bailey model is now given by

$$N_{t+1}=RN_t \exp(-a P_t) \tag{4.4a}$$
$$P_{t+1}=N_t [1-\exp(-a P_t)] \tag{4.4b}$$

The possible equilibrium (N*,P*) is given by

$$N^*=\frac{\lambda \ln \lambda}{a(\lambda-1)},\; P^*=\frac{\ln \lambda}{a}$$

The other equilibrium point is $(0,0)$.

$$J=\begin{pmatrix} Re^{-aP} & -a\lambda N e^{-aP} \\ 1-e^{-aP} & aN e^{-aP} \end{pmatrix}$$

At *(0,0)*,

$$J=\begin{pmatrix} R & 0 \\ 0 & 0 \end{pmatrix}$$

Thus (0,0) is stable if 0<R<1 and unstable for R>1.

At *(N*,P*)*,

$$J=\begin{pmatrix} 1 & -\dfrac{R\ln R}{(R-1)} \\ 1-\dfrac{1}{R} & -\dfrac{\ln R}{(R-1)} \end{pmatrix}$$

Verify that $\left|\mathrm{tr}\, J\right| < 1+\det J < 2$.

$$1-\frac{\ln R}{(R-1)} < 1-2\frac{\ln R}{(R-1)} + \frac{R\ln R}{(R-1)} < 2$$

The left inequality is satisfied for $R > 1$. The right inequality is satisfied if $R <\approx 4.244$

Hence (N^*, P^*) is stable if $1 < R <\approx 4.244$

Bedington, Free and Lawton (1975)

A Predator-Prey Model

Notice that in the absence of parasitoids, the equation of the host (prey) becomes $N_{t+1} = RN_t$ which gives the geometric growth $N_t = R^t N_0$. Such a scenario may be valid for certain hosts but may fail for most prey. Instead, Bedington et al assumed a Ricker-type growth model,

$$N_{t+1} = N_t\, exp(r\ (1\text{-}N_t/K)),\ where\ r = ln$$

Hence the new model is given by

$$N_{t+1} = N_t\, exp\ (r(1\text{-}N_t/K) - aP_t) \quad (4.5a)$$
$$P_{t+1} = N_t\ [1\text{-}exp\ (\text{-}aP_t)] \quad (4.5b)$$

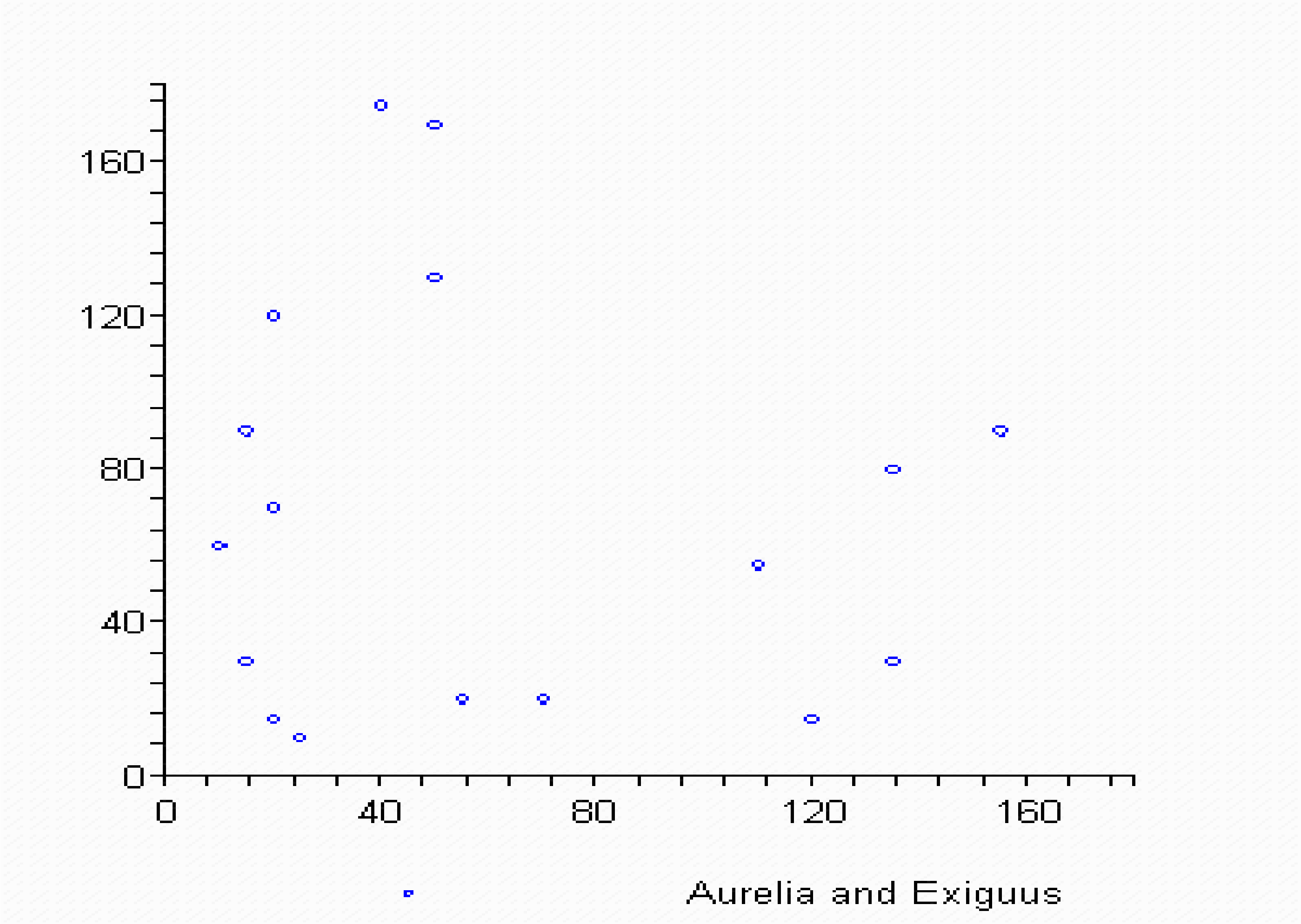
Lab experiment

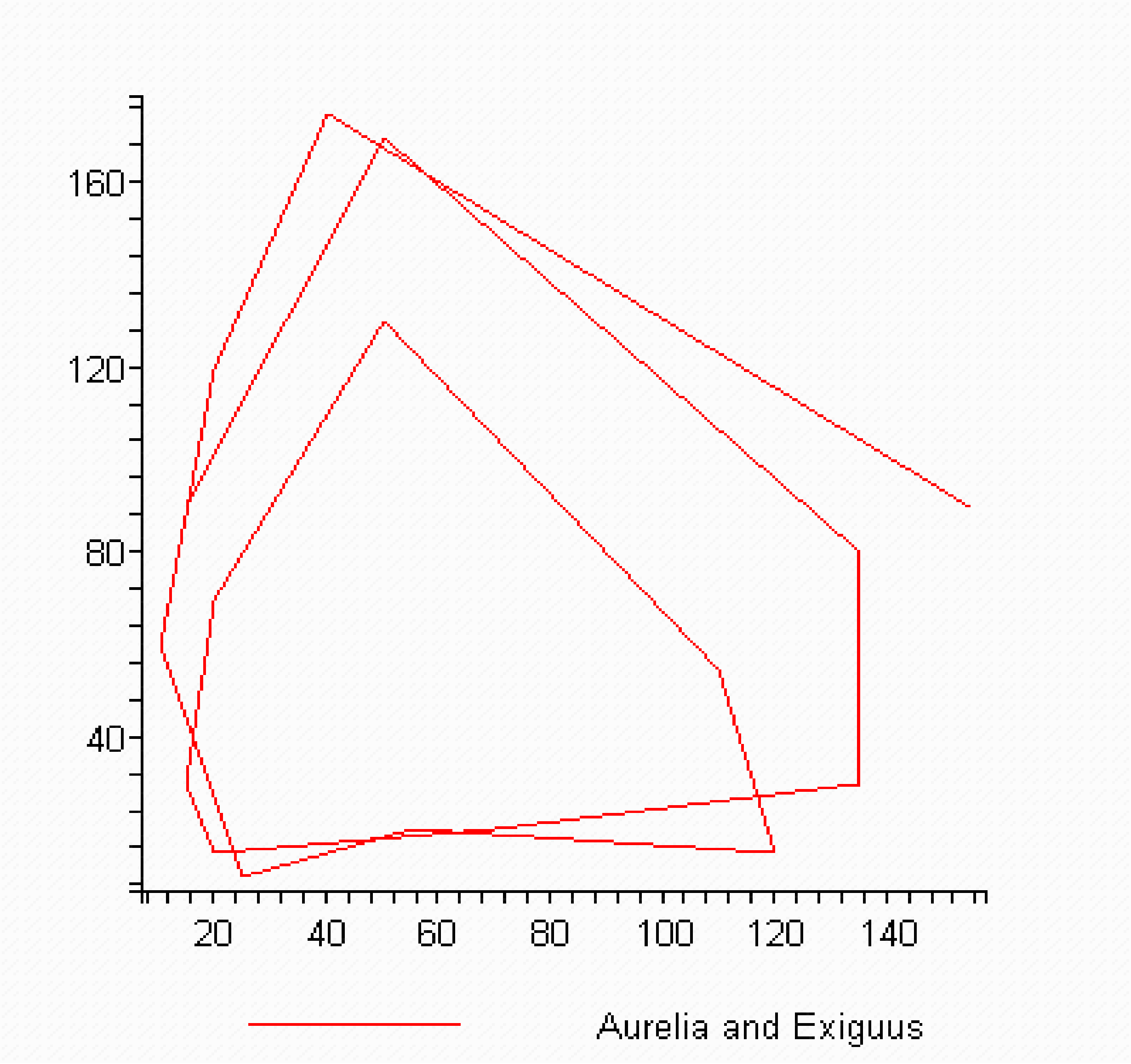
Another experiment performed by Gause (1934) involved Paramecium aurelia and Saccharomyces exiguous (a yeast on which p. Aurelia feeds). Predator-Prey Models:

```
>
restart:with(plots):T:=[155,40,20,10,25,55,120,110,50
,20,15,20,70,135,135,50,15,20];
```

```
T := [155, 40, 20, 10, 25, 55, 120, 110, 50, 20, 15, 20, 70, 135, 135, 50, 15, 20]
```

```
>
S:=[90,175,120,60,10,20,15,55,130,70,30,15,20,30,80,1
70,90,30];
                S := [90, 175, 120, 60, 10, 20, 15, 55, 130, 70, 30, 15, 20, 30, 80, 170, 90, 30]

> pts:=seq([T[k],S[k]],k=1..17);
             pts := [155, 90], [40, 175], [20, 120], [10, 60], [25, 10], [55, 20], [120, 15], [110, 55], [50, 130], [20, 70],

         [15, 30], [20, 15], [70, 20], [135, 30], [135, 80], [50, 170], [15, 90]

>
> plot([pts], style=point,symbol=diamond,color=blue);

      i. plot([pts]);
```


0
40
80
120
160
0
40
80
120
160
Aurelia and Exiguus


160
120
80
40
20
40
60
80
100
120
140
Aurelia and Exiguus