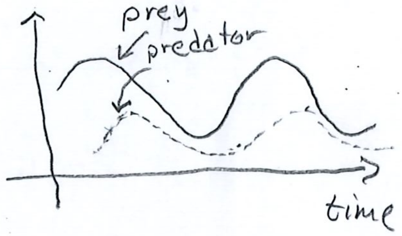
Predator-prey models

Can one model observed oscillating behaviour in predator/prey populations?



From seminar 1: $x(t)$ = prey population
$y(t)$ = predator —"—

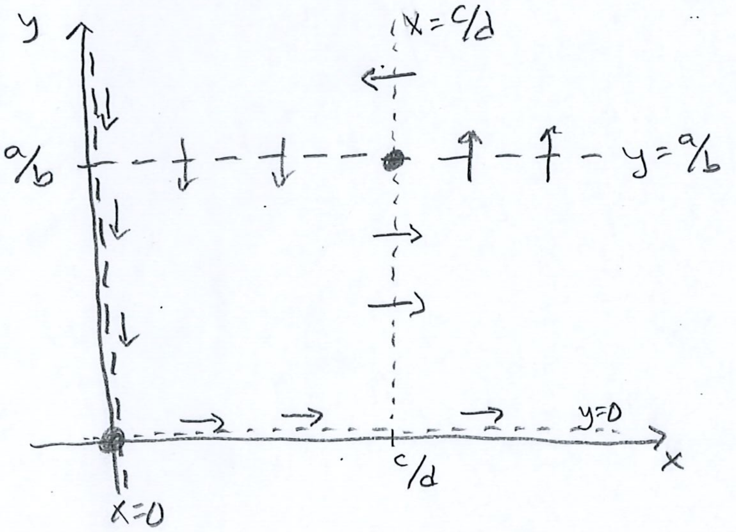
Lotka-Volterra model

$$\begin{cases} \dfrac{dx}{dt} = ax - bxy = F_1(x,y) \\ \dfrac{dy}{dt} = -cy + dxy = F_2(x,y) \end{cases} \qquad a,b,c,d > 0$$

Interpretations
* no predators $(y=0)$ $\Rightarrow$ exp. growth of prey
* no prey $(x=0)$ $\Rightarrow$ exp. decay of predators
* predator growth is proportional to food intake, which depends on likelihood of predators finding prey, a random model for the number of encounters gives the xy-term (non-linear)

To understand solutions, study the phase plane

x nullclines $\quad x(a-by)=0 \Rightarrow x=0$ or $y=a/b$, 2 lines
y nullclines $\quad y(-c+dx)=0 \Rightarrow y=0$ or $x=c/d$, 2 lines



2 steady states
$(\bar{x}_1,\bar{y}_1)=(0,0)$, $(\bar{x}_2,\bar{y}_2)=\left(\frac{c}{d},\frac{a}{b}\right)$

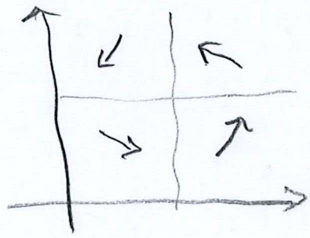
Draw

$\bar{F}=(0, \underbrace{y(dx-c)}_{>0 \text{ if } x>\frac{c}{d}})$ on x nullcline

$\bar{F}=(\underbrace{x(a-by)}_{>0 \text{ if } y<\frac{a}{b}}, 0)$ on y nullcline

$(0,0)$ looks like saddle

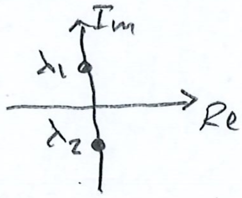
$\left(\frac{c}{d},\frac{a}{b}\right)$?



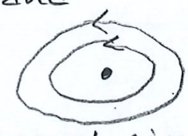
Jacobian $J(x,y) = \begin{pmatrix} \frac{\partial F_1}{\partial x} & \frac{\partial F_1}{\partial y} \\ \frac{\partial F_2}{\partial x} & \frac{\partial F_2}{\partial y} \end{pmatrix} = \begin{pmatrix} a-by & -bx \\ dy & -c+dx \end{pmatrix} \Rightarrow$

$J(0,0) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \Rightarrow \lambda_1 = a > 0, \lambda_2 = -c < 0 \Rightarrow (\bar{x}_1, \bar{y}_1) = (0,0)$ saddle (unstable)

$J(\frac{c}{d}, \frac{a}{b}) = \begin{pmatrix} 0 & -\frac{bc}{d} \\ \frac{ad}{b} & 0 \end{pmatrix} \Rightarrow \lambda^2 + \frac{ad}{b}\frac{bc}{d} = 0 \Rightarrow \lambda^2 = -ac < 0 \Rightarrow \lambda_{1,2} = \pm i\sqrt{ac}$



eigenvalues on imaginary axis $\Rightarrow$
the linearized system has a centre, and
solutions are periodic orbits



This is a sensitive case to drawing conclusions about the original non-linear L-V system (see Hartman-Grobman theorem)

In this case we can do a special analysis [compare problem 6.10 in Ek].
If $(x(t), y(t))$ is a solution curve, L-V $\Rightarrow$

$$\frac{dy}{dx} = \frac{\frac{dy}{dt}}{\frac{dx}{dt}} = \frac{-cy+dxy}{ax-bxy} \Rightarrow x(a-by)\frac{dy}{dx} = y(-c+dx) \Rightarrow$$

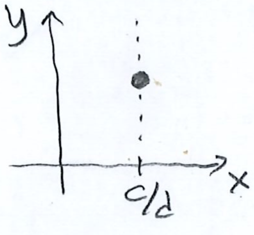
$\left(\frac{a}{y} - b\right)\frac{dy}{dx} = -\frac{c}{x} + d$, separated ODE (y as a function of x)

integrate w.r.t. x $\Rightarrow$ $a\ln|y| - by = -c\ln|x| + dx + k_1$ ← constant, determined by initial values

$$\underset{x>0,y>0}{\Rightarrow} e^{a\ln y - by} = e^{-c\ln x + dx} \cdot \underbrace{e^{k_1}}_{=k_2>0} \Rightarrow \underline{y^a e^{-by} = x^{-c} e^{dx} k_2}$$

(gives level curve for solution)

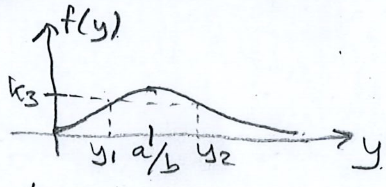
On the y nullcline $x = \frac{c}{d}$: $\underbrace{y^a e^{-by}}_{f(y)} = \left(\frac{c}{d}\right)^{-c} e^c \cdot k_2 = k_3 > 0$



How many solutions can $f(y) = k_3$ have? In how many places can our solution curve cross this nullcline?

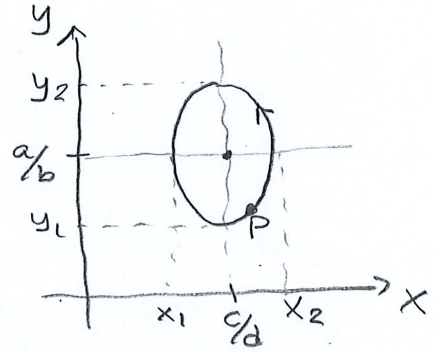
$$f'(y) = ay^{a-1}e^{-by} - by^a e^{-by} = \underbrace{y^{a-1}e^{-by}}_{>0}(a-by) = 0 \text{ if } y = a/b$$

$f'(y) \begin{cases} >0 \text{ if } y < a/b \\ <0 \text{ if } y > a/b \end{cases}$, $f(0) = 0$, $f(y) \to 0, y \to \infty$
$f(y) \geq 0$ for all y



$\Rightarrow$ at most 2 solutions y_1 and y_2 for any k_3

The same holds on the x nullcline $y = a/b$; at most 2 x-values x_1 and x_2



$\Rightarrow$ no spiral around $(\frac{c}{d}, \frac{a}{b})$

(would give more x- and y-values on the nullclines)

$\Rightarrow$ solutions are closed curves

$\Rightarrow$ L-V gives periodic solutions for predator and prey (which has been observed in nature)

Starting at P with plenty of prey x and few predators y, both x and y increase until y big enough to reduce x, after a while lower x leads to decrease in y, so later x increases again, which then again leads to increasing y (back at P).

See Maple plots of phase plane and of $x(t)$ and $y(t)$ as functions of t. There are also interesting Wolfram demonstrations of L-V. (page 9.5)

One modification of L-V (many others possible): logistic growth in prey x if no predators

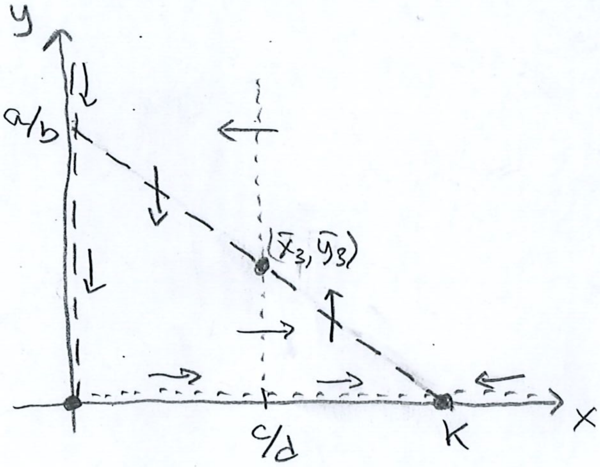
$$\begin{cases} \dfrac{dx}{dt} = ax\underbrace{(1-\frac{x}{K})}_{\text{new term}} - bxy \\ \dfrac{dy}{dt} = -cy + dxy \end{cases}$$

K = carrying capacity of prey

Study phase plane

x nullclines $x(a - \frac{ax}{K} - by) = 0 \Rightarrow x = 0$ or $\frac{ax}{K} + by = a$, 2 lines

y nullclines $y(-c + dx) = 0 \Rightarrow y = 0$ or $x = c/d$ as before (2 lines)



Assume $K > c/d \Rightarrow$ 3 steady states:

$(\bar{x}_1, \bar{y}_1) = (0,0)$

$(\bar{x}_2, \bar{y}_2) = (K, 0)$

$(\bar{x}_3, \bar{y}_3)$ with $\bar{x}_3 = \frac{c}{d}$ and $\frac{a\bar{x}_3}{K} + b\bar{y}_3 = a \Rightarrow$

$\bar{y}_3 = \frac{a}{b}(1 - \frac{c}{Kd})$

Draw $\bar{F}$ on nullclines

$$J(x,y) = \begin{pmatrix} a-\frac{2ax}{K}-by & -bx \\ dy & -c+dx \end{pmatrix} \Rightarrow$$

$$J(0,0) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \Rightarrow \lambda_1 = a>0,\ \lambda_2 = -c<0 \Rightarrow (0,0) \text{ saddle}$$

$$J(K,0) = \begin{pmatrix} -a & -bK \\ 0 & -c+dK \end{pmatrix} \Rightarrow \lambda_1 = -a<0,\ \lambda_2 = -c+dK>0 \Rightarrow (K,0) \text{ saddle}$$

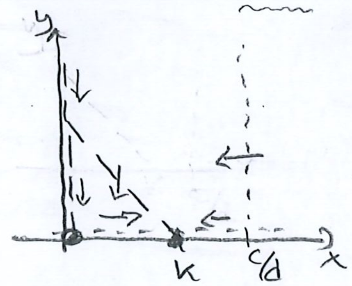
$$J(\bar{x}_3,\bar{y}_3) = \begin{pmatrix} -\frac{ac}{dK} & -\frac{bc}{d} \\ \frac{da}{b}(1-\frac{c}{Kd}) & 0 \end{pmatrix} = J_3 \Rightarrow \left.\begin{array}{l} \operatorname{tr} J_3 = -\frac{ac}{dK} < 0 \\ \det J_3 = ac\underbrace{(1-\frac{c}{Kd})}_{>0} > 0 \end{array}\right\} \Rightarrow (\bar{x}_3,\bar{y}_3) \text{ stable}$$

$(\bar{x}_3,\bar{y}_3)$ can be both spiral (if complex eigenvalues, $(\operatorname{tr} J_3)^2 < 4\cdot\det J_3$) or with 2 real negative eigenvalues.

See Maple plots for $a=2, b=4, c=d=1$ ($K > c/d = 1$), $(\bar{x}_3,\bar{y}_3) = (1, \frac{1}{2}(1-\frac{1}{K}))$ with $K=1.5$ (no spiral) and $K=3$ (spiral). One finds spirals if $K > \frac{\sqrt{3}+1}{2} \approx 1.86$.
[plot on page 9.6]

This shows sensitivity in the original L-V model, a small modification (introducing a large carrying capacity K) changes the solutions from periodic to spiraling towards a stable steady state.

Note that if $K < \frac{c}{d}$, $(\bar{x}_3,\bar{y}_3)$ disappears and $J(K,0)$ gets $\lambda_{1,2} < 0 \Rightarrow$ stable



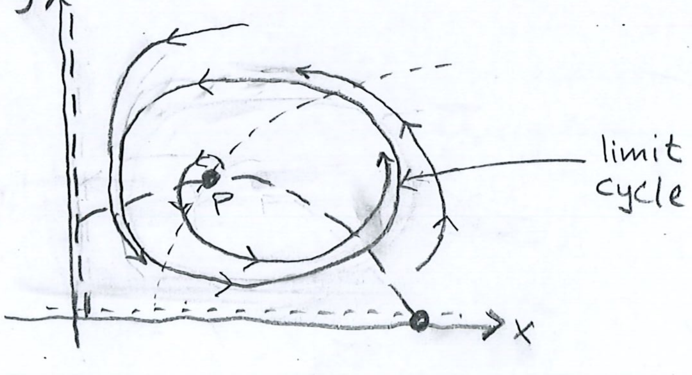
$\Rightarrow (x(t),y(t)) \to (K,0),\ t\to\infty$

K is too small for predators to survive

<u>Remark</u>: There are more general predator-prey models that produce oscillating populations [8.7 in EK].

They have nullclines and phase plane looking like:

(P unstable, solutions approach the limit cycle from inside or outside)

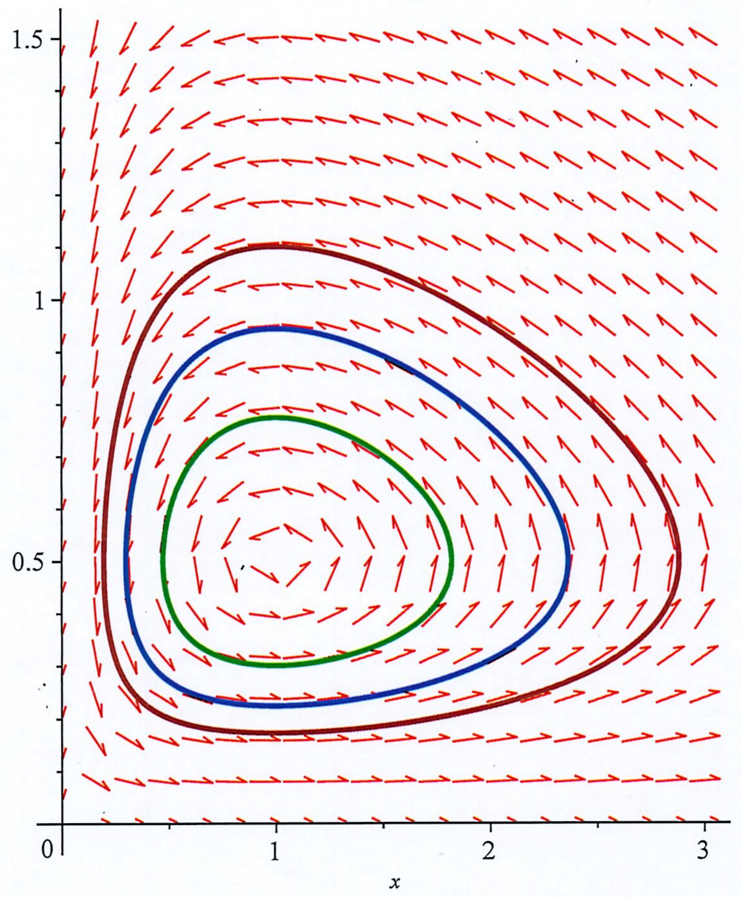


Lotka-Volterra $a=2, b=4, c=d=1 \Rightarrow (1, \tfrac{1}{2})$ steady state

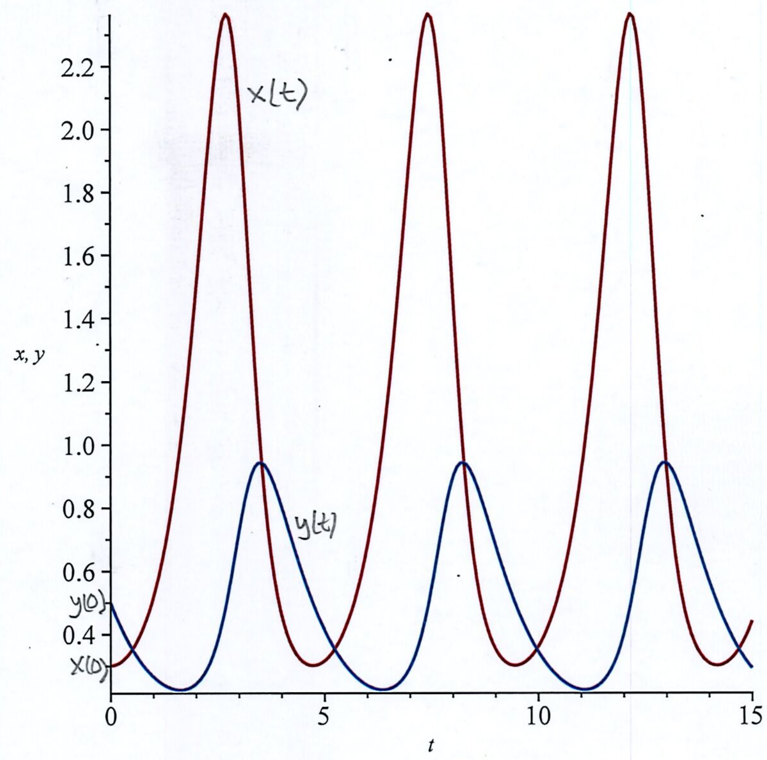
```
> with(DEtools):
> sys := {diff(x(t), t) = 2·x(t) − 4·x(t)·y(t), diff(y(t), t) = x(t)·y(t) − y(t)}
```

$$sys := \left\{ \frac{d}{dt}\, x(t) = 2\,x(t) - 4\,x(t)\,y(t),\ \frac{d}{dt}\, y(t) = x(t)\,y(t) - y(t) \right\} \quad (1)$$

```
> DEplot(sys, [x(t), y(t)], t = 0..15, [[x(0) = 0.3, y(0) = 0.5], [x(0) = 1.0, y(0) = 0.3], [x(0) = 1.0, y(0) = 1.1]], x = 0..3, y = 0..1.5, linecolor = [blue, green, brown], numpoints = 1000)
```




```
p := dsolve({diff(x(t), t) = 2·x(t) − 4·x(t)·y(t), diff(y(t), t) = x(t)·y(t) − y(t), x(0) = 0.3, y(0) = 0.5}, {x(t), y(t)}, type = numeric, range = 0..500):
> with(plots):
> odeplot(p, [[t, x(t)], [t, y(t)]], 0..15)
```



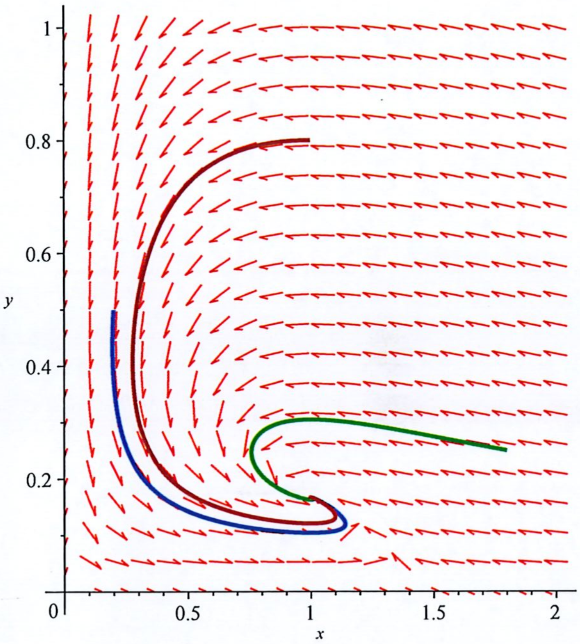
[corresponds to blue curve in phase plane]

Logistic Lotka-Volterra, $a=2, b=4, c=d=1$

```
> with(DEtools) :
> sys := {diff(x(t), t) = 2·x(t) − (4 x(t)·x(t))/3 −4· x(t)·y(t), diff(y(t), t) = x(t)·y(t) − y(t)}
```

$$sys := \left\{\frac{d}{dt}\,x(t) = 2\,x(t) - \frac{4\,x(t)^2}{3} - 4\,x(t)\,y(t),\ \frac{d}{dt}\,y(t) = x(t)\,y(t) - y(t)\right\} \quad (1)$$

```
> DEplot(sys, [x(t), y(t)], t = 0..15, [[x(0) = 0.2, y(0) = 0.5], [x(0) = 1.8, y(0) = 0.25], [x(0)
  = 1.0, y(0) = 0.8]], x = 0..2, y = 0..1, linecolor = [blue, green, brown], numpoints = 1000)
```

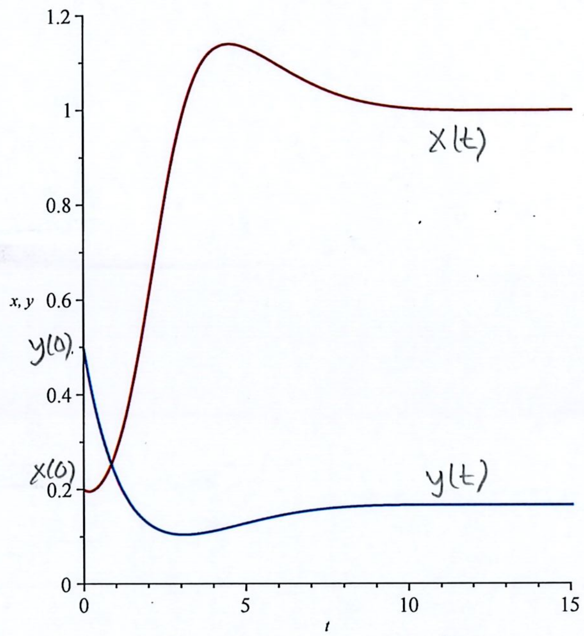


$K=1.5$

$(\bar{x},\bar{y})=(1,\frac{1}{6})$

$\lambda_1<0, \lambda_2<0$ (real)

```
p := dsolve({diff(x(t), t) = 2·x(t) − (4 x(t)·x(t))/3 − 4· x(t)·y(t), diff(y(t), t) = x(t)·y(t)
  − y(t), x(0) = 0.2, y(0) = 0.5}, {x(t), y(t)}, type = numeric, range = 0..500) :
> with(plots) :
> odeplot(p, [[t, x(t)], [t, y(t)]], view = [0..15, 0..1.2], refine = 1)
```

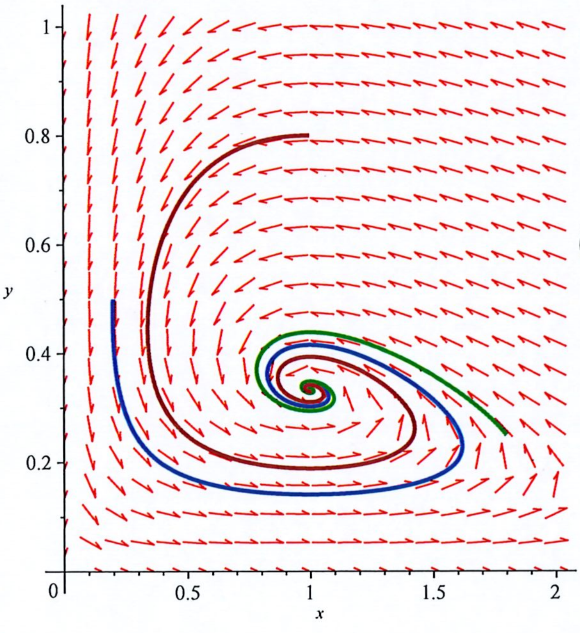


[corresp. to blue curves in phase plane]

```
sys2 := {diff(x(t), t) = 2·x(t) − (2 x(t)·x(t))/3 −4· x(t)·y(t), diff(y(t), t) = x(t)·y(t) − y(t)}
```

$$sys2 := \left\{\frac{d}{dt}\,x(t) = 2\,x(t) - \frac{2\,x(t)^2}{3} - 4\,x(t)\,y(t),\ \frac{d}{dt}\,y(t) = x(t)\,y(t) - y(t)\right\} \quad (2)$$

```
> DEplot(sys2, [x(t), y(t)], t = 0..15, [[x(0) = 0.2, y(0) = 0.5], [x(0) = 1.8, y(0) = 0.25], [x(0)
  = 1.0, y(0) = 0.8]], x = 0..2, y = 0..1, linecolor = [blue, green, brown], numpoints = 1000)
```



$K=3$

$(\bar{x},\bar{y})=(1,\frac{1}{3})$

$\lambda_{1,2}$ complex

$Re(\lambda_{1,2})<0$

```
p2 := dsolve({diff(x(t), t) = 2·x(t) − (2 x(t)·x(t))/3 − 4· x(t)·y(t), diff(y(t), t) = x(t)·y(t)
  − y(t), x(0) = 0.2, y(0) = 0.5}, {x(t), y(t)}, type = numeric, range = 0..500) :
> odeplot(p2, [[t, x(t)], [t, y(t)]], view = [0..15, 0..1.8], refine = 1)
```