

1 Purpose

To examine ODE models of the interactions of species, to make predictions about changes in the populations, and to study sensitivity to changes in rate constants.

Observation These models make sense only in the **population quadrant**, $x \geq 0, y \geq 0$. An orbit starting in that quadrant always stays there since the positive axes are unions of orbits; the Uniqueness Principle prevents any other orbit from touching the axial orbits.

Observation The models have their flaws. No account is taken of the time delay between an action and its effect on population rates. Averaging the rates of change over all categories of age, sex, fertility, and health is of dubious validity. More intricate models could be (and have been) constructed, but most of these have their origins in the models presented above.

1. Consider the Lottka-Volterra model for predator/prey interaction below:

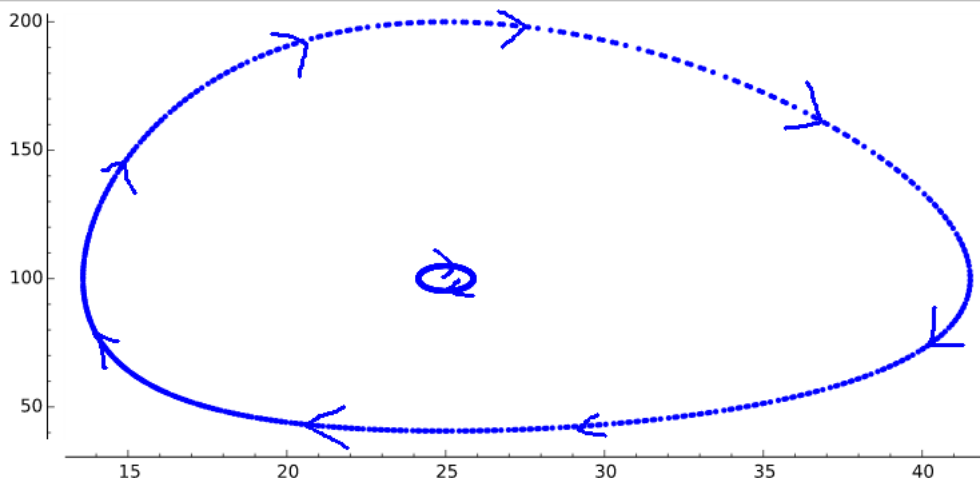
$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} -1 & x/100 \\ -2y/25 & 2 \end{bmatrix} \cdot \begin{bmatrix} x \\ y \end{bmatrix}$$

Use a computer to graph the population cycles of the following instance of Volterra's equations. Draw these in the xy -plane. Draw arrowheads on the orbits to show the direction of increasing time.

I experimented with various initial conditions using code like this:

```
x,y,t=var('x y t')
P=desolve_system_rk4([-x+x*y/100,-2*x*y/25+2*y],[x,y],ics=[0,25,105],ivar=t,step=0.1,end_points=5)
P=P+desolve_system_rk4([-x+x*y/100,-2*x*y/25+2*y],[x,y],ics=[0,25,200],ivar=t,step=0.1,end_points=5)
Q=[ [j,k] for i,j,k in P]
LP=list_plot(Q)
show(LP)
tx = [[q[0],q[1]] for q in P]
line(tx)
```

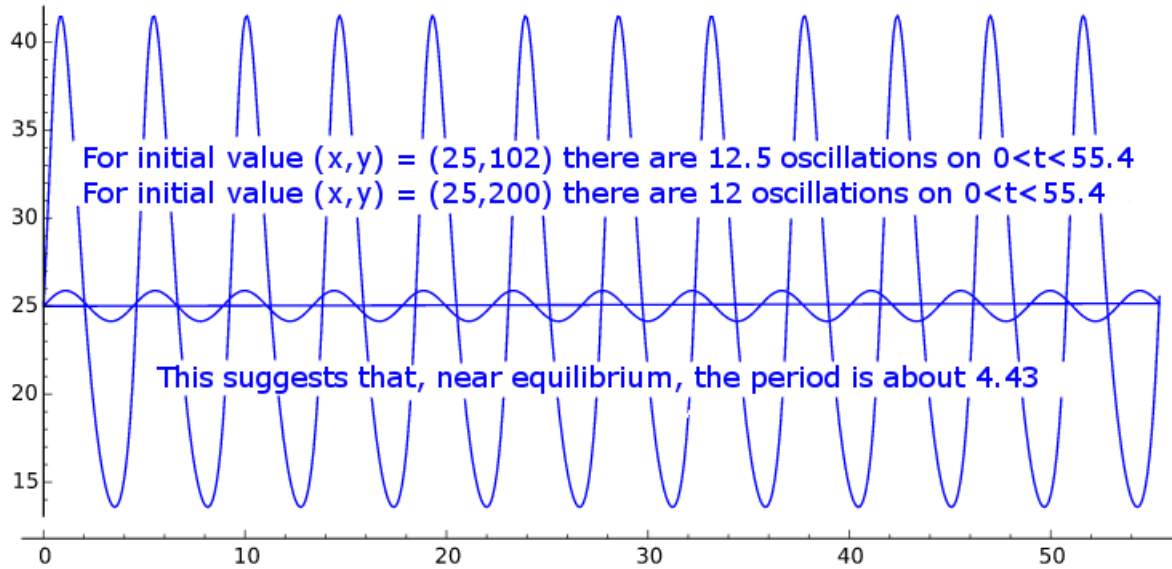
The first initial condition gives a point where x is at equilibrium and y is just 5 units above. The second also has x starting at 25 but with a much larger displacement for $y = 200$. Here is the phase plane portrait for these two orbits, with arrows indicating the direction of change.



Plot component curves for $0 \leq t \leq 20$ in the tx -plane and in the ty -plane and estimate the period T of each. Does T diminish, increase, or stay fixed as the starting points (x_0, y_0) of distinct orbits are chosen closer to the

equilibrium point $(25, 100)$? Plot enough component curves near equilibrium to estimate the limiting value of the period as $(x_0, y_0) \rightarrow (25, 100)$. Write your answers on the graphs.

Here's my first attempt at writing on the graph:



2. The system of ODEs in the previous problem may be linearized in a region about the equilibrium point $(25, 100)$ by rewriting the ODEs in new variables $u = x - 25$ and $v = y - 100$ and discarding all nonlinear terms. Show that the new system is $u' = v/4$, $v' = -8u$.

ANS: Substituting, we have

$$\begin{bmatrix} u' \\ v' \end{bmatrix} = \begin{bmatrix} -1 & (u+25)/100 \\ -2(v+100)/25 & 2 \end{bmatrix} \cdot \begin{bmatrix} u+25 \\ v+100 \end{bmatrix}$$

or, expanding:

$$\begin{aligned} u' &= -u - 25 + (uv + 25v + 100u + 2500)/100 = \frac{v}{100}(25 + u) \\ v' &= 2v + 200 - 2uv/25 - 2v - 8u - 200 = -\frac{2u}{25}(100 + v) \end{aligned}$$

Discarding the nonlinear terms leads to

$$\begin{bmatrix} u' \\ v' \end{bmatrix} = \begin{bmatrix} 0 & 1/4 \\ -8 & 0 \end{bmatrix} \cdot \begin{bmatrix} u \\ v \end{bmatrix}$$

The characteristic equation for the system has zeros $\lambda = \pm\sqrt{2}i$ leading to the eigenpairs $\left(\sqrt{2}i, \begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 \\ 4\sqrt{2} \end{pmatrix}i\right)$ and $\left(-\sqrt{2}i, \begin{pmatrix} -1 \\ 0 \end{pmatrix} + \begin{pmatrix} 0 \\ 4\sqrt{2} \end{pmatrix}i\right)$. This leads to (see case 2 on page 162 of the text) the general solution

$$\begin{pmatrix} u \\ v \end{pmatrix} = C_1 \left[\cos(\sqrt{2}t) \begin{pmatrix} 1 \\ 0 \end{pmatrix} - \sin(\sqrt{2}t) \begin{pmatrix} 0 \\ 4\sqrt{2} \end{pmatrix} \right] + C_2 \left[\cos(\sqrt{2}t) \begin{pmatrix} 0 \\ 4\sqrt{2} \end{pmatrix} + \sin(\sqrt{2}t) \begin{pmatrix} 1 \\ 0 \end{pmatrix} \right]$$

In Sage:

```
t=var('t')
u=function('u',t)
v=function('v',t)
sol=desolve_system([diff(u,t)==v/4,diff(v,t)==-8*u],[u,v],ivar=t)
show(sol)
```

produces this result: $u(t) = \frac{1}{8}\sqrt{2}\sin(\sqrt{2}t)v(0) + \cos(\sqrt{2}t)u(0)$, $v(t) = -4\sqrt{2}\sin(\sqrt{2}t)u(0) + \cos(\sqrt{2}t)v(0)$ which can be written this way

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \cos \sqrt{2}t & \frac{\sqrt{2}}{8} \sin \sqrt{2}t \\ -4\sqrt{2} \sin \sqrt{2}t & \cos \sqrt{2}t \end{pmatrix} \begin{pmatrix} u(0) \\ v(0) \end{pmatrix}$$

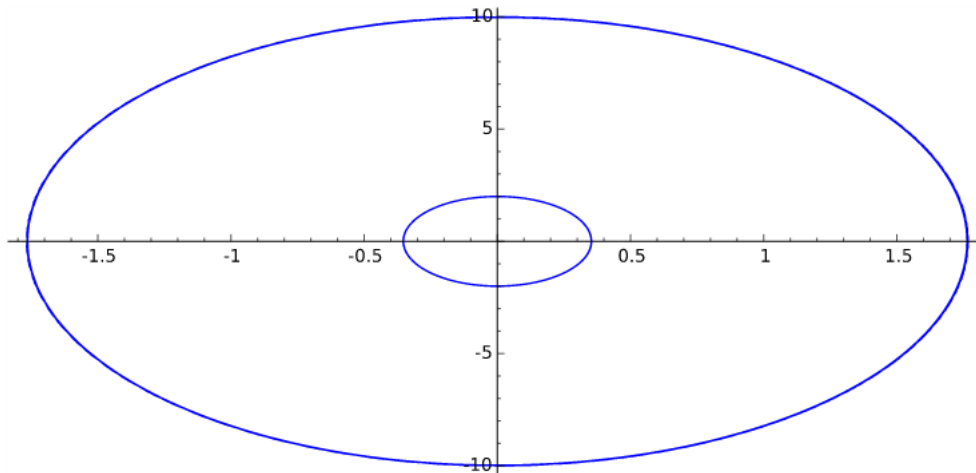
This is in normal form, and will work for any specified initial conditions. Note that the period of oscillation is $\frac{2\pi}{\sqrt{2}} \approx 4.4$, the period we found experimentally in part (1).

Graph orbits and component curves for the linear system, and calculate the (constant) period. Explain why the period should be the same as the limiting period estimated in Problem 1. Write explanations on your graphs.

ANS: We can use `desolve_odeint` like so:

```
from sage.calculus.desolvers import desolve_odeint
u,v=var('u,v')
f=[v/4,-8*u]
sol=desolve_odeint(f,[0,2],srange(0,20,0.1),[u,v])
p=line(zip(sol[:,0],sol[:,1]))
sol=desolve_odeint(f,[0,10],srange(0,20,0.1),[u,v])
p=p+line(zip(sol[:,0],sol[:,1]))
p.show()
```

and we see the two elliptical solutions to the linear system:



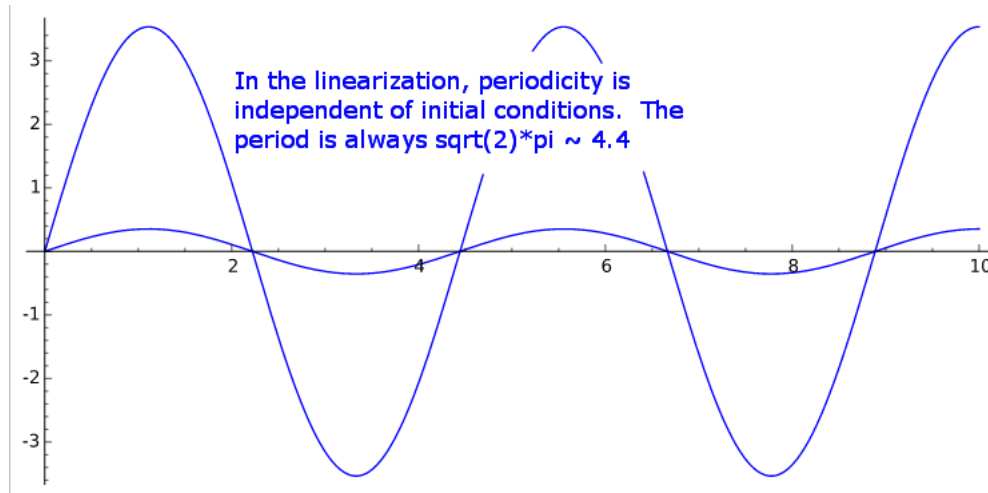
I needed to rework this to access the component curves:

```
from sage.calculus.desolvers import desolve_system
t=var('t')
u=function('u',t)
v=function('v',t)
f=[diff(u,t)==v/4,diff(v,t)==-8*u]
#sol=desolve_odeint(f,[0,2],srange(0,20,0.1),[u,v])
#p=line(zip(sol[:,0],sol[:,1]))
#sol=desolve_odeint(f,[0,10],srange(0,20,0.1),[u,v])
#p=p+line(zip(sol[:,0],sol[:,1]))
sol=desolve_system(f,[u,v],[0,0,2])
show(sol)
```

```

solnu, solnv = sol[0].rhs(), sol[1].rhs()
p=plot(solnu, (0,10))
sol=desolve_system(f, [u,v], [0,0,20])
solnu, solnv = sol[0].rhs(), sol[1].rhs()
p=p+plot(solnu, (0,10))
p.show()

```



3. Consider the system with constant effort harvesting:

$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} -1 - H & x \\ -y & 1 - H \end{bmatrix} \cdot \begin{bmatrix} x \\ y \end{bmatrix}$$

Use initial conditions $x(0) = 0.5, y(0) = 1$ on the interval $0 \leq t \leq 15$ to plot orbits for $H = 0, 0.25, 0.50, 0.75, 1.00, 3.00$ on the same phase plane (x vs. y). Draw arrowhead to show the direction of increasing time on the orbits. For each of the harvesting values, mark the locations of all equilibrium points inside or on the edge of the population quadrant. Explain what happens to the time-average populations as the harvesting is increase from 0 to 1 and beyond.

First, the case $H = 0$ is special, since in that case we have

$$\frac{dy}{dx} = \frac{y(1-x)}{x(y-1)} \Leftrightarrow \frac{y}{y-1} dy = \frac{1-x}{x} dx$$

is separable. Solve by integrating:

$$\int \frac{y-1}{y} dy = \int \frac{1-x}{x} dx \Leftrightarrow \ln y - y + \ln x - x = k \Leftrightarrow \frac{xy}{e^{x+y}} = K$$

This last equation defines a family of closed curves in the first quadrant. To see this, consider the functions

$$f(y) = \frac{y}{e^y}, g(x) = \frac{x}{e^x}$$

Note that $f(0) = 0, f(\infty) = 0$ and $f(y) > 0$. Computing the derivative:

$$f'(y) = \frac{1-y}{e^y}$$

we see that $f(y)$ has a critical point at $y = 1$ and so $f(y)$ achieves its maximum value $M_y = \frac{1}{e}$ at $y = 1$. Similarly, $g(x)$ achieves its maximum $\frac{1}{e}$ where $x = 1$. Thus $0 < K \leq \frac{1}{e^2}$ and if $K = \frac{1}{e^2}$ then there is only one

solution: $(x, y) = (1, 1)$, an equilibrium. Now suppose that $K = \frac{\lambda}{e}$ where $\lambda < \frac{1}{e}$. Then we have $\frac{x}{e^x} = \lambda$ has exactly two solutions: one for $x_m < 1$ and another for $x_M > 1$. Hence the equation

$$f(y) = \frac{y}{e^y} = \frac{\lambda}{xe^{1-x}}$$

has no solution when $x < x_m$ or $x > x_M$ and the single solution $y = 1$ when $x = x_m$ or $x = x_M$. As $x \rightarrow x_m$ or $x \rightarrow x_M$ both the y values approach 1 and so the solution is a closed curve. Phew!

As to the time-average populations, these are, in fact, the equilibrium populations, as we can show without directly computing x and y . The population averages are given by the formulas:

$$\bar{x} = \frac{1}{T} \int_0^T x(t) dt, \quad \bar{y} = \frac{1}{T} \int_0^T y(t) dt$$

where T is the period of oscillation. Now consider this:

$$0 = \frac{1}{T} (\ln(x(T)) - \ln(x(0))) = \frac{1}{T} \int_0^T \frac{\dot{x}}{x} dt [1 - y(t)] dt$$

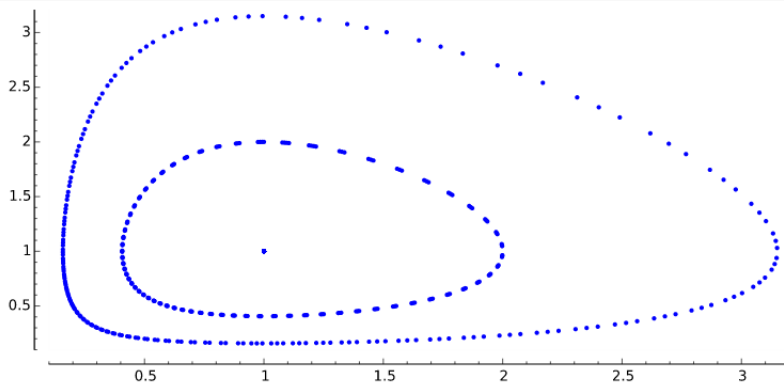
so

$$\frac{1}{T} \int_0^T y(t) dt = \frac{1}{T} \int_0^T dt = 1$$

and thus $\bar{y} = 1$ and similarly, $\bar{x} = 1$

The orbits shown by using these Sage commands:

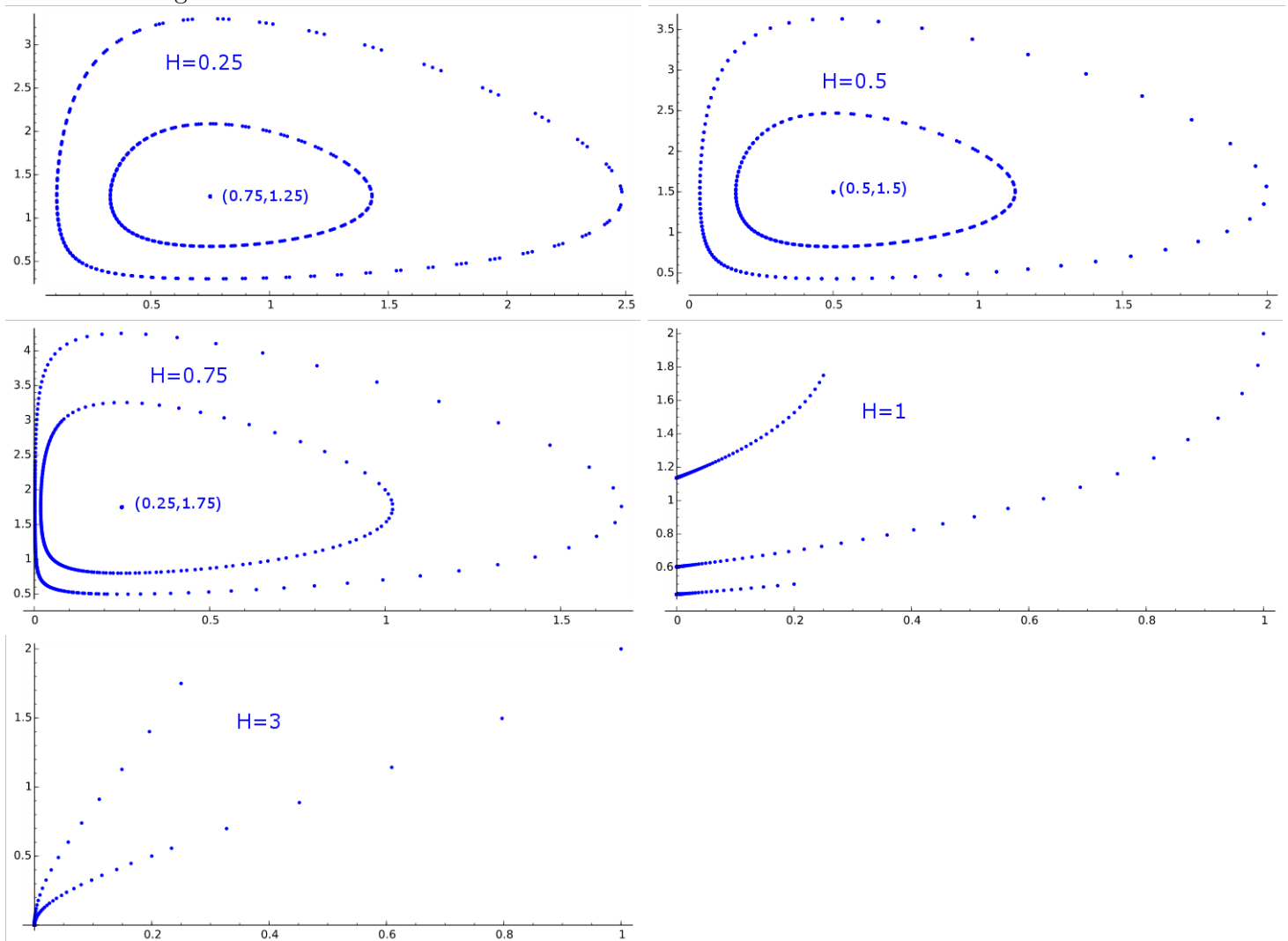
```
t,H,x,y=var('t H x y')
H=0
sol=desolve_system_rk4([- (1+H)*x+x*y, -x*y+(1-H)*y], [x,y], [0,0.20,0.50], ivar=t, end_points=20)
Q=[ [j,k] for i,j,k in sol]
LP=list_plot(Q)
sol=desolve_system_rk4([- (1+H)*x+x*y, -x*y+(1-H)*y], [x,y], [0,1,2], ivar=t, end_points=20)
Q=[ [j,k] for i,j,k in sol]
LP=LP+list_plot(Q)
sol=desolve_system_rk4([- (1+H)*x+x*y, -x*y+(1-H)*y], [x,y], [0,1,1], ivar=t, end_points=20)
Q=[ [j,k] for i,j,k in sol]
LP=LP+list_plot(Q)
show(LP)
```



Show that while the equilibrium is not the midpoint of extremes, it gives the time-average populations since the populations linger more in the small

zones than in the larger zones.

Now what about the harvesting? Let us put off analytical methods for another day, and just concentrate on interpreting the numerical solutions. Here is a sequence of results of several orbits for each of the constant harvesting schemes:



Apparently, the time average populations are $(1 - H, 1 + H)$ unless $H \geq 1$ in which cases, if $H = 1$ the predator dies out and leaves some vestige of prey, whereas, if $H > 1$ then both populations go extinct.

4. On the basis of problem 3, explain why limited harvesting of both species is a boon to the prey, but not to the predator. A species of ladybug once kept the cottony cushion scale pest of California orange trees under control. During the 1950s the broad-range insecticide DDT was applied to further control the scale. Why did that turn out to be a bad idea?

ANS: The constant harvesting affects the predator more than the prey. While the maximum predator populations diminish, the opposite occurs for the prey. Spraying DDT has an effect that is probably more like proportional harvesting than constant harvesting, but to the degree that it is like constant harvesting, we can see that a likely outcome is that the ladybug population would be exterminated, leaving the cottony cushion scale to persist. Worse, once you stop the spraying, the pest will rebound without the natural check on its population.

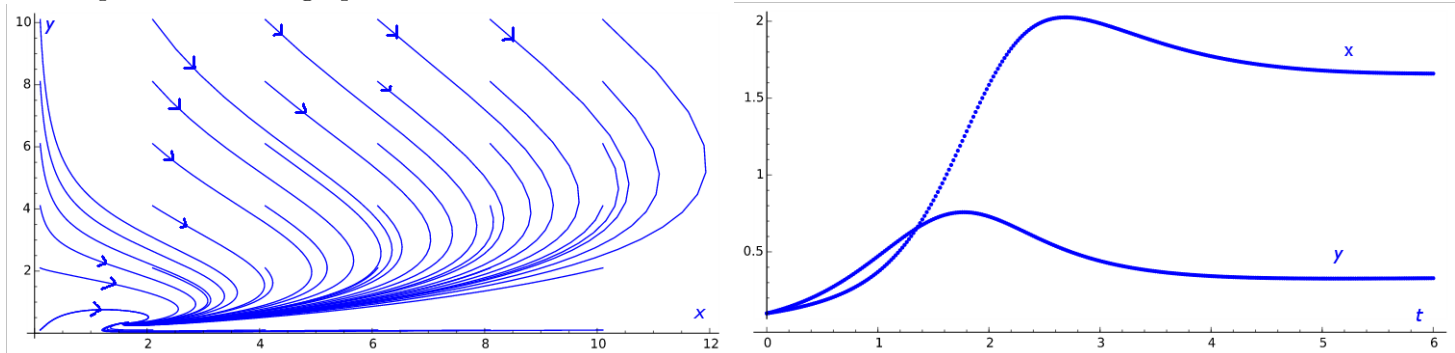
5. Overcrowding further limits the growth of the predator-prey community. Set $a = d = \alpha = \gamma = 1, b = c = 2$ in the overcrowding model and plot several orbits inside the population quadrant and the corresponding component curves. Explain what is happening. Mark all the equilibrium populations inside or on the edge of the

population quadrant. Replot with $\gamma = 2, 3, 4, 5$. Explain any significant changes in the nature of the orbits, the component curves, and the periods of cycles.

ANS: I wrote this Sage code to impose a grid of initial conditions:

```
t,a,b,c,d,alpha,gamma,x,y=var('t a b c d alpha gamma x y')
(a,b,c,d,alpha,gamma)=(1,2,2,1,1,1)
sol=desolve_system_rk4([(1-x)*x+2*x*y,-x*y+(2-y)*y],[x,y],[0,0.1,0.1],ivar=t,step=0.02,end_points=6)
Q=[ [j,k] for i,j,k in sol]
X=[ [i,j] for i,j,k in sol]
Y=[ [i,k] for i,j,k in sol]
LP=list_plot(Q,plotjoined=True)
LX=list_plot(X)
LX=LX+list_plot(Y)
for n in range(6):
    for m in range(6):
        sol=desolve_system_rk4([(1-x)*x+2*x*y,-x*y+(2-y)*y],[x,y],[0,0.1+2*n,0.1+2*m],
            ivar=t,step=0.01,end_points=6)
        Q=[ [j,k] for i,j,k in sol]
        LP=LP+list_plot(Q,plotjoined=True)
show(LP)
show(LX)
```

Which produced these graphs:

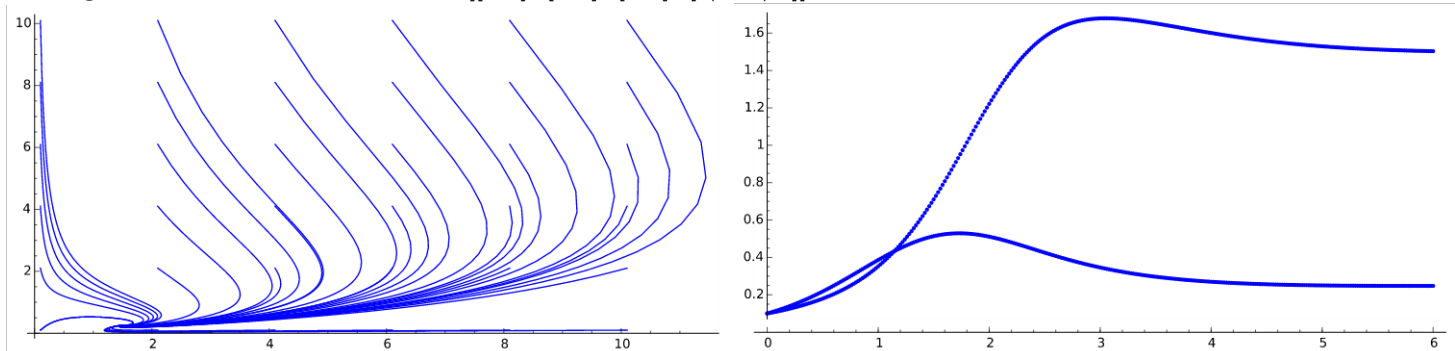


Evidently, the plots all approach an equilibrium near $(1.6, 0.3)$

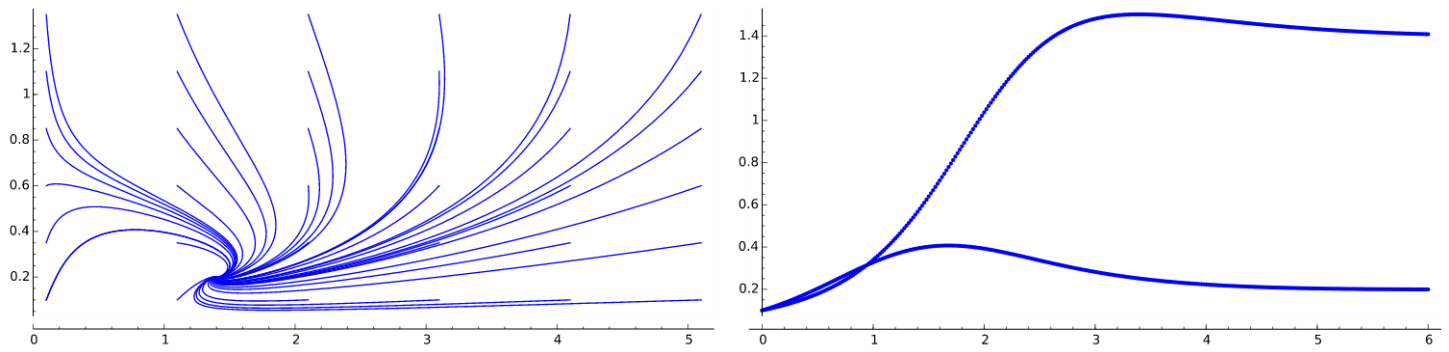
To be sure, we can find all equilibrium points by setting the rate of change to zero and solving for x and y :

```
solve([(1-x)*x+2*x*y==0, -x*y+(2-y)*y==0], x, y)
[[x == 0, y == 0], [x == 1, y == 0], [x == 0, y == 2], [x == (5/3), y == (1/3)]]
```

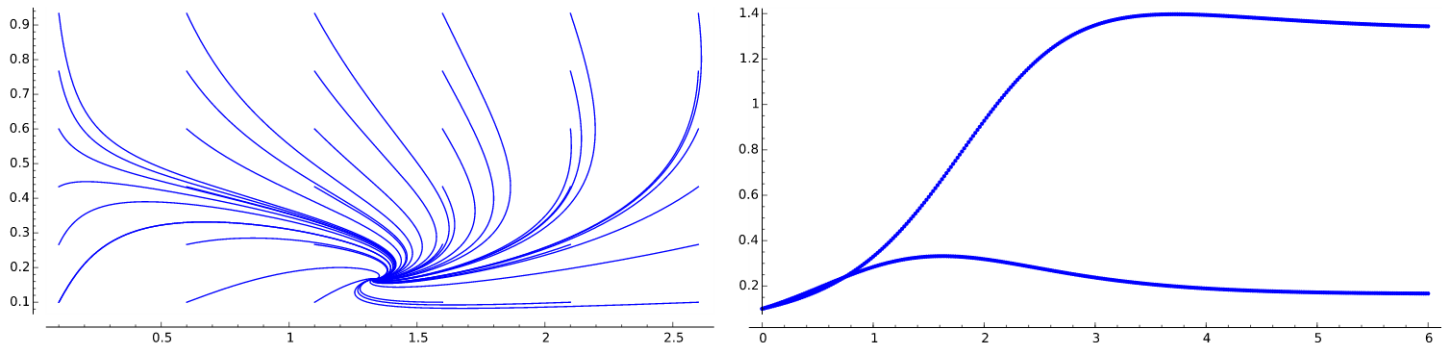
With $\gamma = 2$ we have equilibria $[[0,0], [1,0], [0,1], [3/2,1/4]]$



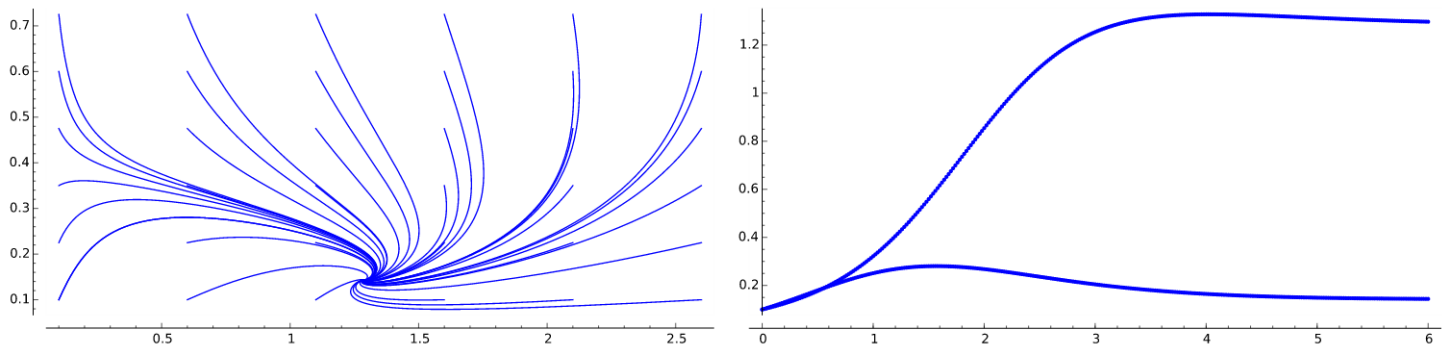
With $\gamma = 3$ we have equilibria $[[0,0], [1,0], [0,2/3], [7/5,1/5]]$



With $\gamma = 4$ we have equilibria $[[0,0], [1,0], [0,1/2], [4/3,1/6]]$



With $\gamma = 5$ we have equilibria $[[0,0], [1,0], [0,2/5], [9/7,1/7]]$



6. The competition model models the dynamics of a pair of species that compete for a common resource that is in limited supply. Explain the meaning of each term in the x -rate equation.

ANS: The x -rate equation is $\frac{dx}{dt} = (a - \alpha x)x + bxy$. The first term, $(a - \alpha x)x$ models logistic growth and has the non-trivial zero at $x = \frac{a}{\alpha}$. Think of a as measuring the predator's tolerance for crowding and α as measuring the environment's harshness. The second term, bxy models the predator-prey interaction and the parameter b combines the measures of how good the predator is at hunting, how poor the prey is at escaping and how nutritious the prey are for the predator.

7. In the competing species model, introduce new variables by letting $x = A\tilde{x}, y = B\tilde{y}, t = C\tilde{t}$, where $A = a/b, B = a/c, C = 1/a$, and then using the old variables names the system can be written as

$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} 1 - x & -x \\ -a_2y & a_1 - a_3y \end{bmatrix} \cdot \begin{bmatrix} x \\ y \end{bmatrix}$$

where $a_1 = d/a, a_2 = e/b, a_3 = f/c$, using three parameters instead of six.

Plot many orbits for

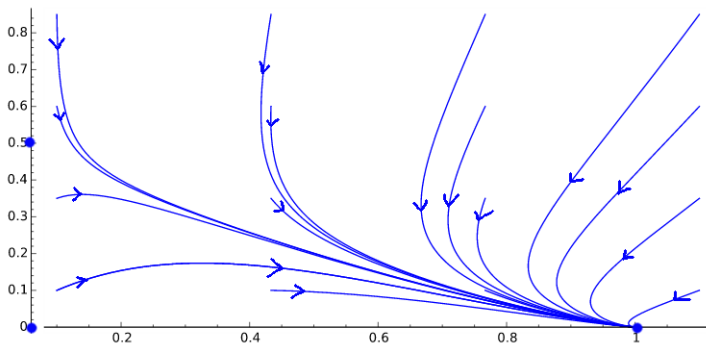
$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} 1-x & -x \\ -2y & 1-2y \end{bmatrix} \cdot \begin{bmatrix} x \\ y \end{bmatrix}$$

(where x survives and y does not) and

$$\begin{bmatrix} x' \\ y' \end{bmatrix} = \begin{bmatrix} 1-x & -x \\ -y & 2-3y \end{bmatrix} \cdot \begin{bmatrix} x \\ y \end{bmatrix}$$

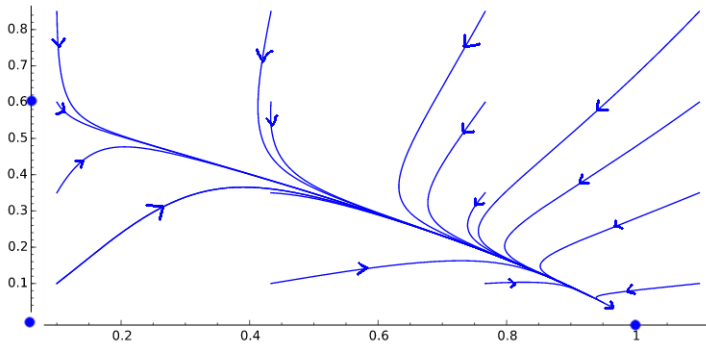
where x and y coexist, marking all equilibrium points inside and on the edge of the population quadrant and inserting arrowheads on the orbits to show the direction of increasing time. Beginning with the values of a_1, a_2, a_3 in the first model, change the parameters by small amounts, plotting orbits after each change, until you reach the picture of the second model. Continue making small change until a system is obtained in which y survives by x does not. On your last graph write your conclusions.

ANS: In the first model we have $a_1 = 1, a_2 = 2, a_3 = 2$ with equilibria at $[[0,0], [1,0], [0,1/2]]$ As the orbits below suggest, only the equilibrium at $[1,0]$ is a sink:



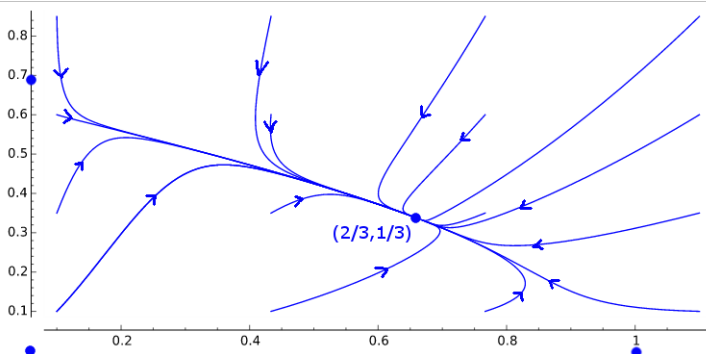
At a sort of "halfway" point, choose $a_1 = 1.5, a_2 =$

$1.5, a_3 = 2.5$. The equilibria are at $[0,0], [0,0.6], [1,0]$ with, again $[1,0]$ as the stable equilibrium, though somewhat less within reach:

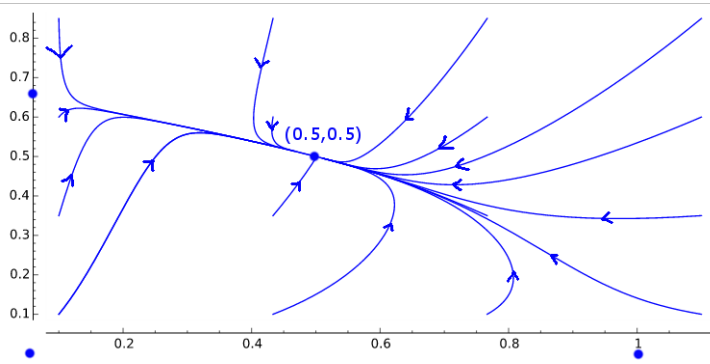


At a kind of "three quarters" point, choose $a_1 =$

$1.75, a_2 = 1.25, a_3 = 2.75$. The equilibria are now four: $[0,0], [1,0], [0,7/11], [2/3,1/3]$ with the last of these the stable equilibrium, as indicated by these orbits:



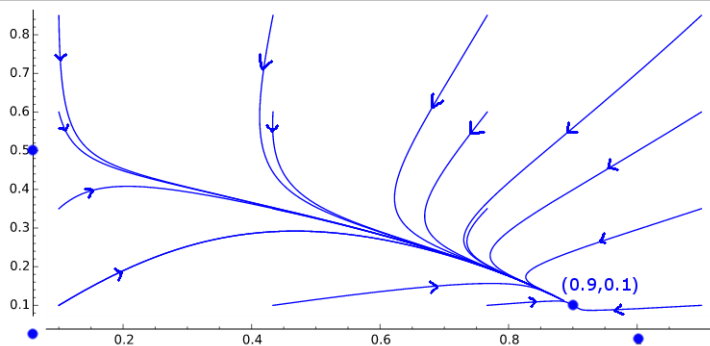
Here's the last model with $a_1 = 2, a_2 = 1, a_3 = 3$ equilibria $[[0,0], [1,0], [0,2/3], [0.5,0.5]]$ As the orbits below suggest, only the equilibrium at $[1,0]$ is a sink:



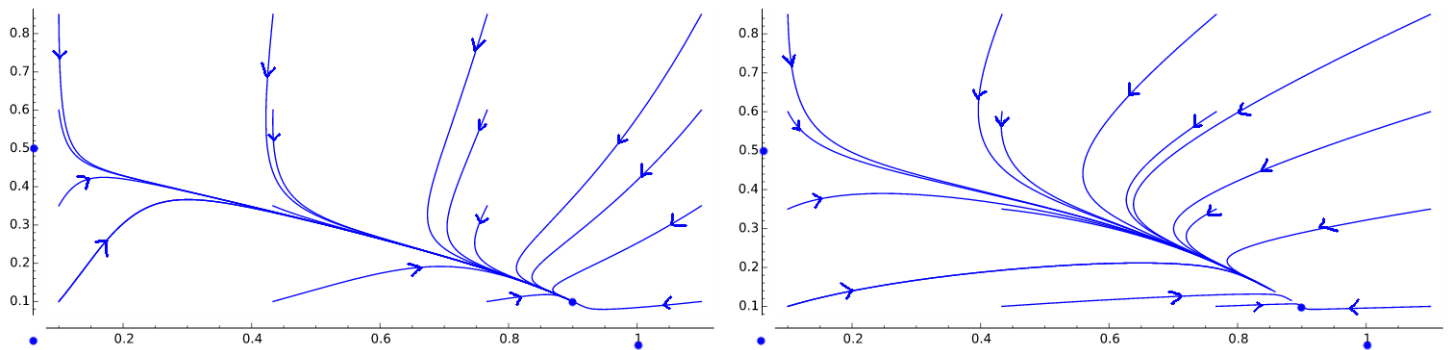
A little analysis shows that the equilibrium points are the solution to the system

$$\begin{aligned} (1 - x - y)x &= 0 \\ (a_1 - a_2x - a_3y)y &= 0 \end{aligned}$$

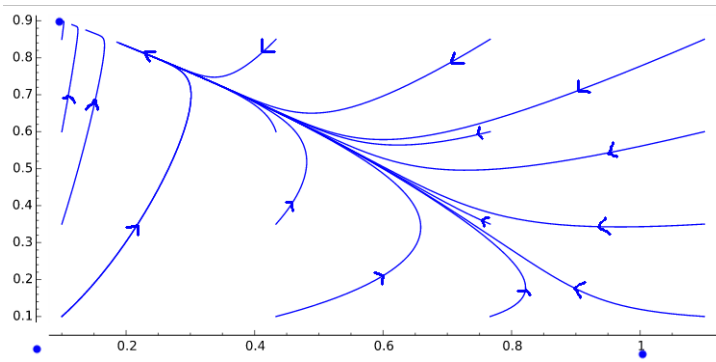
If an equilibrium point is not on the boundary of the first quadrant, $x \neq 0$ and $y \neq 0$ so that, from the first equation, $x = 1 - y$. Substituting this into the second equation, we have $y = \frac{a_2 - a_1}{a_2 - a_3}$. If this turns out to be 0, or undefined, then the only equilibria are on the boundary. If it comes out to a value between 0 and 1, then we're in business for a non-trivial equilibrium. We might eliminate another degree of freedom by using the variables $u = \frac{a_1}{a_2}$ and $v = \frac{a_3}{a_2}$ so that the y -coordinate of the sink equilibrium is $y = \frac{u - 1}{v - 1}$ where $x = 1 - y$. Then you could start with the coordinates of the equilibrium, say $(x, y) = (0.9, 0.1)$ and work your way outwards to $y = \frac{1}{10} = \frac{u - 1}{v - 1} = \frac{1/8}{5/4} = \frac{9/8 - 1}{9/4 - 1}$. Taking (somewhat arbitrarily) $a_2 = 1$, we'd have $a_1 = \frac{9}{8}$ and $a_3 = \frac{9}{4}$. This leads to sequence of orbits shown below:



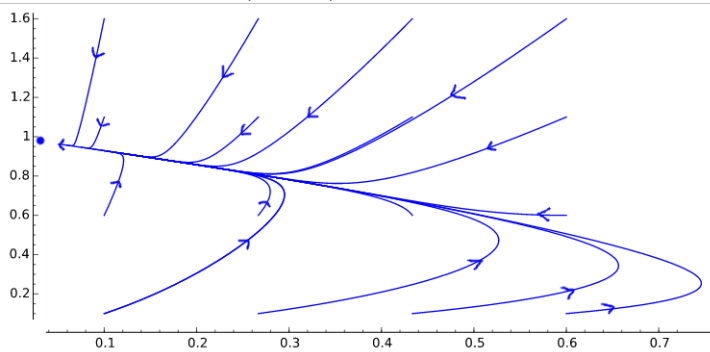
In this way, we can produce phase portraits with the same equilibria but different values of a_2 . On the left below, $a_2 = 2$, while on the right $a_2 = 1/2$:



If we want y to survive and x to die off, simply choosing $a_1 = a_3 = 1$ and $a_2 = 2$, say, doesn't do it. So let's ease our way there. We can get an equilibrium at $(0.1, 0.9)$ by choosing $\frac{9}{10} = \frac{1/2}{5/9} = \frac{\frac{3}{2} - 1}{\frac{14}{9} - 1}$ so that with $a_2 = 1$, $a_1 = \frac{3}{2}$ and $a_3 = \frac{14}{9}$ we get this phase portrait, with equilibria at $[0, 0]$, $[1, 0]$, $[0, 27, 28]$, $[0.1, 0.9]$:



Continuing in this fashion, choose $a_2 = 1$, $a_1 = 1.5$ and $a_3 = \frac{149}{99}$ to get a sink equilibrium at $(0.01, 0.99)$ (also at $(1,0), (0,0)$ and $(0, \frac{297}{298})$) and the phase portrait below:



The trouble appears to be that

$\frac{dx}{dt}$ has a factor of x , so as $x \rightarrow 0$, $\frac{dx}{dt} \rightarrow 0$ and it'll never get there (or approaches asymptotically).

However, we can make the the sink equilibrium as close to $(0,1)$ as we like. To go again closer, choose $a_2 = 1$, $a_1 = 1.5$ and $a_3 = \frac{14999}{9999}$ to get equilibria at $[[0,0],[1,0],[0,29997/29998],[1/10000,9999/10000]]$ and the phase portrait:

