This is the basic model of Tyson et al., built to reproduce the code that we assembled in InsightMaker.

Reference: Tyson, Rebecca, Sheena Haines, Karen Hodges. *Modelling the Canada lynx and snowshoe hare population cycle: The role of specialist predators*. Theoretical Ecology. 3, 97–111 (2010). https://doi.org/10.1007/s12080-009-0057-1

This is the documentation that I included in that InsightMaker model (https://insightmaker.com/insight/188321/Basic-Model-Tyson-Lynx-and-Hare#):

The basic model of Tyson, et al. demonstrates logistic growth in prey, and in predator (with prey dependence for carrying capacity).

The differential equations looks like

x'(t)=rx(1-x/K)-gamma x^2/(x^2+eta^2) - alpha y x/(x+mu)

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \frac{\gamma N^2}{N^2 + \eta^2} - \frac{\alpha NP}{N + \mu}, \tag{1a}$$

$$\frac{dP}{dt} = sP\left(1 - \frac{qP}{N}\right), \tag{1b}$$

where K is the carrying capacity of the prey, in the absence of predation.

y'(t)=sy(1- y/(x/q))

is the predator (lynx) equation. The growth term suggests exponential growth, but there is a loss term of the form sy^2/(x/q)) -- loss is proportional to population (crowding), and inversely proportional to prey density.

In this model, I scale the second equation by multiplying by q, then replace y by qy. This requires a slight change in the prey equation -- alpha replaced by the ratio of alpha/q.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{\gamma N^2}{N^2 + \eta^2} - \frac{\frac{\alpha}{q} N w}{N + \mu}$$
$$\frac{dw}{dt} = sw\left(1 - \frac{w}{N}\right)$$

Tyson, et al. took q to be about 212 for hare and lynx -- so that it requires about 212 hare to allow for one lynx to survive at “equilibrium”. However, when alpha -- the hares/lynx/year -- gets sufficiently large (e.g. 1867 -- and that does seem like a lot of hares per lynx per year...:), limit cycles develop (rather than a stable equilibrium).

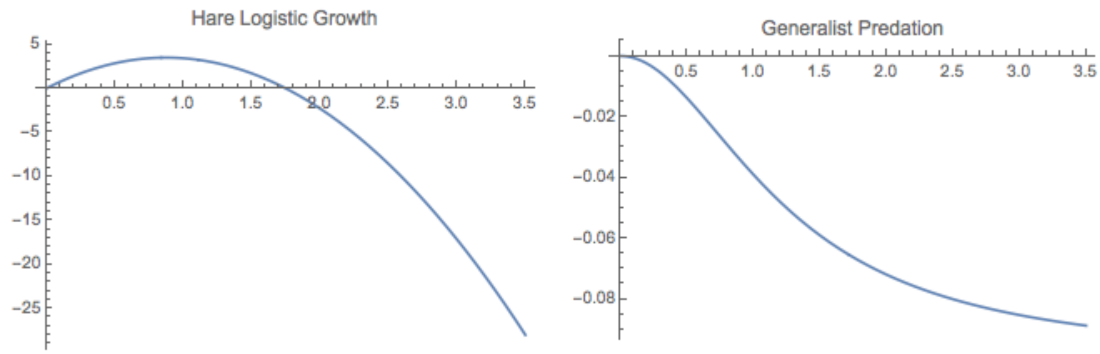
Author: Andy Long, Northern Kentucky University (2020)

Reference: Tyson, Rebecca, Sheena Haines, Karen Hodges. Modelling the Canada lynx and snowshoe hare population cycle: The role of specialist predators.

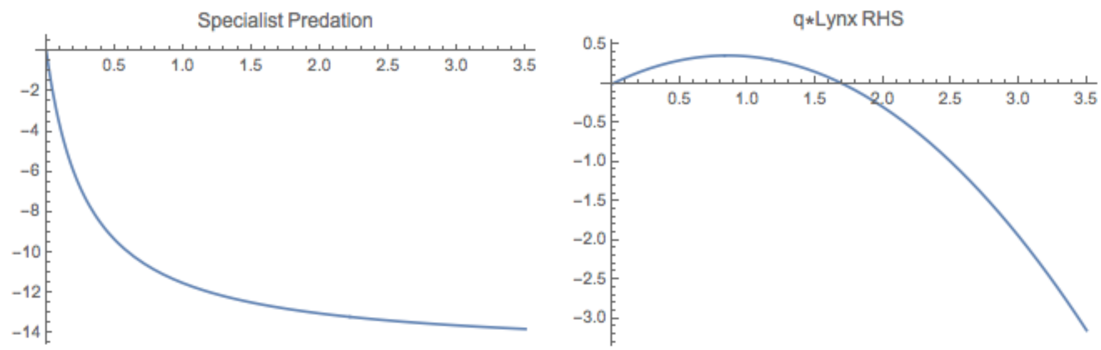
Theoretical Ecology. 3, 97–111 (2010). https://doi.org/10.1007/s12080-009-0057-1

```
In[•]:= Clear["Global`*"]

In[•]:= Manipulate[
   lv =
    NDSolve[
     {(* x is prey: *)
      x'[t] == r x[t] (1 - x[t] / k)
         - gamma x[t]^2 / (x[t]^2 + eta^2)
         - (alpha / q) x[t] * y[t] / (x[t] + mu),
      (* y is predator: *)
      y'[t] == s y[t] (1 - y[t] / x[t]),
      x[0] == xnot,
      y[0] == ynot
     },
     {x[t], y[t]},
     {t, 0, tend}];
   popvals = Table[Evaluate[{x[t], y[t]} /. lv], {t, 0, tend, .1}];
```

```
r1 = Plot[r x (1 - x / k), {x, 0, 2 * k}, PlotLabel → "Hare Logistic Growth"];
r2 = Plot[- gamma x^2 / (x^2 + eta^2),
  {x, 0, 2 * k}, PlotLabel → "Generalist Predation"];
r3 = Plot[- (alpha / q) x * ynot / (x + mu), {x, 0, 2 * k},
  PlotLabel → "Specialist Predation", PlotRange → All];
r4 = Plot[s y (1 - y / xnot), {y, 0, 2 * k}, PlotLabel → "q*Lynx RHS"];

p1 = ListPlot[popvals,
  PlotLabel → "Phase Portrait",
  AxesLabel → {"Hare", "q*Lynx"}];
timeseries = Table[f, {f,
   {Evaluate[x[t] /. lv][[1]] / k, Evaluate[y[t] /. lv][[1]] / k}}, {t, 0, tend, .1}];
p2 = ListLinePlot[timeseries,
  DataRange → {0, tend},
  PlotLegends → Placed[{"Hare", "q*Lynx"}, Below],
  PlotLabel → "Populations, relative to K",
  AxesLabel → {"Years"}
 ];

Show[GraphicsGrid[{{p1, p2}, {r1, r2}, {r3, r4}}]],
{{lv, {}}, None},
{{tend, 28}, 2, 100, 1},
{{xnot, 1.7}, .01, 10, .1},
{{ynot, 1.7}, .01, 10, .1},
{{r, 8}, 0.1, 20, .1},
{{eta, 1.25}, .5, 5, .1},
{{mu, 0.3}, .01, 1, .01},
{{gamma, .1}, .01, 1, .01},
{{alpha, 1867}, 100, 10 000, 1},
{{q, 212}, 1, 600, 1},
{{s, 0.85}, 0.1, 2, .1},
{{k, 1.75}, 1, 6, .1}
]
```



In[∘]:=



In[∘]:=

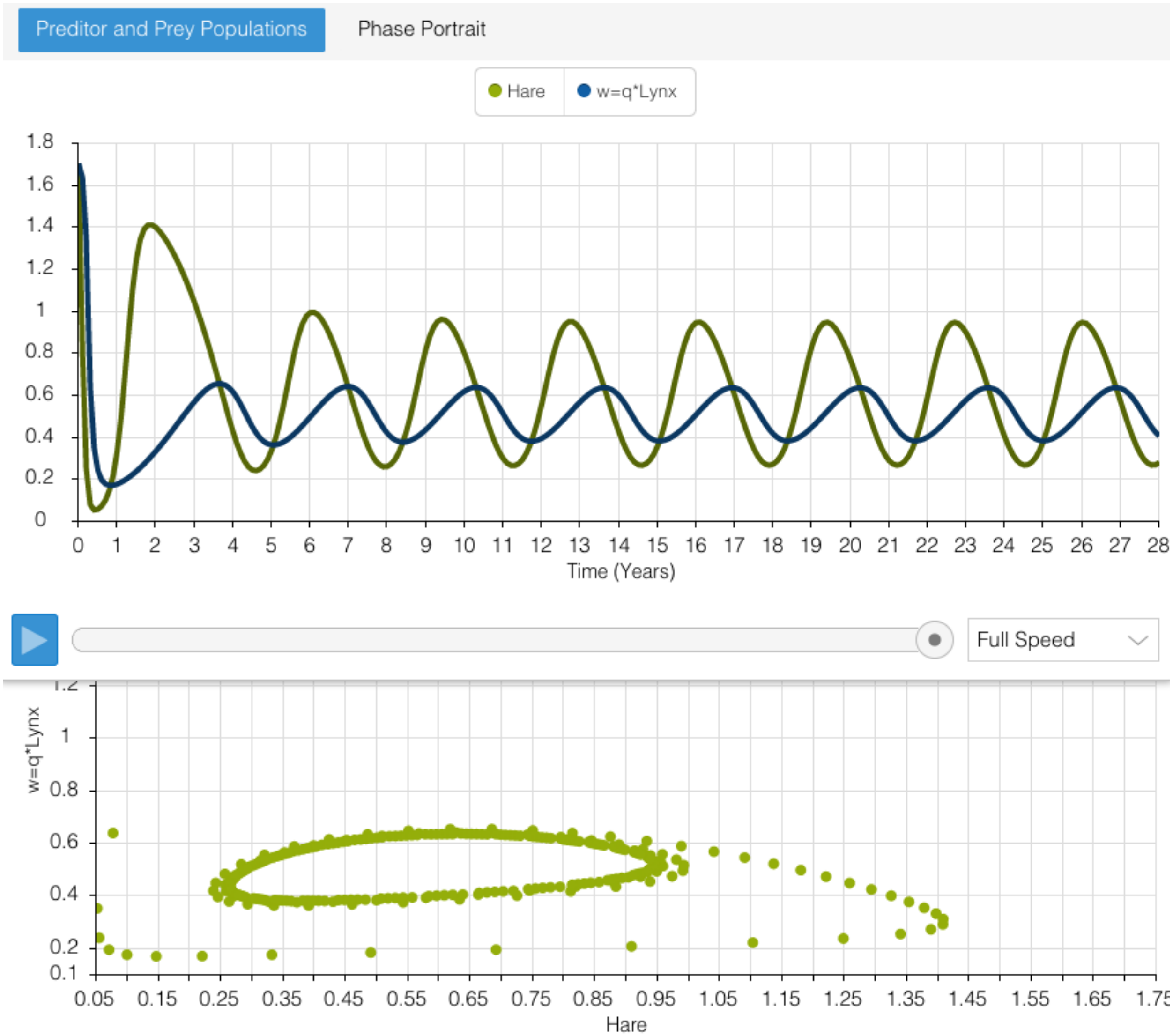
So the Hare Logistic Growth term is fairly self-explanatory. When hares are few, the derivative is positive, pushing the hare population up; when the hare head past the carrying capacity, the hare derivative becomes negative, and the population falls.

The generalist predation graph starts 0, then is always negative and decreasing; starts off slow, then builds as the hare population gets bigger. The bigger the hare population the bigger the generalist predation.

The specialist predation starts off at 0, and also always negative and decreasing; but it rockets off -- as soon as some hares appear the specialist predator is on them like a fox! :) Like when the first blueberries of the year appear, we're on 'em.... My family is a bunch of specialist blueberry predators....

The predator equation is logistic looking, because we've assumed a constant value of hare -- so this is how the lynx would behave (actually q*lynx) with a given level of hare: there's essentially a carrying capacity level of hare. Unfortunately, what we'll see is that in chasing that, the lynx population may chase the hare away from its carrying capacity, so the two won't agree, and we'll get oscillations.

In[∘]:=

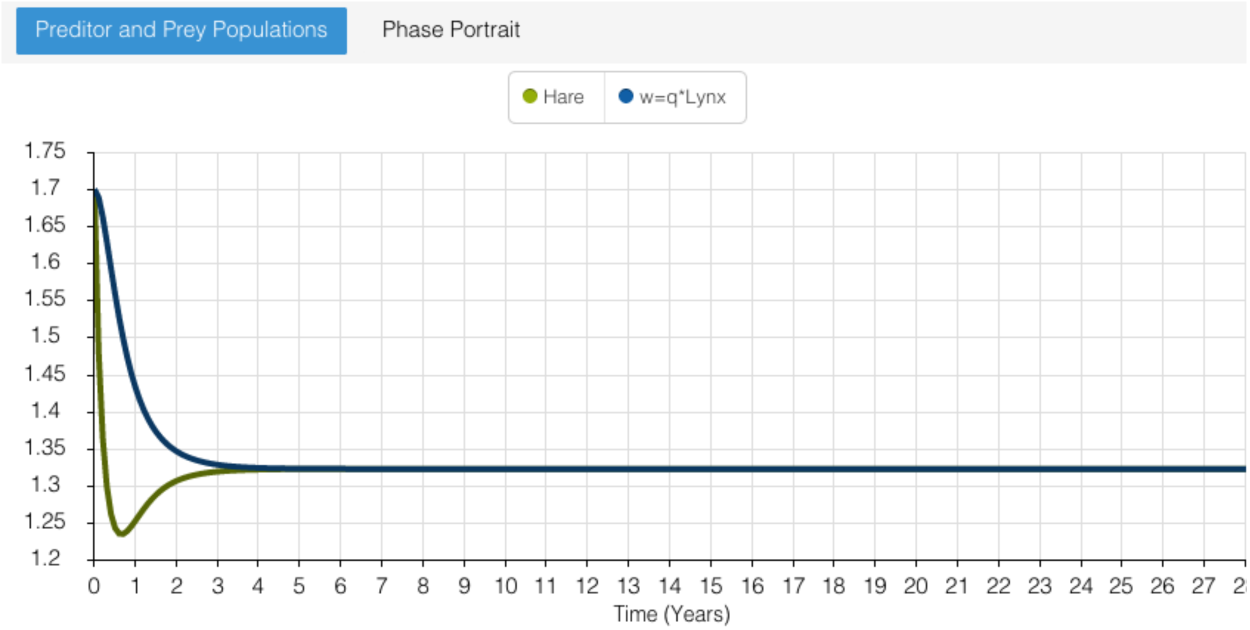


In[∘]:=

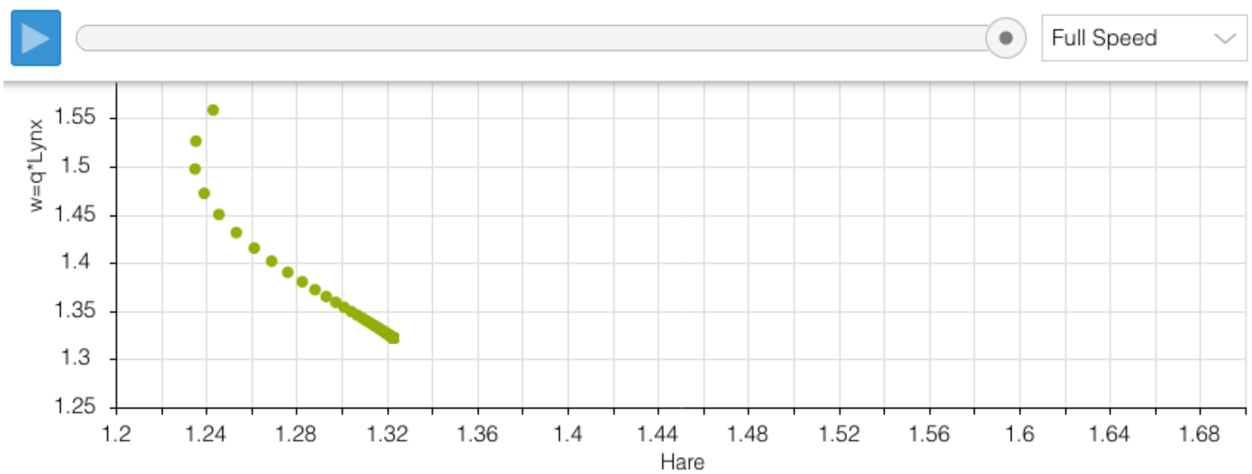
At the outset it seems that both are chasing each other! As the hare population drops low, the lynx drop low afterwards; then, as the hare pick up, the lynx tear off after them -- so to me it seems that the lynx are chasing the hare. Without the hare, the lynx die out. So the hare are sort of primary.

After a few years, the system seems to settle down to a steady cycle, as shown in the phase portrait. So as time goes to infinity this will just closer and closer to a curve, called the **limit cycle**.

If we set alpha to 505, the system settles down quickly, without oscillation, to a stable equilibrium -- both populations head to 1.32something. It will set there forever, as the right hand sides of the system will be 0 -- no change in the populations.



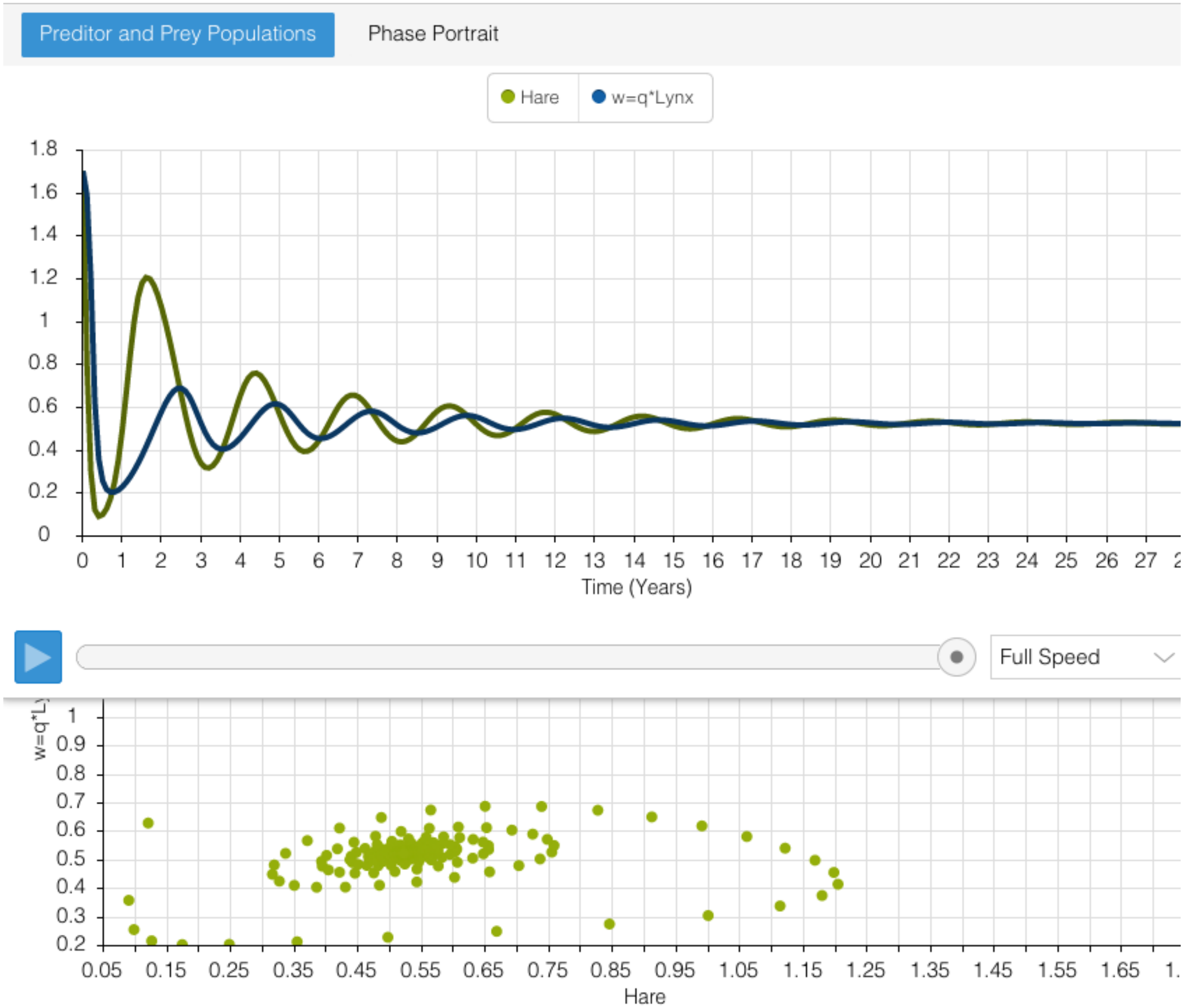
In[∘]:=



In[∘]:=

In this case, the system oscillates with a successively decreasing amplitude, as it heads towards its equilibrium. The phase portrait shows the system spiraling in towards that point.

In[∘]:=



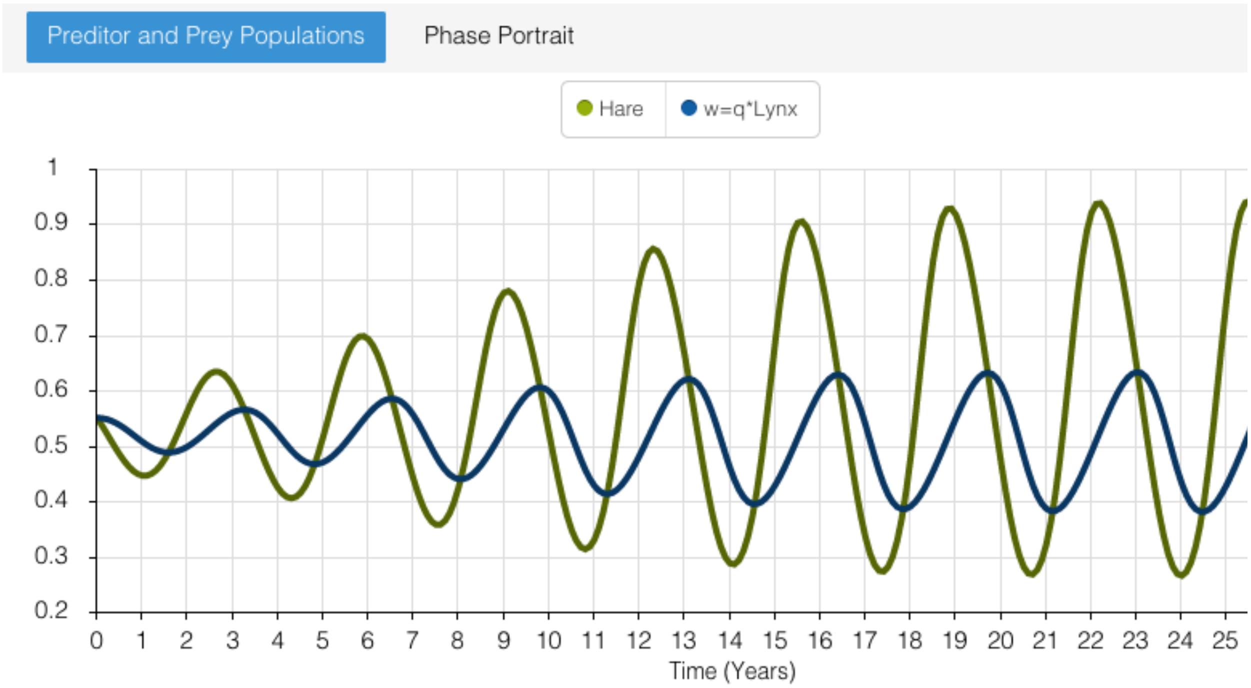
In[∘]:=

In[∘]:=
```
Manipulate[
 lv =
  NDSolve[
   {(* x is prey: *)
    x'[t] == r x[t] (1 - x[t] / k)
      - gamma x[t]^2 / (x[t]^2 + eta^2)
      - (alpha / q) x[t] * y[t] / (x[t] + mu),
    (* y is predator: *)
    y'[t] == s y[t] (1 - y[t] / x[t]),
    x[0] == xnot,
    y[0] == ynot
   },
   {x[t], y[t]},
```

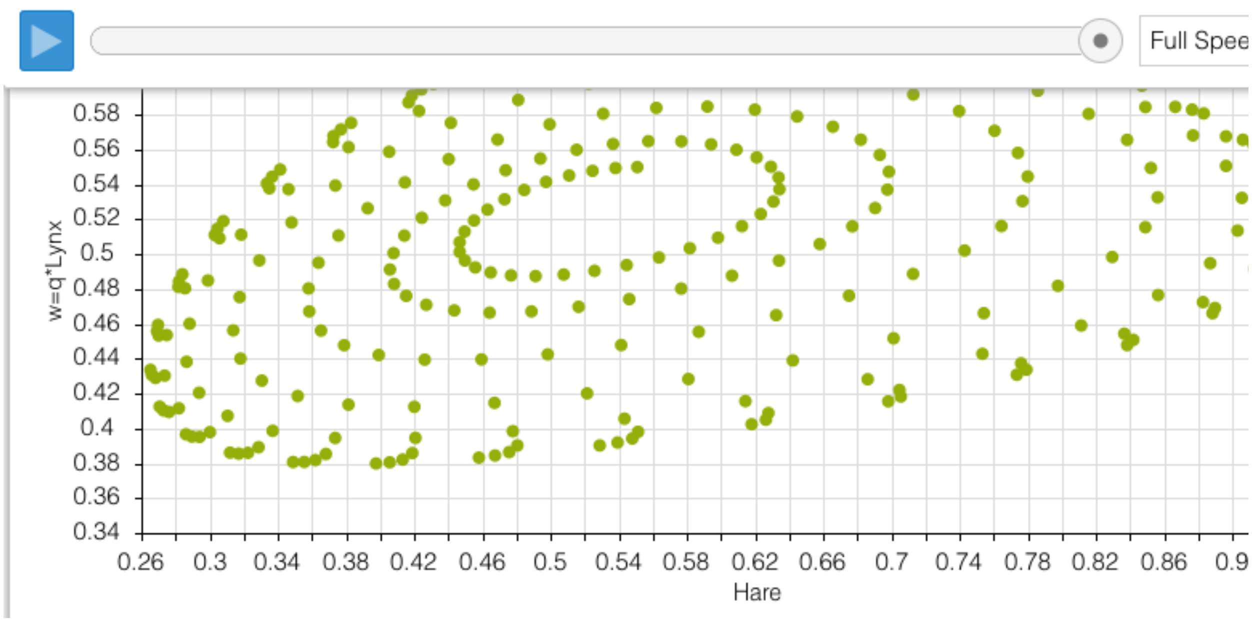
```
    {t, 0, tend}];
  popvals = Table[Evaluate[{x[t], y[t]} /. lv], {t, 0, tend, .1}];

  r1 = Plot[r x (1 - x / k), {x, 0, 2 * k}, PlotLabel → "Hare Logistic Growth"];
  r2 = Plot[- gamma x^2 / (x^2 + eta^2),
    {x, 0, 2 * k}, PlotLabel → "Generalist Predation"];
  r3 = Plot[- (alpha / q) x * ynot / (x + mu), {x, 0, 2 * k},
    PlotLabel → "Specialist Predation", PlotRange → All];
  r4 = Plot[s y (1 - y / xnot), {y, 0, 2 * k}, PlotLabel → "q*Lynx RHS"];

  p1 = ListPlot[popvals,
    PlotLabel → "Phase Portrait",
    AxesLabel → {"Hare", "q*Lynx"}];
  timeseries = Table[f, {f,
     {Evaluate[x[t] /. lv][[1]] / k, Evaluate[y[t] /. lv][[1]] / k}}, {t, 0, tend, .1}];
  p2 = ListLinePlot[timeseries,
    DataRange → {0, tend},
    PlotLegends → Placed[{"Hare", "q*Lynx"}, Below],
    PlotLabel → "Populations, relative to K",
    AxesLabel → {"Years"}
   ];

  Show[GraphicsGrid[{{p1, p2}, {r1, r2}, {r3, r4}}]],
  {{lv, {}}, None},
  {{tend, 28}, 2, 100, 1},
  {{xnot, .55}, .01, 10, .1},
  {{ynot, .55}, .01, 10, .1},
  {{r, 8}, 0.1, 20, .1},
  {{eta, 1.25}, .5, 5, .1},
  {{mu, 0.3}, .01, 1, .01},
  {{gamma, .1}, .01, 1, .01},
  {{alpha, 1867}, 100, 10000, 1},
  {{q, 212}, 1, 600, 1},
  {{s, 0.85}, 0.1, 2, .1},
  {{k, 1.75}, 1, 6, .1}
]
```

Now it's challenge time: two challenges. Find starting values for the populations so that the cycles start small, and get bigger; and so that the system approaches a limit cycle (which is the sort of thing we expect biologically). You may also alter other parameters. Report your parameter choices, and show a graph of the population time series.

So the easy way to do this is to start inside a cycle that we already have! The first graph led inward to a cycle, so I simply chose a starting initial condition inside the limit cycle: (.55, .55); now the system is spiralling out to the edge of the limit cycle. It's a sort of equilibrium in motion! The system is drawn to this cycle, from within or from without. It's the black hole of mathematics....:)



In[∘]:=



In[∘]:=

Second challenge: find starting values so that your solutions look qualitatively like those waves of the hare and lynx of Figure 2, p. 102. Show a graph, and report parameter values. (I think that there's more of a "forward lean" to the solutions than you see in our initial graph.)

Remember that the authors have scaled their population to 0 to 1, so that they can plot them together (see the caption to Figure 2).

This is fundamentally the goal of the authors -- they seek to match oscillations in real data with their models. We'll do something easier here: try to match the oscillations in their model with oscillations from the same model! (Important Note -- the parameter values given in the paper don't work, which I found out early when I was trying to replicate their work. So I had to hunt around to find parameter values that would give the cycles they illustrated.

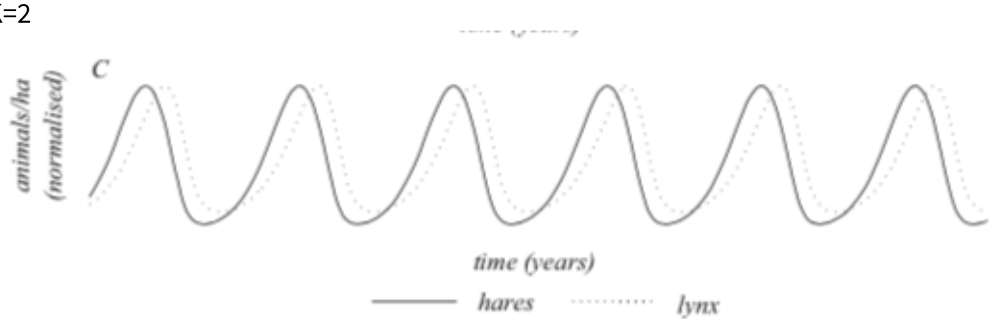
Stuff happens....).

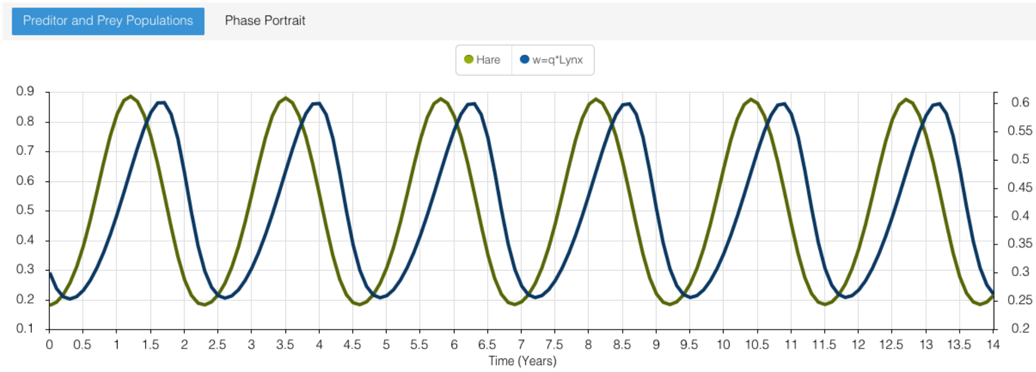
So for this one I simply played around until I got something that looked qualitatively like the results in Tyson, et al.

```
In[•]:= Manipulate[
 lv =
  NDSolve[
   {(* x is prey: *)
    x'[t] == r x[t] (1 - x[t] / k)
      - gamma x[t]^2 / (x[t]^2 + eta^2)
      - (alpha / q) x[t] * y[t] / (x[t] + mu),
    (* y is predator: *)
    y'[t] == s y[t] (1 - y[t] / x[t]),
    x[0] == xnot,
    y[0] == ynot
   },
   {x[t], y[t]},
   {t, 0, tend}];
 popvals = Table[Evaluate[{x[t], y[t]} /. lv], {t, 0, tend, .1}];

 r1 = Plot[r x (1 - x / k), {x, 0, 2 * k}, PlotLabel → "Hare Logistic Growth"];
 r2 = Plot[- gamma x^2 / (x^2 + eta^2),
   {x, 0, 2 * k}, PlotLabel → "Generalist Predation"];
 r3 = Plot[- (alpha / q) x * ynot / (x + mu), {x, 0, 2 * k},
   PlotLabel → "Specialist Predation"];
 r4 = Plot[s y (1 - y / xnot), {y, 0, 2 * k}, PlotLabel → "q*Lynx RHS"];

 p1 = ListPlot[popvals,
   PlotLabel → "Phase Portrait",
   AxesLabel → {"Hare", "q*Lynx"}];
 timeseries = Table[f, {f,
    {Evaluate[x[t] /. lv][[1]] / k, Evaluate[y[t] /. lv][[1]] / k}}, {t, 0, tend, .1}];
 p2 = ListLinePlot[timeseries,
```

```
   DataRange → {0, tend},
   PlotLegends → Placed[{"Hare", "q*Lynx"}, Below],
   PlotLabel → "Populations, relative to K",
   AxesLabel → {"Years"}
  ];

 Show[GraphicsGrid[{{p1, p2}, {r1, r2}, {r3, r4}}]],
 {{lv, {}}, None},
 {{tend, 14}, 2, 100, 1},
 {{xnot, 0.18}, .01, 10, .1},
 {{ynot, 0.3}, .01, 10, .1},
 {{r, 8}, 0.1, 20, .1},
 {{eta, 1.2}, .5, 5, .1},
 {{mu, 0.26}, .01, 1, .01},
 {{gamma, 0.33}, .01, 1, .01},
 {{alpha, 2193}, 100, 10 000, 1},
 {{q, 212}, 1, 600, 1},
 {{s, 1.8}, 0.1, 2, .1},
 {{k, 2.0}, 1, 6, .1}
]
```

tend=14
xnot=0.18
ynot=0.3
r=8
eta=1.2
mu=0.26
gamma=0.33
alpha=2193
q=212
s=1.8
K=2




Preditor and Prey Populations
Phase Portrait
Hare
w=q*Lynx
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5 5 5.5 6 6.5 7 7.5 8 8.5 9 9.5 10 10.5 11 11.5 12 12.5 13 13.5 14
Time (Years)