```
In[322]:= sysid

        Mathematica 4.1, DynPac 10.65, 2/16/2002
```

ME 406
Predator-Prey Example
Part 1 - Equilibrium

■ Introduction

This is a simple model of an ecological system with three components: a plant, a small mammal called the Murat which eats the plant, and a carnivorous predator called the Vekton which eats the mammal. We are using the model to test our belief that we can control this ecosystem by controlling the plant population. Our goal is to maintain both species at healthy numbers. We denote the population of the plant eater by M and the population of the carnivore by V. The basic equations governing this system were set-up in class. They are

$$\frac{dM}{dt} = rM\left(1 - \frac{M}{A}\right) - \frac{\beta MV}{M+H} ,$$

$$\frac{dV}{dt} = \frac{bMV}{M+H} - cV .$$

The parameters were explained in class, so we just review them very briefly here. The parameter A is the maximum sustainable population of the plant-eaters in the absence of the carnivores, and the model incorporates this via a logistic law. The parameter A is the one we control, by controlling the plant population, and this is our only management tool for this system. In the limit M << A, the constraint represented by A is unimportant, and the net birth rate of of the plant eaters is r, and they will grow like e^{rt} until M becomes comparable with A. The second, negative, term in the M-equation models the effects of the predators. The loss is proportional to the product of the populations, because this product is proportional to the encounter rate. The denominator is a saturation effect, accounting for the fact that if the population of plant eaters is large, predators won't be as hungry and there will be fewer kills per encounter. In the predator equation, the first term models the birth rate, and accounts for the fact that it will be higher if food is more plentiful. If food is very plentiful (M much larger than H), this birth term saturates with a rate b*V, so b is the natural birth rate with ample food. It is an artificial simplification of the model that the saturation parameter has the same value H in both equations.

■ Defining the System for Mathematica

We define the system for DynPac.

```
In[323]:= setstate[{M, V}];

In[324]:= setparm[{A}];

In[325]:= slopevec = {r * M * (1 - M / A) - (β * M * V) / (M + H), (b * M * V) / (M + H) - c * V};
```

With so many parameters, the exploration of the system could take a very long time. To keep things simple, we choose values for all of the parameters except A (our management variable), and then study the system as we vary A. This is why we have included only A in the parameter vector. The units for the population quantities V, M, H, and A are in millions of individuals. The units of the time constants r, beta, b and c are in inverse years. We will assume that A can be varied from 0 up to a maximum of 15. We specify now all of the parameters that will be fixed throughout this study.

```
In[326]:=  r = 12 (** yr^-1 **);

In[327]:=  β = 20 (** yr^-1 **);

In[328]:=  b = 4(** yr^-1 **);

In[329]:=  c = 8 / 5 (** yr^-1 **);

In[330]:=  H = 4 (** millions **);
```

In our evaluations below of the effects of changing A, we adopt the following criterion for a healthy ecosystem: if the population of each species remains above 1 million, we count this as a successful preservation strategy.

■ Locating the Equilibrium States

We first find the equilibrium states in terms of the parameter A.

```
In[331]:=  eqstates = findpolyeq
```

Out[331]= $\left\{\{0, 0\}, \{A, 0\}, \left\{\frac{8}{3}, \frac{4\,(-8+3\,A)}{3\,A}\right\}\right\}$

We see that there are three equilibrium states. The first is {0,0}, in which no animals of either species are present. The second is {A,0}, in which the Vektons are absent, and the Murats are living free of fear at their maximum sustainable population A. In the third state, both species are present. We give each of these states a name.

```
In[332]:=  nulleq = eqstates[[1]]

Out[332]=  {0, 0}

In[333]:=  murateq = eqstates[[2]]

Out[333]=  {A, 0}

In[334]:=  coeq = eqstates[[3]]
```

Out[334]= $\left\{\frac{8}{3}, \frac{4\,(-8+3\,A)}{3\,A}\right\}$

From these formulas, we can deduce the existence of some interesting transitions. For example, when A = 8/3, coeq reduces to murateq. In other words, at A = 8/3, those two equilibria coincide. For A < 8/3, coeq has a negative value of V. Such a state exists mathematically, but can never be reached in the model as long as we start in the first quadrant (because the V and M axes are orbits and cannot be crossed). Thus for 0 < A < 8/3, there are two equilibrium states in the relevant first quadrant -- nulleq and murateq. At A = 8/3, coeq moves up from the fourth quadrant and coalesces with murateq. For any A > 8/3, all three equilibria exist in the first quadrant. In particular, there is a state (coeq) with both species present. Whether these states are relevant depends on their stability. We examine that next.

Stability of Equilibrium

We begin by calculating the derivative matrix at the three equilibria.

```
In[335]:= dmatnull = dermat /. Thread[statevec -> nulleq]
```

Out[335]=

$$\left\{\{12, 0\}, \left\{0, -\frac{8}{5}\right\}\right\}$$

```
In[336]:= dmatmurat = dermat /. Thread[statevec -> murateq]
```

Out[336]=

$$\left\{\left\{-12, -\frac{20\,A}{4+A}\right\}, \left\{0, -\frac{8}{5}+\frac{4\,A}{4+A}\right\}\right\}$$

```
In[337]:= dmatco = dermat /. Thread[statevec -> coeq]
```

Out[337]=

$$\left\{\left\{12\left(1-\frac{8}{3\,A}\right)-\frac{32}{A}-\frac{12\,(-8+3\,A)}{5\,A}, -8\right\}, \left\{\frac{12\,(-8+3\,A)}{25\,A}, 0\right\}\right\}$$

We first see if we can draw any general stability conclusions for all values of A.

```
In[338]:= Eigensystem[dmatnull]
```

Out[338]=

$$\left\{\left\{-\frac{8}{5}, 12\right\}, \{\{0, 1\}, \{1, 0\}\}\right\}$$

Here is our first result: the {0,0} equilibrium is always a saddle point and hence always unstable. If any Murats are introduced, they will increase in number. If both Vektons and Murats are introduced, they will increase. If only Vektons are introduced, they will die out (no food), and thus the Vekton axis is the stable manifold for this saddle.

Now we try the Murat equilibrium.

```
In[339]:= Eigensystem[dmatmurat]
```

Out[339]=

$$\left\{\left\{-12, -\frac{8}{5}+\frac{4\,A}{4+A}\right\}, \left\{\{1, 0\}, \left\{-\frac{25\,A}{2\,(26+9\,A)}, 1\right\}\right\}\right\}$$

We see from the eigenvalues that this is a strictly stable node for A < 8/3, and is a saddle and therefore unstable for any A > 8/3.

Finally we look at the equilibrium coeq.

```
In[340]:= eigenco = Eigensystem[dmatco]
```

Out[340]=

$$\left\{\left\{\frac{4\left(-28+3\,A-\sqrt{784-120\,A-9\,A^2}\right)}{5\,A}, \frac{4\left(-28+3\,A+\sqrt{784-120\,A-9\,A^2}\right)}{5\,A}\right\}, \left\{\left\{\frac{5\left(-28+3\,A-\sqrt{784-120\,A-9\,A^2}\right)}{3\,(-8+3\,A)}, 1\right\}, \left\{\frac{5\left(-28+3\,A+\sqrt{784-120\,A-9\,A^2}\right)}{3\,(-8+3\,A)}, 1\right\}\right\}\right\}$$

This is a little more complicated, but we can still look for bifurcations. We start by defining expresssions for the eigenvalues.

```
In[341]:= lamco1 = First[First[eigenco]]
```

Out[341]=

$$\frac{4\left(-28+3\,A-\sqrt{784-120\,A-9\,A^2}\right)}{5\,A}$$

```
In[342]:= lamco2 = Last[First[eigenco]]
```

Out[342]= $$\frac{4\left(-28+3\,A+\sqrt{784-120\,A-9\,A^2}\right)}{5\,A}$$

The transition between real and complex roots occurs when the discriminant vanishes, hence for

```
In[343]:= Solve[lamco1 - lamco2 == 0, A]
```

Out[343]= $$\left\{\left\{A\to\frac{4}{3}\left(-5-\sqrt{74}\right)\right\},\left\{A\to\frac{4}{3}\left(-5+\sqrt{74}\right)\right\}\right\}$$

Only the second of these is positive and hence relevant.

```
In[344]:= Atran = Last[%]
```

Out[344]= $$\left\{A\to\frac{4}{3}\left(-5+\sqrt{74}\right)\right\}$$

The numerical value is

```
In[345]:= N[A /. Atran]

Out[345]= 4.8031
```

At this transition, the eigenvalues are equal and are

```
In[346]:= N[lamco1 /. Atran]

Out[346]= -2.26365
```

Thus at Atran, the equilibrium makes a transition between a stable node and a stable spiral.

Does coeq ever become unstable as A increases? We ask whether the real parts of the eigenvalues ever vanish:

```
In[347]:= Solve[lamco1 + lamco2 == 0, A]
```

Out[347]= $$\left\{\left\{A\to\frac{28}{3}\right\}\right\}$$

At this point we have a rather complete picture of the equilibria of the system and the stability. Here is a summary of the results.

(a) For 0 < A < 8/3, the only stable equilibrium state is the all-Murat state at the maximum sustainable population A.

(b) For 8/3 < A < $\frac{4}{3}\left(-5+\sqrt{74}\right)$ = 4.8031, the only stable equilibrium state is the state coeq in which members of both species are present. This equilibrium is a stable node.

(c) For $\frac{4}{3}\left(-5+\sqrt{74}\right)$ < A < 28/3, the only stable equilibrium state is coeq, and the state is a stable spiral.

(d) For 28/3 < A, there are no stable equilibrium states.

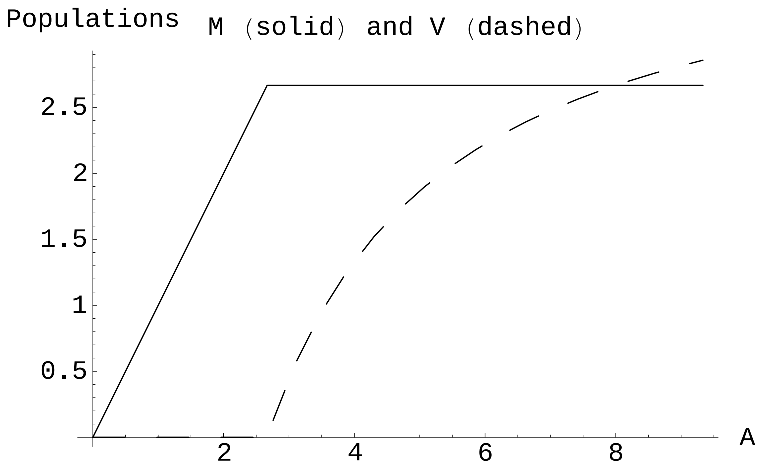
This last result raises an interesting question: For A > 28/3, just where does this system spend its time? We will defer a discussion of this question to Part 2 of this example. In the remainder of Part 1 we study the equilibrium states in their dependence on A, and we look at some representative phase plane plots. As a last task in this section, we plot the equilibrium populations as a function of A, from 0 to 28/3. We define these, on the basis of the above calculations, as Meq[A], and Veq[A].

```
In[348]:=  Meq[A_] := If[A < 8 / 3, A, 8 / 3]
```

```
In[349]:=  Veq[A_] := If[A < 8 / 3, 0, 4 - 32 / (3 * A)]
```

These are valid for A up to 28/3. Let's plot them.

```
In[350]:=  Plot[{Meq[A], Veq[A]}, {A, 0, 28 / 3}, AxesLabel -> {"A", "Populations"},
             PlotLabel -> "M (solid) and V (dashed)", PlotStyle -> {Dashing[{}], Dashing[{0.05}]}];
```



As the graph shows (and as we may show analytically), both populations exceed 1 million for A > 32/9 = 3.56. Once A reaches 8/3, the equilibrium Murat population does not increase further. As we increase A beyond that value, we get more Vektons -- thus more Murats are born but more are eaten by Vektons.

At the risk of being somewhat redundant, we use classify2D to verify our stability results for a selection of A values.

First we look at a value between 0 and 8/3.

```
In[351]:=  parmval = {1};
```

```
In[352]:=  classify2D[murateq]

             Abbreviations used in classify2D.

             L = linear, NL = nonlinear, R2 = repeated root.

             Z1 = one zero root, Z2 = two zero roots.

             This message printed once.


             strictly stable - node
```

```
In[353]:=  classify2D[coeq]

             unstable - saddle
```

We verify that murateq is stable and coeq is unstable. Now we look at the transition value of A = 8/3.

```
In[354]:= parmval = {8 / 3};
```

```
In[355]:= classify2D[murateq]

        stable (L), indeterminate (NL) - saddle-node trans.(Z1)
```

```
In[356]:= classify2D[coeq]

        stable (L), indeterminate (NL) - saddle-node trans.(Z1)
```

We see clearly the transition. Now we look at a value above the transition.

```
In[357]:= parmval = {3};
```

```
In[358]:= classify2D[coeq]

        strictly stable - node
```

```
In[359]:= classify2D[murateq]

        unstable - saddle
```

The event associated with A passing through 8/3 is sometimes called an exchange of stabilities. As A passes through that value, the two relevant equilibria interchange their roles. The next transition occurs at $A = \frac{4}{3}\left(-5+\sqrt{74}\right)$.

```
In[360]:= parmval = {(4 / 3) * (-5 + Sqrt[74])};
```

```
In[361]:= tranmat = dermatval[coeq]
```

Out[361]=
$$\left\{\left\{-\frac{24}{-5+\sqrt{74}}+12\left(1-\frac{2}{-5+\sqrt{74}}\right)-\frac{9\left(-8+4\left(-5+\sqrt{74}\right)\right)}{5\left(-5+\sqrt{74}\right)},\ -8\right\},\ \left\{\frac{9\left(-8+4\left(-5+\sqrt{74}\right)\right)}{25\left(-5+\sqrt{74}\right)},\ 0\right\}\right\}$$

```
In[362]:= Eigenvalues[tranmat]
```

Out[362]=
$$\left\{\frac{12}{35}\left(2-\sqrt{74}\right),\ \frac{12}{35}\left(2-\sqrt{74}\right)\right\}$$

The two eigenvalues are equal and negative, so we are at a spiral-node transition. If we increase A further, the system becomes oscillatory and the equilibrium is a stable spiral:

```
In[363]:= parmval = {6};
```

```
In[364]:= classify2D[coeq]

        strictly stable - spiral
```

The final transition is at A = 28/3.

```
In[365]:= parmval = {28 / 3};
```

```
In[366]:= classify2D[coeq]

        stable (L), indeterminate (NL) - center
```

```
In[367]:= Eigenvalues[dermatval[coeq]]
```

Out[367]=
$$\left\{-12\,i\sqrt{\frac{2}{35}},\ 12\,i\sqrt{\frac{2}{35}}\right\}$$

The eigenvalues have become pure imaginary, and stability by linearization is inconclusive. If we go slightly above A = 28/3, we get

```
In[368]:= parmval = {10};
```

```
In[369]:= classify2D[coeq]

          unstable - spiral
```

```
In[370]:= classify2D[murateq]

          unstable - saddle
```

```
In[371]:= classify2D[nulleq]

          unstable - saddle
```

This raises again our question: where does this system spend its time? It has no stable equilibria, and it doesn't seem to run off to infinity. We will answer that question in Part 2. We conclude our study here with some phase portraits for various values of A.

■ Some Phase Portraits

In constructing the phase portrait, one of the most important integral curves will be the curve leaving murateq when A is large enough for this point to be a saddle point. We obtained the relevant eigenvector earlier, and we repeat it here:

```
In[372]:= evec = Eigensystem[dmatmurat]
```

Out[372]=

$$\left\{\left\{-12,\ -\frac{8}{5}+\frac{4\,A}{4+A}\right\},\ \left\{\{1,\ 0\},\ \left\{-\frac{25\,A}{2\,(26+9\,A)},\ 1\right\}\right\}\right\}$$

```
In[373]:= muratvec = Last[Last[evec]]
```

Out[373]=

$$\left\{-\frac{25\,A}{2\,(26+9\,A)},\ 1\right\}$$

We use this to find an initial condition displaced very slightly from the equilibrium along the eigenvector:

```
In[374]:= mursadinit = murateq + muratvec / 100
```

Out[374]=

$$\left\{A-\frac{A}{8\,(26+9\,A)},\ \frac{1}{100}\right\}$$

When we use this as an initial condition, we will evaluate it at the current value of A by

```
In[375]:= eqstateval[mursadinit]
```

Out[375]=

$$\left\{\frac{4635}{464},\ \frac{1}{100}\right\}$$

which is correct for the current value of A = 10. This initial condition will be useful only for A > 4.8031, for which the all-Murat state is a saddle.

Now we set some integration parameters. We use range checking to prevent overflows.

```
In[376]:=  ranger = {{0, 15}, {0, 15}};
```

```
In[377]:=  rangeflag = True;
```

```
In[378]:=  plrange = {{-1, 12}, {-1, 12}};
```

```
In[379]:=  nsteps = 400;
```

We set the spacing and the initial time.

```
In[380]:=  h = 0.015;
```

```
In[381]:=  t0 = 0.0;
```

We set the graph aspect ratio to 1, and we give the system a name.

```
In[382]:=  asprat = 1.0;
```

```
In[383]:=  sysname = "Murats and Vektons";
```

We put arrows on the curves, although sparingly.

```
In[384]:=  arrowflag = True;
```

```
In[385]:=  arrowvec = {1 / 3};
```

Now we are ready to construct the phase plane pictures. We do this for A = 2, 6, and 9.

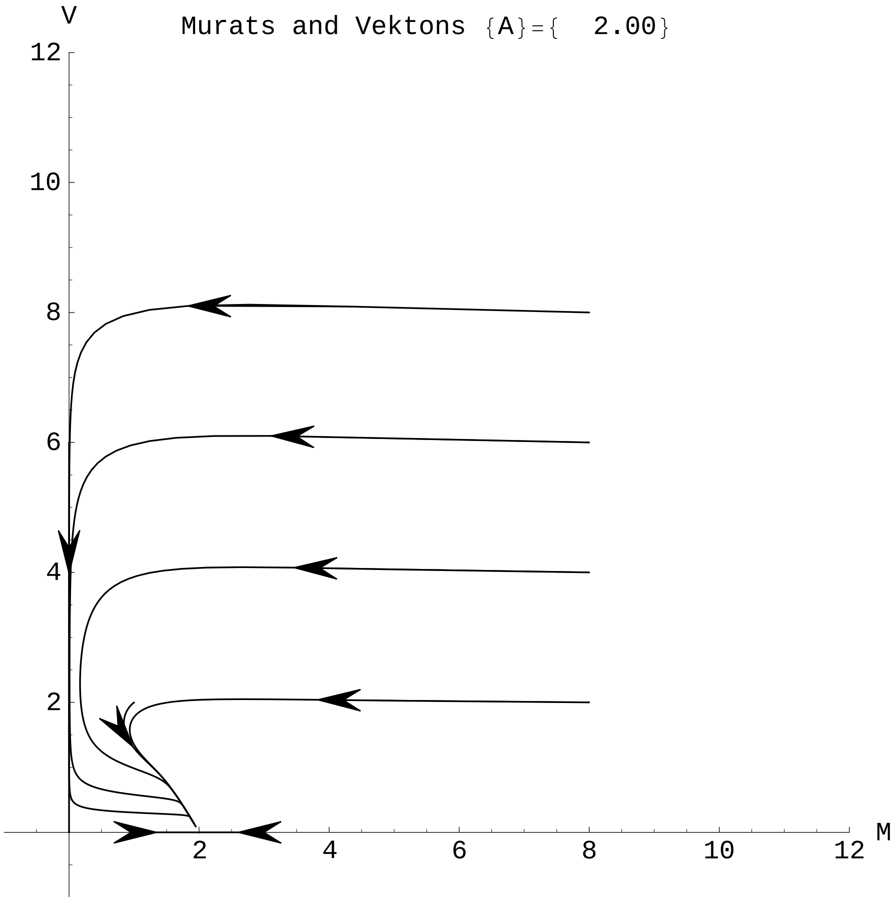
■ Portrait for A = 2

For this value of A, the system attractor is the all-Murat state at A = 2. We choose a variety of initial conditions around the first quadrant and on the quadrant axes.

```
In[386]:=  parmval = {2};
```

```
In[387]:=  initlist = {{0, 6}, {1, 0}, {3, 0}, {8, 2}, {8, 4}, {8, 6}, {8, 8}, {1, 2}};
```

```
In[388]:= portrait[initlist, t0, h, nsteps, 1, 2];
```



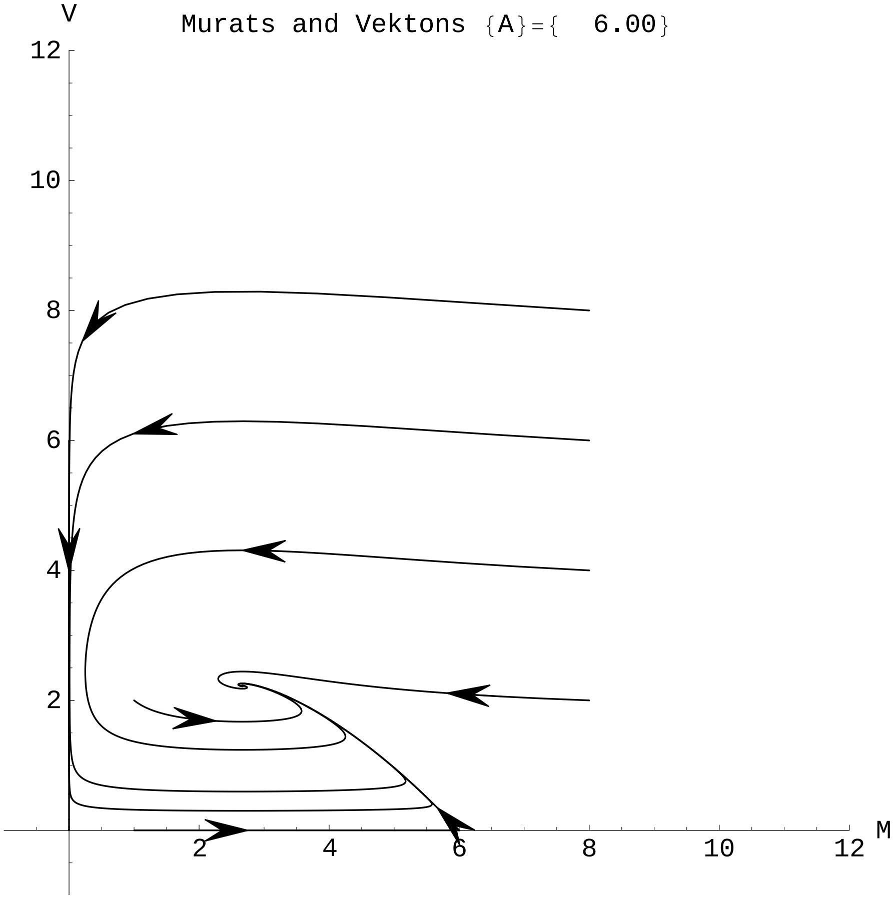
■ Portrait for A = 6

In this case, the equilibrium state is coeq, in which both species are present, and the all Murat state is a saddle. We include the initial condition near the saddle.

```
In[389]:= parmval = {6};
```

```
In[390]:= initlist = {eqstateval[mursadinit], {0, 6}, {1, 0}, {8, 2}, {8, 4}, {8, 6}, {8, 8}, {1, 2}};
```

```
In[391]:= portrait[initlist, t0, h, nsteps, 1, 2];
```



The spiral nature of the equilibrium is fairly evident here. It will be more pronounced in the last case A = 9.

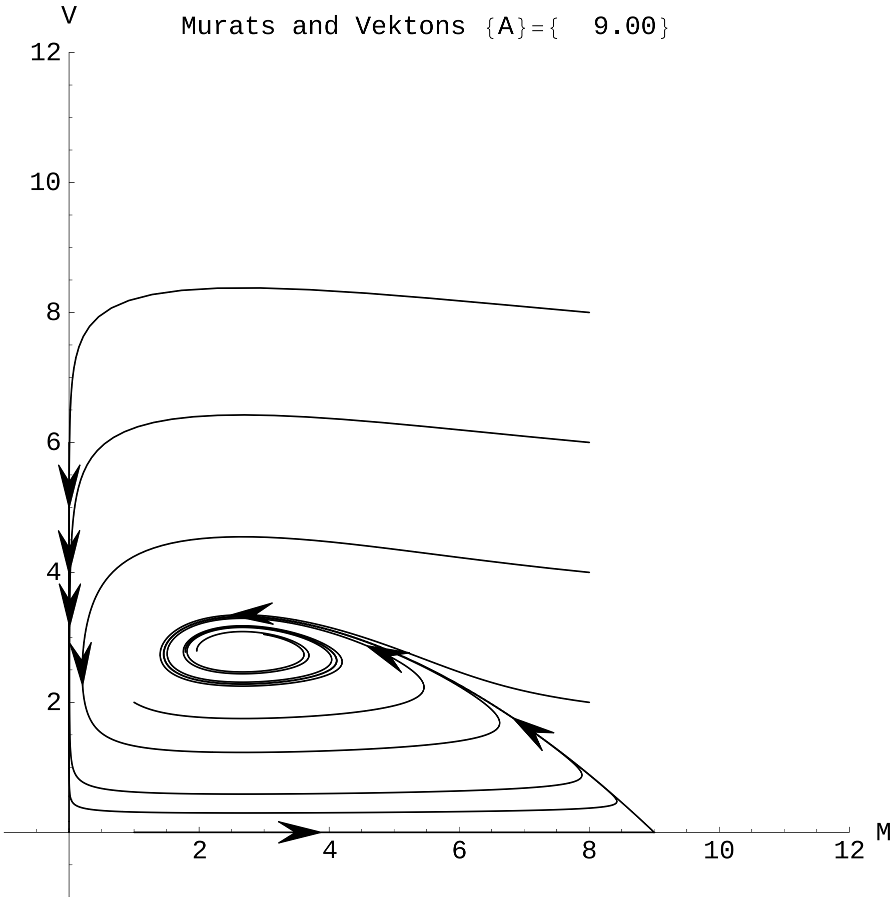
■ Portrait for A = 9

Once again we have a stable spiral at coeq. We use the same set of initial conditions.

```
In[392]:= parmval = {9};
```

```
In[393]:= initlist = {eqstateval[mursadinit], {0, 6}, {1, 0}, {8, 2}, {8, 4}, {8, 6}, {8, 8}, {1, 2}};
```

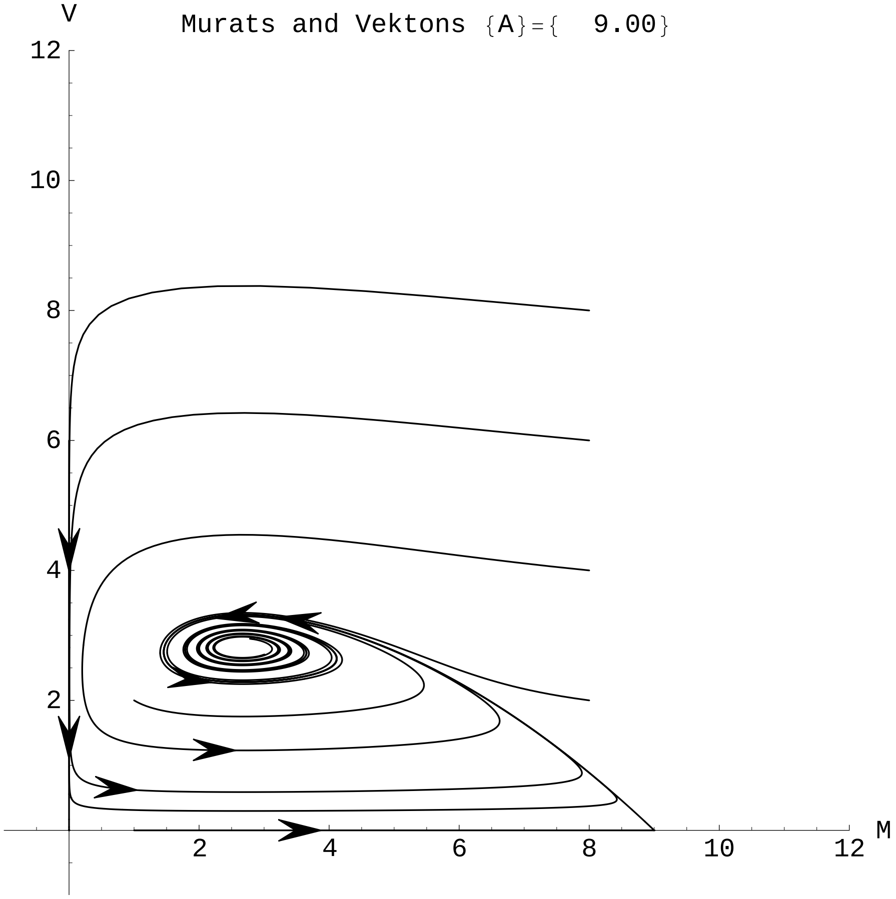
```
In[394]:=  portrait[initlist, t0, h, nsteps, 1, 2];
```



The solution is much more oscillatory for A = 9 than it was for A = 6. In fact, we have not reached equilibrium even after 400 time steps. We increase the number of steps to 800 and repeat.

```
In[395]:=  nsteps = 800;
```

```
In[396]:= portrait[initlist, t0, h, nsteps, 1, 2];
```



We are getting there but it is a slow process. As we saw earlier, a further increase of A to beyond 28/3 leads to the strange result that there are NO stable equilibria for the system. The behavior of the A = 9 case is a strong clue as to what actually happens for A > 28/3. We will come back to this soon in Part 2.

■ What is the Stability of Coeq for A = 28/3 ?

As we saw above, linearization is inconclusive for the case A = 28/3, because the eigenvalues for the equilibrium at coeq are pure imaginary. We begin our attempt to determine stability or instability by looking at an orbit starting near coeq. First we set A = 28/3, then we review the locations and linearized stabilities of the equilibria.

```
In[397]:= parmval = {28 / 3};

In[398]:= eqstateval[nulleq]

Out[398]= {0, 0}

In[399]:= eqstateval[murateq]
```

Out[399]= $\left\{\frac{28}{3}, 0\right\}$

```
In[400]:= eqstateval[coeq]
```

Out[400]= $\left\{\frac{8}{3}, \frac{20}{7}\right\}$

```
In[401]:= classify2D[nulleq]

        unstable – saddle

In[402]:= classify2D[murateq]

        unstable – saddle

In[403]:= classify2D[coeq]

        stable (L), indeterminate (NL) – center
```

Now we construct an orbit starting fairly close to coeq.

```
In[404]:= initvec = eqstateval[coeq + {0.1, 0.1}]

Out[404]= {2.76667, 2.95714}
```

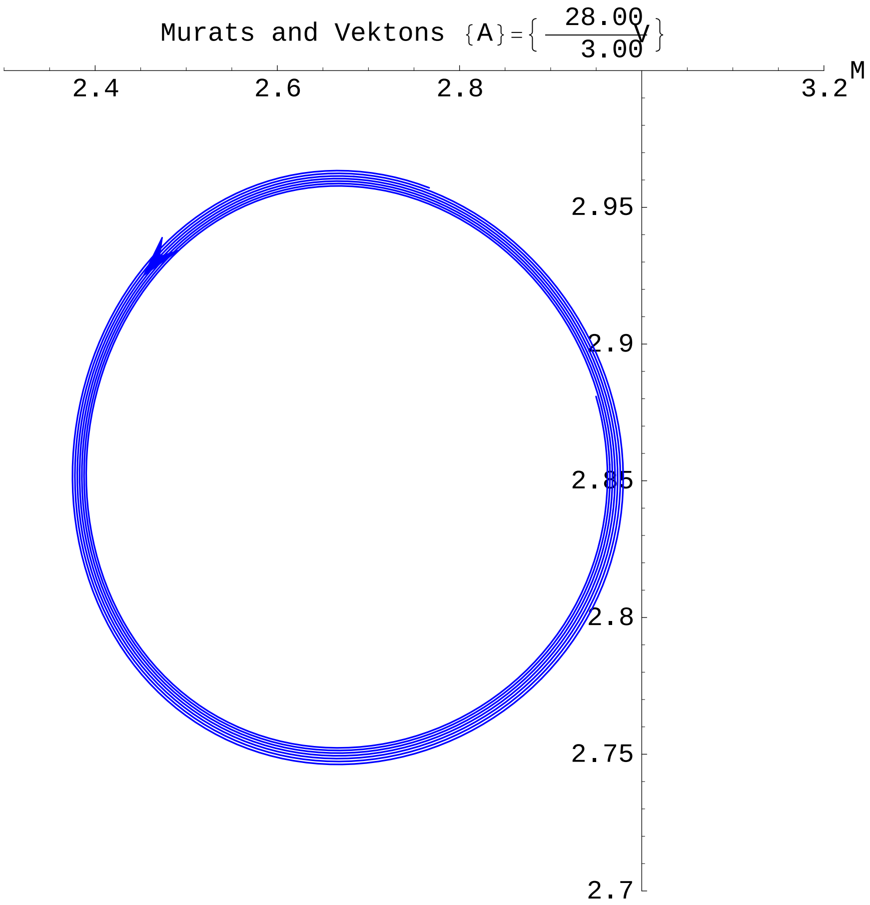
We take 1000 steps.

```
In[405]:= nsteps = 1000;

In[406]:= soltrans = integrate[initvec, t0, h, nsteps];
```

We narrow the plotting window to the immediate neighborhood of coeq. We set the color to Blue.

```
In[407]:= setcolor[{Blue}];

In[408]:= plrange = {{2.3, 3.2}, {2.7, 3.0}};
```

```
In[409]:=  graph1 = phaser[soltrans];
```

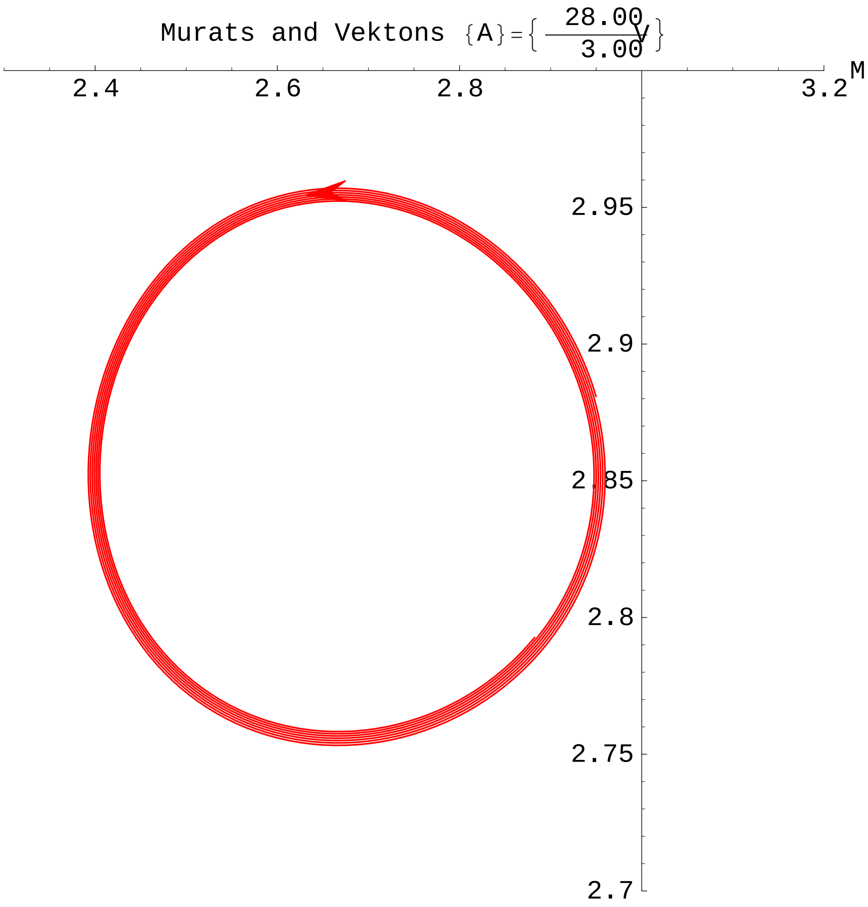


Now we continue the integration and plot, after setting the color to red.

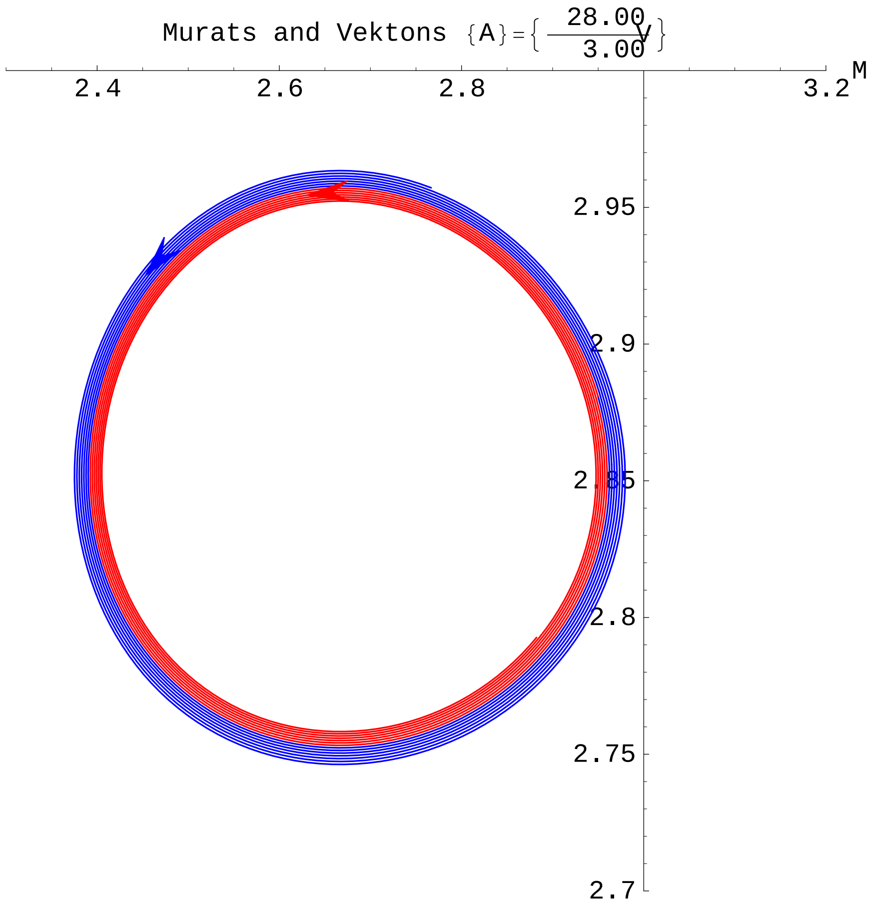
```
In[410]:=  soltrans2 = integrate[lastx, lastt, h, nsteps];
```

```
In[411]:=  setcolor[{Red}];
```

```
In[412]:=  graph2 = phaser[soltrans2];
```



```
In[413]:= show[graph1, graph2];
```



This suggests that the equilibrium is stable, although the approach is very slow indeed. To prove stability, we would have to find a suitable Liapunov function, which could be difficult in this case. Even without such a proof, we already know the most important result about stability: for A < 28/3, there is exactly one stable equilibrium for every value of A. For A > 28/3, all the equlibria are unstable, so the system must have some other kind of attractor. The main point is that there is a bifurcation at A = 28/3.

A Bifurcation Movie of the Equilbria

To give a fairly complete overview of the change of the system with the parameter A, we construct a movie that shows how the three equilibria change as A is changed. Stable equilibria are marked by a blue dot and unstable equilibria by a red dot. We let A run from 1 to 10. We start with the expressions for the three equilibria as a function of A.

```
In[414]:= nulleq

Out[414]= {0, 0}
```

```
In[415]:= murateq

Out[415]= {A, 0}
```

```
In[416]:= coeq
```

Out[416]= $\left\{\frac{8}{3}, \frac{4\,(-8+3\,A)}{3\,A}\right\}$

As we saw earlier, nulleq is always a saddle and hence always unstable. Murateq on the other hand is stable until A reaches 8/3. It is unstable for A larger than 8/3. Something else important also happens at A = 8/3: the state coeq moves from the irrelevant fourth quadrant into the first quadrant. Let's check the stability on both sides of the A = 8/3 transition. We will also verify the change in stability of murateq as we cross A = 8/3.

```
In[418]:= parmval = {2.6};

In[419]:= classify2D[murateq]

        strictly stable - node

In[420]:= classify2D[coeq]

        unstable - saddle

In[421]:= parmval = {2.8};

In[422]:= classify2D[murateq]

        unstable - saddle

In[423]:= classify2D[coeq]

        strictly stable - node
```

Thus as we discussed briefly in class, the two equilibria coalesce at A = 8/3 and there is an exchange of stabilities.

We set the plotting window to {0,10}, {-10,10} which will include all the equilibria in the A-range we have chosen.

```
In[417]:= plrange = {{0, 10}, {-10, 10}};
```

We set a value for ptsize, which determines the size of dots plotted.

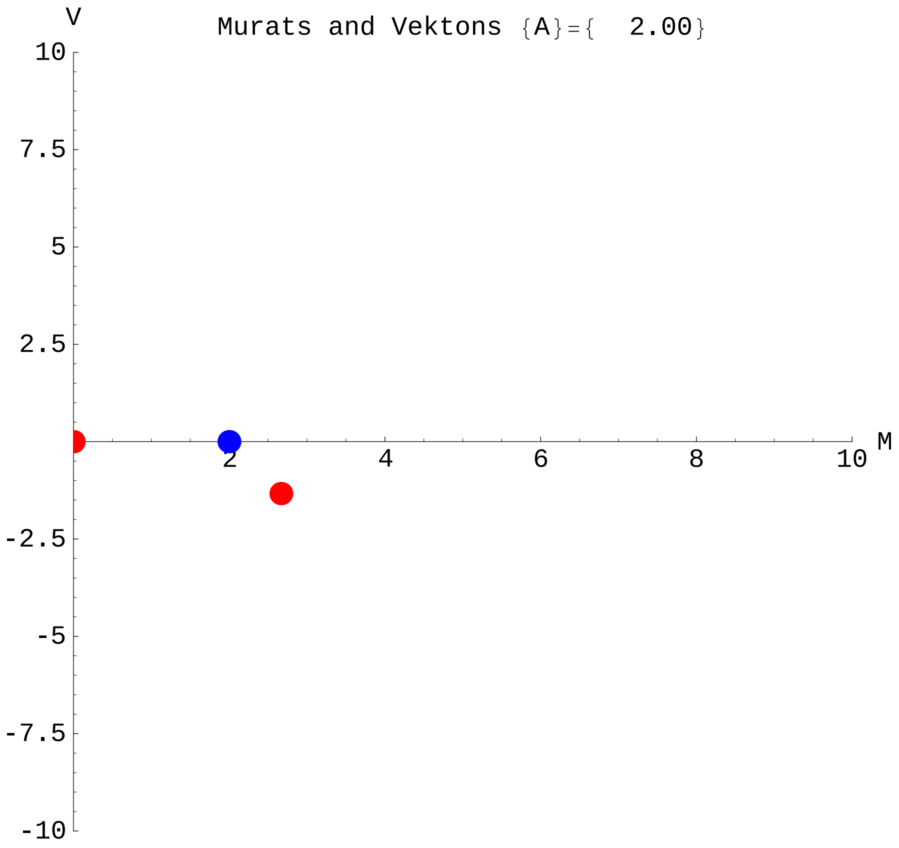
```
In[430]:= ptsize = 0.03;
```

We define a function of A which produces a graph showing a dot at each equilibria.

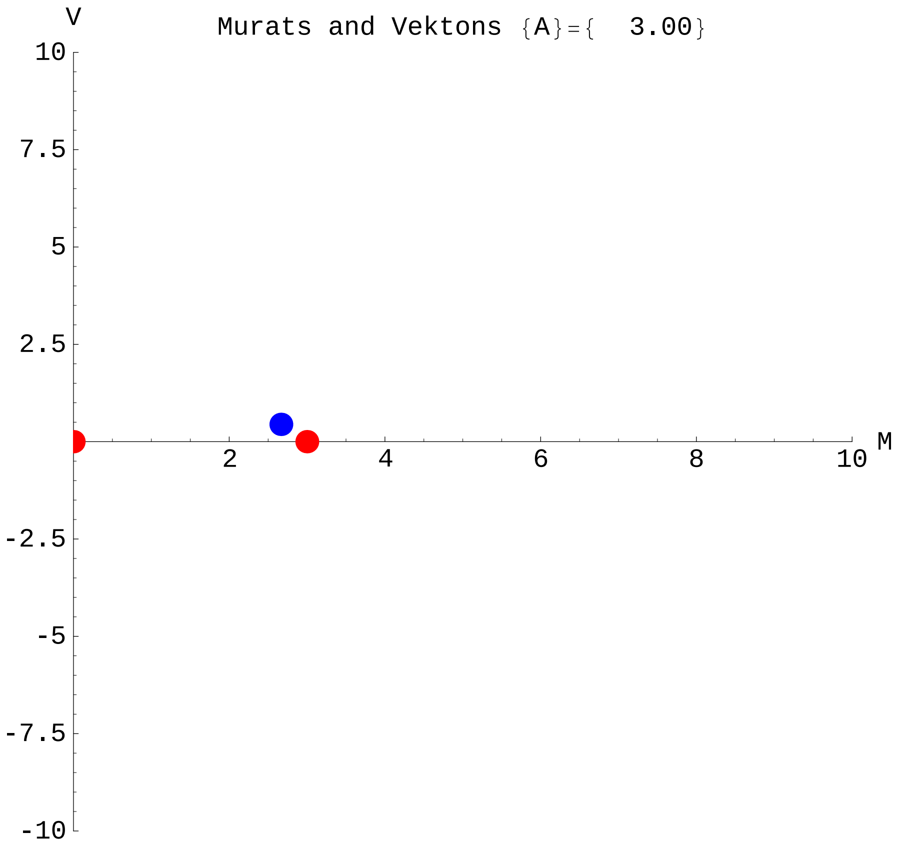
```
In[446]:= eqgraph[Aval_] :=
           Module[{st1, st2, st3, gr1, gr2, gr3}, parmval = {Aval}; If[(Aval < 28 / 3),
             (setcolor[{Red, Blue, Red}]), (setcolor[{Red, Red, Red}])]; st1 = eqstateval[nulleq];
            If[(Aval < 8 / 3), (st2 = eqstateval[murateq]; st3 = eqstateval[coeq]),
             (st3 = eqstateval[murateq]; st2 = eqstateval[coeq])];
            display = False; gr1 = dots[{st1}]; gr2 = dots[{st2}];
            gr3 = dots[{st3}]; display = True; show[gr1, gr2, gr3]]
```

We try this for A = 2, 3, and 10.

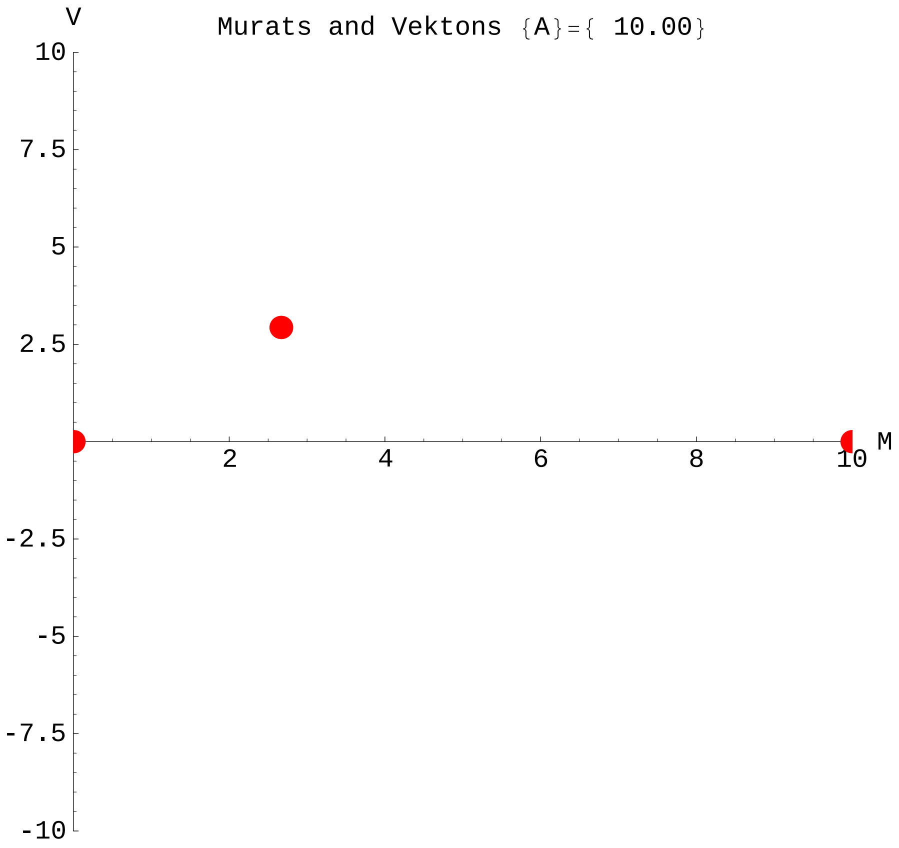
```
In[447]:= eqgraph[2];
```



```
In[448]:= eqgraph[3];
```

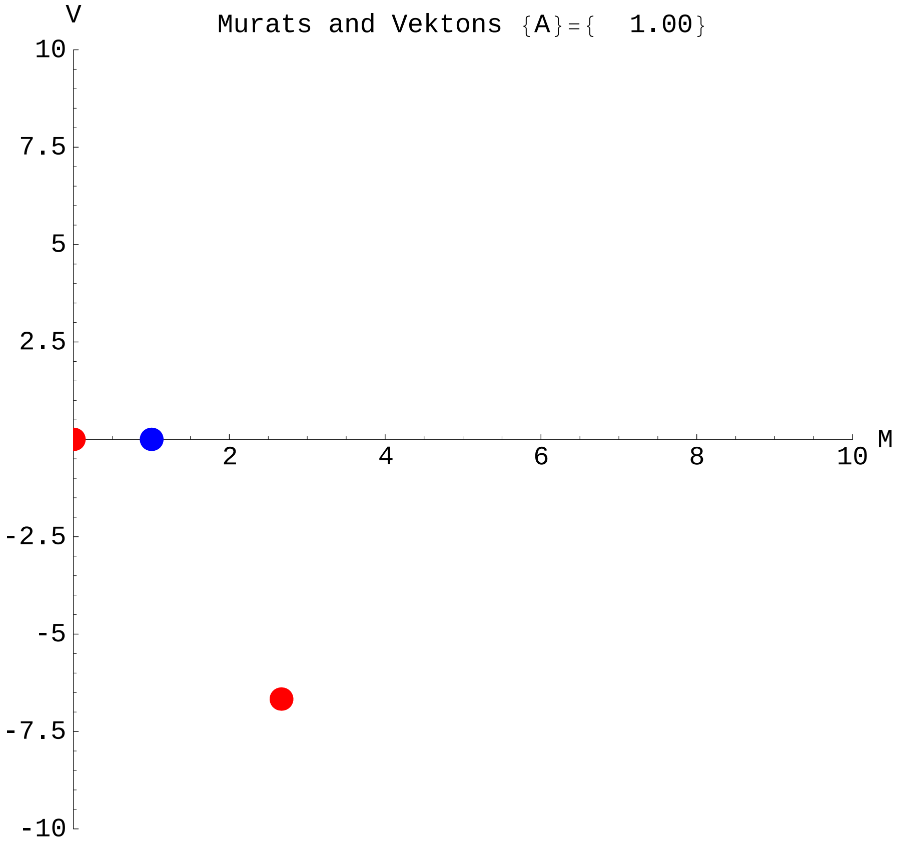


```
In[449]:= eqgraph[10];
```



Now we use a Do loop to make a 91 frame movie going from A = 1 to A = 10 in increments of 0.1. In the printed version of the notebook, only the first frame of the movie is shown.

```
In[450]:= Do[eqgraph[1.0 + 0.1 * i], {i, 0, 90}];
```


V
Murats and Vektons {A}={ 1.00}
10
7.5
5
2.5
-2.5
-5
-7.5
-10
2
4
6
8
10
M