Stability Analysis

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January 11, 2024

1 Introduction

We provide a few examples of stability analysis and bifurcations arising in differential equations coming from an ecological context. There is also an example with the theta logistic equation and mathematically resolving the "Paradox of Biological Control".

2 Examples

1. (Refuge) Consider the differential equations

$$\frac{\mathrm{d}N}{\mathrm{d}T} = rN - c(N-s)P$$

$$\frac{\mathrm{d}P}{\mathrm{d}T} = b(N-s)P - mP$$

for a predator P and its prey N. In this model,s of the prey may hide in a refuge and avoid predation.

a) Non-dimensionalize the system.

Proof. Let $x = \frac{N}{s}$ then $N = xs$ so we have

$$s\frac{\mathrm{d}x}{\mathrm{d}T} = rxs - c(xs - s) = s(rx - c(x-1)P)$$

$$\frac{\mathrm{d}P}{\mathrm{d}T} b(xs - s)P - mP = bs(x-1)P - mP.$$

Canceling out the s from above and let $y = \frac{c}{r}P$ then $P = \frac{r}{c}y$ so we have

$$\frac{\mathrm{d}x}{\mathrm{d}T} = rx - c(x-1)\frac{r}{c}y = r(x - y(x-1))$$

$$\frac{r}{c}\frac{\mathrm{d}y}{\mathrm{d}T} = bs(x-1)\frac{r}{c}y - m\frac{r}{c}y = y(\frac{bsr}{c}(x-1) - \frac{mr}{c}).$$

Canceling out the r/c and taking $t = rT$ we have that $\frac{\mathrm{d}}{\mathrm{d}T} = r\frac{\mathrm{d}}{\mathrm{d}t}$ so our equation become

$$\frac{\mathrm{d}x}{\mathrm{d}t} = (x - y(x-1))$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = y(\alpha(x-1) - \beta)$$

where $\alpha = \frac{bs}{r}, \beta = \frac{m}{r}$. ∎

b) Determine the zero-growth isoclines of your non-dimensionalized system.

Proof. The prey zero-growth iscolines are the curves where $\frac{\mathrm{d}x}{\mathrm{d}t} = 0$ and the predator zero-growth iscolines are the curves where $\frac{\mathrm{d}y}{\mathrm{d}t} = 0$.

Starting with prey zero-growth isoclines $\frac{\mathrm{d}x}{\mathrm{d}t} = 0 \implies x - y(x-1) = 0$. Solving for y gives the curve,

$$y = \frac{x}{x-1}.$$

Solving for x gives the curve,

$$x = -\frac{y}{1-y} = \frac{y}{y-1}$$

which is the same curve as above.

Now for the predator zero-growth isocline we have $\frac{\mathrm{d}y}{\mathrm{d}t} = 0 \implies \alpha y(x-1) - \beta y = 0$. Solving for x gives the line,

$$x = \frac{\beta}{\alpha} + 1.$$

Solving for y gives the line,

$$y = 0.$$

∎

c) Find the equilibria.

Proof. We can find the equilibria of the system where the predator and prey zero-growth isoclines intersect.

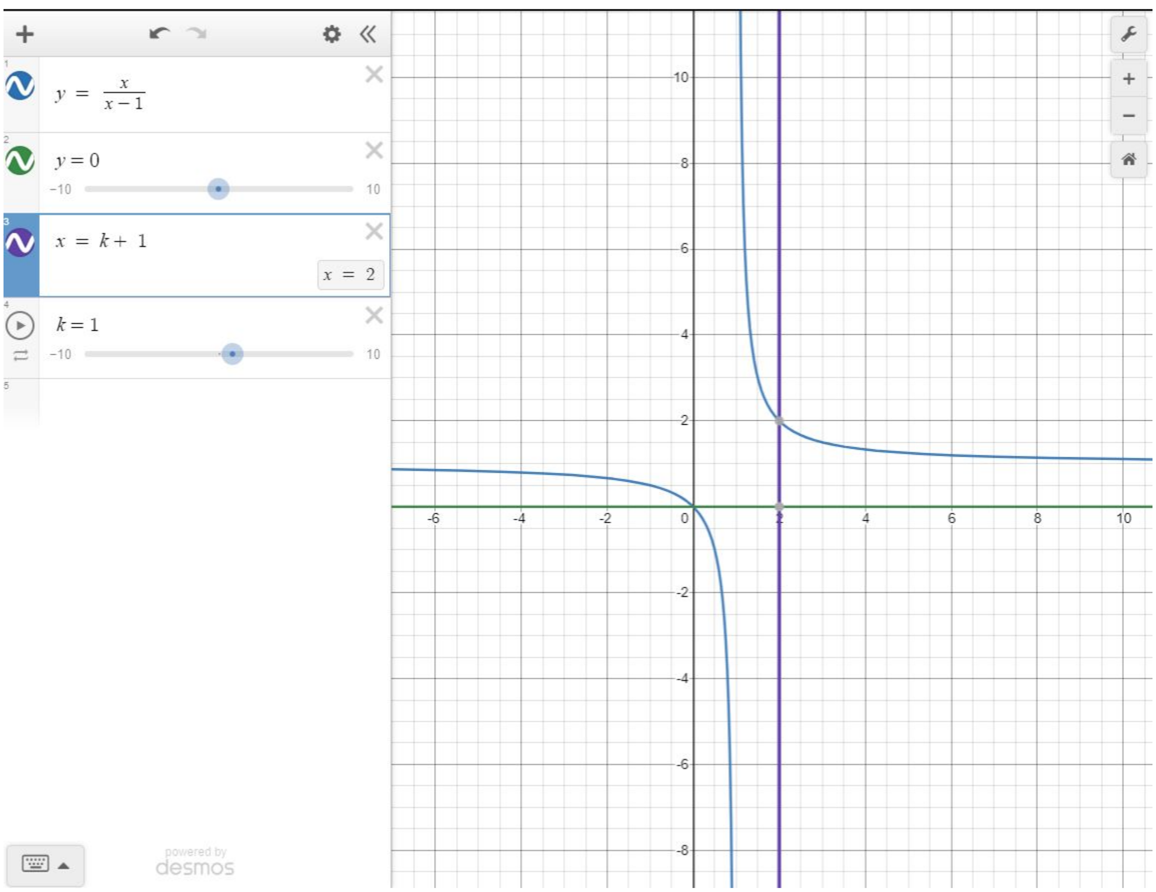

Figure 1: example of isoclines for non-dimensionalized system

The curve $y = \frac{x}{x-1}$ intersects the line $y = 0$ at $(x_1^*, y_1^*) = (0,0)$. The final equilibrium point occurs when $x = \frac{\beta}{\alpha} + 1$ intersects the curve $y = \frac{x}{x-1}$ which gives the equilibrium $(x_2^*, y_2^*) = (\frac{\beta}{\alpha} + 1, \frac{\frac{\beta}{\alpha}+1}{\frac{\beta}{\alpha}})$. Where the lines $x = \frac{\beta}{\alpha} + 1$ and $y = 0$ intersect both correspond to predator zero-growth isocline so that intersection point is not of interest. ■

d) Find the stability of each equilibrium using a linearized stability analysis.

Proof. To determine stability we will calculate the Jacobian of our system at each equilibrium point.

$$J(x,y) = \begin{bmatrix} (1-y) & (1-x) \\ \alpha y & \alpha(x-1) - \beta \end{bmatrix}$$

Recall that all constant coefficients are taken to be positive so that $\alpha, \beta > 0$ as well. Let $p(\lambda)$ be the characteristic polynomial.

$(0,0)$

$$J = \begin{bmatrix} 1 & 0 \\ 1 & -(\alpha+\beta) \end{bmatrix}$$

Then $p(\lambda) = (1-\lambda)(-(\alpha+\beta) - \lambda)$. So $\lambda_1 = 1$, $\lambda_2 = -(\alpha+\beta)$ since we have two real eigenvalues with one positive and one negative we have a saddle node.

$(\frac{\beta}{\alpha} + 1, \frac{\frac{\beta}{\alpha}+1}{\frac{\beta}{\alpha}})$

$$J = \begin{bmatrix} -\frac{\alpha}{\beta} & -\frac{\beta}{\alpha} \\ \frac{\alpha(\alpha+\beta)}{\beta} & 0 \end{bmatrix}$$

then $p(\lambda) = \lambda^2 + \lambda\frac{\alpha}{\beta} + (\alpha+\beta)$. Using the quadratic formula we have

$$\lambda_{1,2} = \frac{\frac{\alpha}{\beta} \pm \sqrt{(-\frac{\alpha}{\beta})^2 - 4(\alpha+\beta)}}{2}.$$

We will use the guide from the Topic 5 notes on page 12. First notice that the trace is negative and the determinant is positive. So if det < trace^2/4 we will have a stable node/ sink. If det > trace^2/4 then we have a stable focus.

■

e) Use whatever other techniques you have at your disposal to analyze this system.

Proof. Consider the strip $D = 0 < y < 1$ and take $B = \frac{1}{y}$. Then if we take $F = s(x - y(x-1))$ and $G = y(\alpha(x-1) - \beta)$ we have that

$$BF = (\frac{x}{y} + 1 - x) \implies \frac{\partial[BF]}{\partial x} = (\frac{1}{y} - 1)$$

$$BG = \alpha x - (\alpha + \beta) \implies \frac{\partial[BG]}{\partial y} = 0.$$

Then for $x, y \in D$, $\frac{\partial[BF]}{\partial x} + \frac{\partial[BG]}{\partial y} = (\frac{1}{y} - 1) > 0$ so by Bendixson-Dulac we have no closed orbits in the strip D. Now notice that if we consider $y > 1$ for any x the sum of partials is strictly negative so there are no closed orbits above $y > 1$. If we take $D = x \in \mathbb{R}, y < 0$ then the sum of the partials is strictly negative so there are no closed orbits in the 3rd and 4th quadrants either.

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f) Draw typical phase portraits for this system.

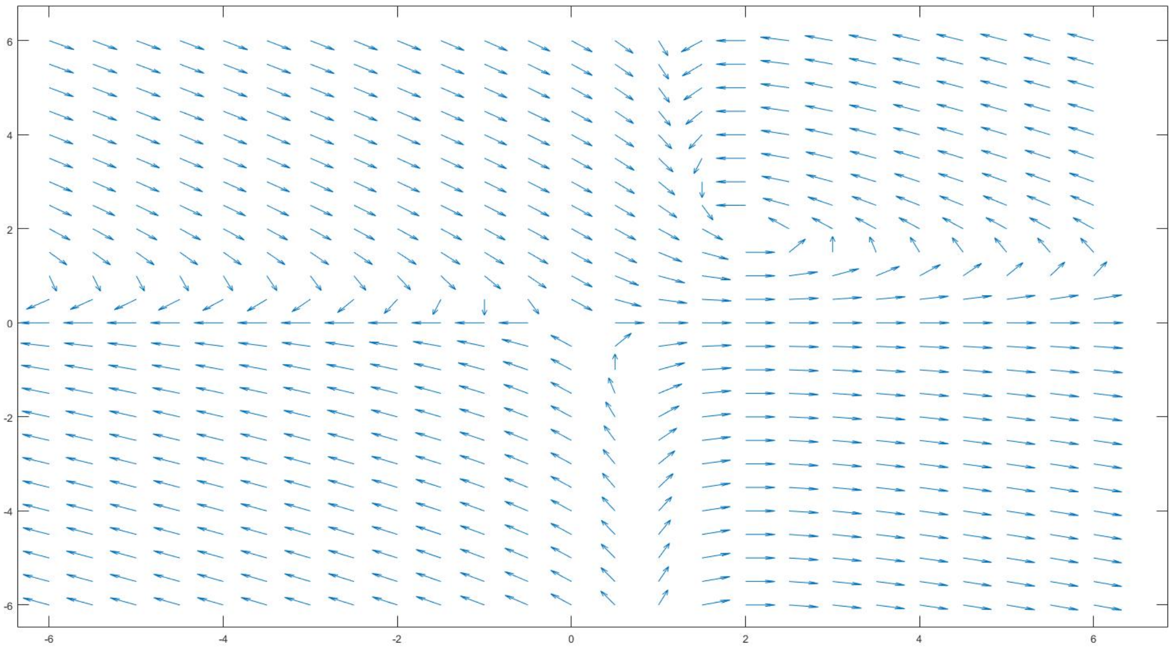

Figure 2: Phase plane with $\alpha = .5, \beta = .5$

Note that vectors were normalized to have same length. Now we check our previous work/sanity check with the α and β values from the phase plane above. We indeed see a saddle node at $(0,0)$. At $(\frac{\beta}{\alpha}+1, \frac{\frac{\beta}{\alpha}+1}{\frac{\beta}{\alpha}}) = (2{,}2)$ and our determinant $= 1$ and trace$^2/4 = .25$ so we should expect a stable focus which is what we have.

2. (Theta-Logistic Predator-Prey Model) At the start of the quarter we studied the theta-logistic equation

$$\frac{\mathrm{d}N}{\mathrm{d}T} = rN[1 - (\frac{N}{K})^{\theta}].$$

Consider the predator-prey model

$$rN[1 - (\frac{N}{K})^{\theta}] - \frac{cNP}{a+N}$$
$$\frac{\mathrm{d}P}{\mathrm{d}T} = \frac{bNP}{a+N} - mP$$

Analyze and discuss the effects of the parameter θ on the occurrence of limit cycles for the above predator-prey model. Explain how your results resolve the biological control paradox.

Proof. We follow along with the topic 5 notes and introduce a change of variable $N = ax$, $P = r\frac{a}{c}y$, $T = \frac{1}{r}t$

and we obtain the dimensionless system

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x\left(1 - (\frac{x}{\gamma})^{\theta}\right) - \frac{xy}{1+x}$$

$$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta\left(\frac{x}{1+x} - \alpha\right)y$$

where $\alpha = \frac{m}{b}$, $\beta = \frac{b}{r}$, $\gamma = \frac{K}{a}$.

We obtain the prey zero-growth isoclines by taking $\frac{\mathrm{d}x}{\mathrm{d}t} = 0$ which gives

$$x = 0,\ y = (1+x)\left(1 - (\frac{x}{\gamma})^{\theta}\right).$$

The predator zero-growth isoclines are obtained by $\frac{\mathrm{d}y}{\mathrm{d}t} = 0$ which gives

$$y = 0,\ x = \frac{\alpha}{1-\alpha}.$$

The equilibria occur at the intersections of the predator-prey zero-growth isoclines. We obtain 3 equilibria

$$(x_1^*, y_1^*) = (0,0)$$
$$(x_2^*, y_2^*) = (\gamma, 0)$$
$$(x_3^*, y_3^*) = (x_0, (1+x_0)\left(1 - (\frac{x^*}{\gamma})^{\theta}\right)$$

where $x_0 = \frac{\alpha}{1-\alpha}$.

Following the notes we make the simplification

$$f(x) = \frac{x}{1+x}, g(x) = (1+x)\left(1 - (\frac{x}{\gamma})^{\theta}\right)$$

which reduces our system to

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)(g(x) - y)$$
$$\frac{\mathrm{d}y}{\mathrm{d}t} = \beta(f(x) - \alpha)y.$$

To analyze the stability we need to look at the Jacobian,

$$J = \begin{bmatrix} f(x)g'(x) + f'(x)g(x) - yf'(x) & -f(x) \\ \beta f'(x)y & \beta(f(x) - \alpha) \end{bmatrix}.$$

We focus our attention on the third equilibrium. Here $f(x_0) = \alpha$ and so our Jacobian,

$$J = \begin{bmatrix} \alpha g'(x_0) & -\alpha \\ \beta f'(x_0)g(x_0) & 0 \end{bmatrix}$$

which has characteristic polynomial $p(\lambda) = \lambda^2 - \alpha g'(x_0)\lambda + \alpha\beta f'(x_0)g(x_0)$.

The Routh-Hurwitz criterion (pg. 12 of Predator-Prey notes) gives us stability if the coefficients are positive. Since

$$f'(x) = \frac{1}{(1+x)^2}$$

then $f'(x)$ is strictly positive and by assumption α, β are strictly positive. $g(x_0)$ is positive on $-1 < x_0 < \gamma$. So the stability at this equilibrium is determined by $g'(x_0)$. The equilibrium is stable if $g'(x_0) < 0$ and unstable if $g'(x_0) > 0$.

We want to see the effect that θ has on our system. If we consider populations less than the parameter encoding carrying capacity which corresponds to $0 < x < \gamma$ then $\frac{x}{\gamma} < 1$ so if we let

$$g_{\theta}(x) = (1+x)\left(1 - (\frac{x}{\gamma})^{\theta}\right)$$

$$g_\theta(x) \to 1 + x$$

pointwise on $0 < x < \gamma$. So (in a handwavy fashion since uniform convergence wasn't proven) $g'(x) = 1 > 0$. So for large θ by the Routh-Hurwitz criterion we destabilize the equilibrium and this causes large oscillations. This resembles the idea of the Enrichment Paradox when $\theta = 1$ - if we fix the prey isocline then as we increase the carrying capacity we pull the peak of the parabola to the right so that the slope of the predator isocline at the equilibrium point (similar to our case the sign of the derivative of the predator isocline determines the stability) is positive. So as we pull the carrying capacity further we would need to adjust the prey isocline to be larger so the intersection occurs on the side of the parabola where the slope is positive. In the theta-logistic case, we are not changing the carrying capacity, but as $\theta \to \infty$ we approach a line that has a positive slope up to the carrying capacity so really no matter where the prey isocline intersects the predator isocline that point has a positive slope (for $x \in (0, \gamma)$).

Running this idea in the other direction, as $\theta \to 0$ we are pushing the peak of the parabolic-like curve to the left. So that $g'(x_0)$ is more likely to be negative and hence our system is stable.

For numerical plots we use the fix the parameters $\alpha = .75$, $\beta = .9$, $\gamma = 5$, and we vary θ. We plot the derivative of g and vary θ (t in the image) around x_0 to to get an idea for when the equilibrium should destabilize (Fig 1). We see that θ a bit larger than 3 for the fixed parameters α, β is where the destabilization should begin.

Notice that Fig 3 and 4 are in agreement with the results we found from plotting the derivative. That is, we see the destabilization of the equilibrium occurs just after $\theta = 3$ in this case. Now we address the paradox of biological control - from Fig.3 and Fig. 4 we see that for certain theta values if we were to drive the prey zero growth isocline to the left then we would destabilize and get large oscillations. So the question is: in reality when we see prey zero-growth isoclines pushed to the left why aren't they exhibiting this Hopf bifurcation going from stable to large oscillations? It is because they must have a small theta parameter! Since for small theta, even as you drive the prey isocline closer to zero, the slope of $g'(x_0)$ is negative and hence the equilibrium is stable. Paradox = resolved.

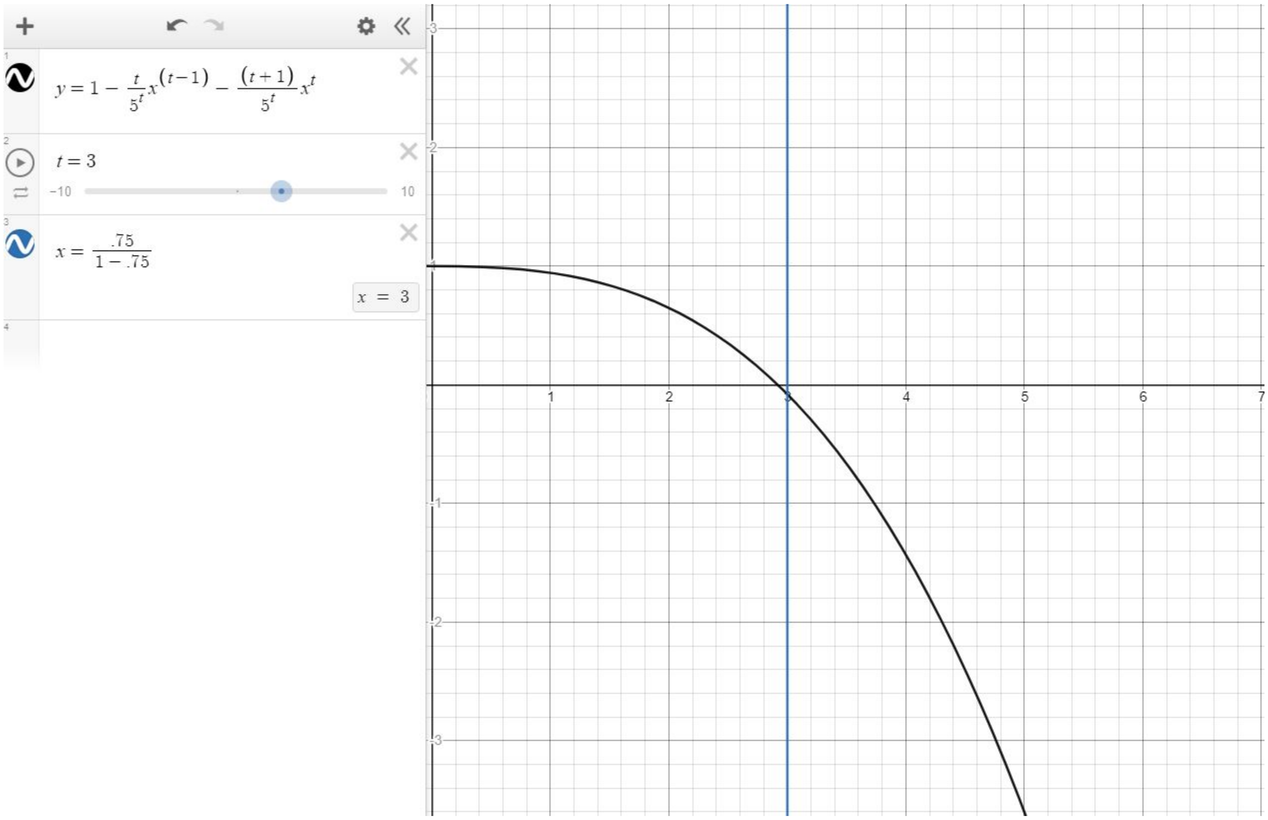

Figure 3: Derivative around critical point x_0

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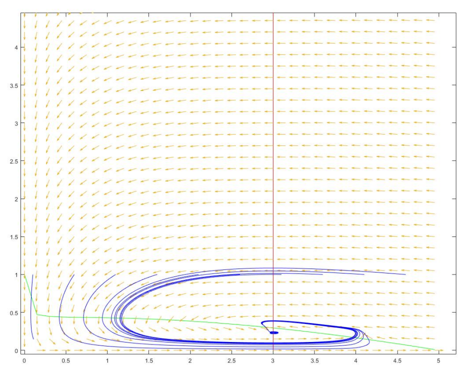
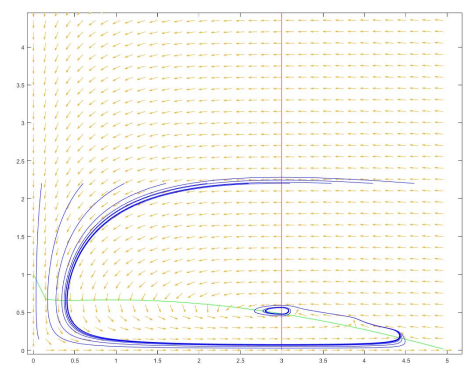
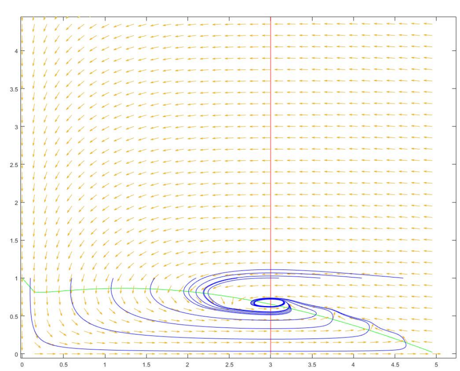


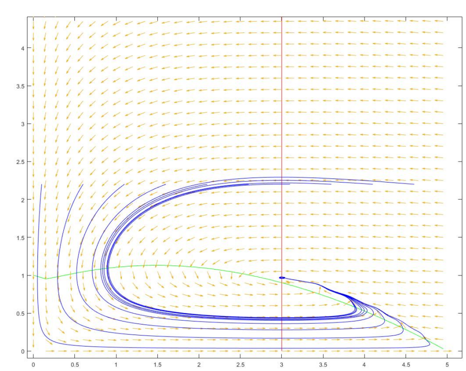
(a) $\theta = 0.15$



(b) $\theta = 0.25$

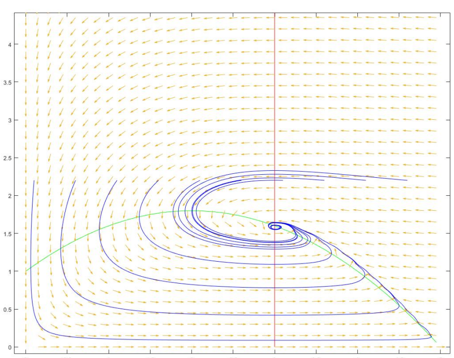


(c) $\theta = 0.35$

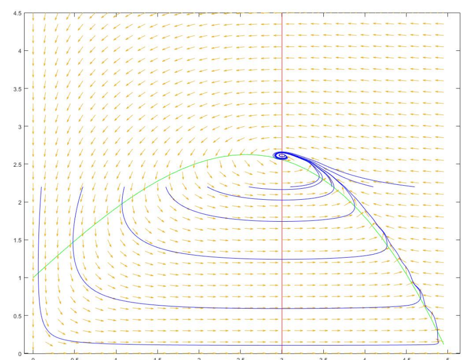


(d) $\theta = 0.5$

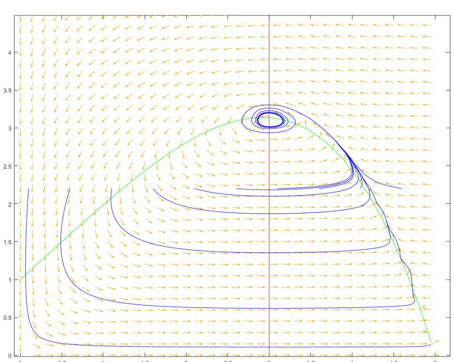
Figure 4: Small θ with stable equilibrium



(a) $\theta = 1$

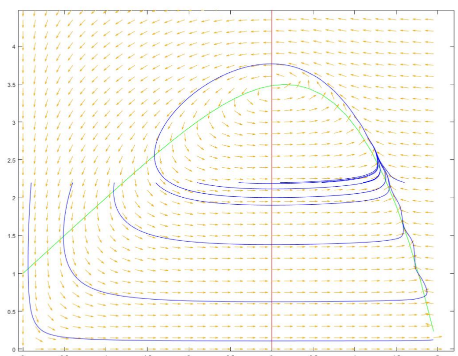


(b) $\theta = 2$

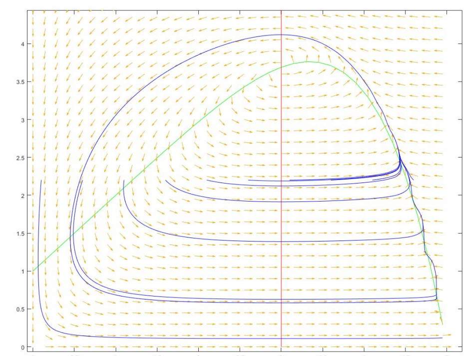


(c) $\theta = 3$

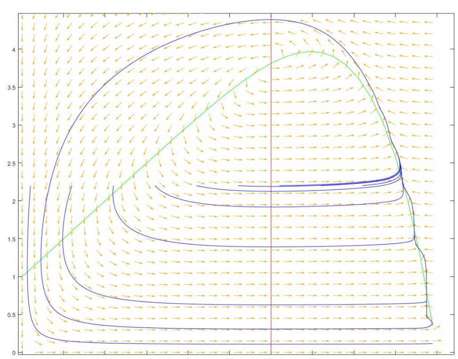
Figure 5: θ that have stable equilibrium



(a) $\theta = 4$



(b) $\theta = 5$



(c) $\theta = 6$

Figure 6: θ that do not have stable equilibrium

3. Consider dimensionless version of generalist predator and prey model,

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)[g(x,\alpha) - \beta y]$$
$$\frac{\mathrm{d}x}{\mathrm{d}t} = \gamma y\left[1 - \frac{y}{h(x,\delta)}\right]$$

Where

$$f(x) = \frac{x}{1+x}$$
$$g(x,\alpha) = (1+x)(1-\alpha x)$$
$$h(x,\delta) = 1 + \delta x.$$

$$\alpha = \frac{a}{K}$$
$$\beta = \frac{cL}{ar}$$
$$\delta = \frac{ba}{L}$$
$$\gamma = \frac{s}{r}.$$

a) (Zero growth isoclines) Find and dray the prey and predator zero-growth isoclines in the first quadrant of the predator-prey plane. Draw all *reasonable* (qualitatively different, biologically plausible) configurations for your zero-growth isoclines. (Looking for several configurations that differ with respect to a) number of intersections between isoclines, b)the signs of the slope of the prey zero-growth isoclines at these intersections.) What are the directions of the vector fields in each portion of your subdivided phase planes?

Proof. The prey zero-growth isoclines correspond to

$$\frac{\mathrm{d}x}{\mathrm{d}t} = 0$$

that is

$$f(x)[g(x,\alpha) - \beta y] = 0$$

so the prey zero-growth isoclines are

$$f(x) = \frac{x}{x+1} = 0 \implies x = 0$$

$$g(x,\alpha) - \beta y = 0 \implies y = \frac{g(x,\alpha)}{\beta} = \frac{1}{\beta}(1+x)(1-\alpha x).$$

Similarly for the predator zero-growth isoclines we want

$$\frac{\mathrm{d}y}{\mathrm{d}t} = 0$$

that is

$$\gamma y\left[1 - \frac{y}{h(x,\delta)}\right]$$

so they predator zero-growth isoclines are

$$y = 0$$

$$1 - \frac{y}{h(x,\delta)} = 0 \implies y = h(x,\delta) = 1 + \delta x.$$

See attached for pictures of isoclines. ■

b) (Equilibria and Bifurcations) Characterize your equilibria. How many equilibria are there and where are they? What bifurcations do you expect to occur as you change the various (nondimensionalized) parameters in your model?

We have equilibrium at the intersection of the prey and predator zero-growth isoclines. We could have up to 4 equilibrium points.

1) We will have the trivial equilibrium $(0, 0)$ which is unstable.
2) We have where $x = 0$ intersects $y = 1 + \delta x$ which occurs at $(0, 1)$. This equilibrium is stable when it lies above $y = \frac{g(x,\alpha)}{\beta}$ and unstable when it lies below $y = \frac{g(x,\alpha)}{\beta}$. So there is a bifurcation that occurs when we change the value of β. As we vary β across 1 we have isoclines colliding and the stability exchanges so we have a Transcritical bifurcation.
3) We have the intersection of $y = 0$ and $y = \frac{1}{\beta}(1 + x)(1 - \alpha x)$ which corresponds to the root of our quadratic. In the first quadrant this gives $(\frac{1}{\alpha}, 0)$. We have a saddle node at this equilibrium.
4) Depending on the value of β we could have an intersection of $y = \frac{1}{\beta}(1 + x)(1 - \alpha x)$ and $y = 1 + \delta x$. If $\beta \leq 1$ we will get an intersection and $\beta > 1$ we will not get an intersection of these isoclines. If we are in the case where $\beta < 1$ then as we vary δ we can force $h(x, \delta)$ to pass through the peak of the parabola. If $h(x, \delta)$ intersects where $\frac{g'(x,\alpha)}{\beta} < 0$ we have a stable equilibrium and if we intersect where $\frac{g'(x,\alpha)}{\beta} > 0$ then we see limit cycle behavior so we expect a Hopf bifurcation.

   Computation for more precise location of intersection of isoclines in case 4.

$$1 + \delta x = \frac{1}{\beta}(1 + x)(1 - \alpha x) \implies 0 = (1 - \beta) + (1 - \alpha - \beta\delta)x - \alpha x^2$$

$$\implies x_{\pm} = \frac{\alpha + \beta\delta - 1 \pm \sqrt{(1 - \alpha - \beta\delta)^2 + 4\alpha(1 - \beta)}}{2(1 - \beta)}$$

   So the location of the intersection is $x_+ = x^*$ and $y^* = 1 + \delta x^*$.

c) (Easy Stability Analysis) Determine the stability and nature of equilibrium at $(0, 1)$, corresponding to extinction of the starfish, but survival of the predators, using a linearized stability analysis. Be sure to state your Jacobian and eigenvalues. Keep your analysis lean and clean (no ugly algebra).

Proof. Our general Jacobian in terms of our functions f, g, h is

$$J(x, y) = \begin{bmatrix} f'(x)[g(x,\alpha) - \beta y] + g'(x,\alpha)f(x) & -\beta f(x) \\ \gamma y^2 \frac{h'(x,\delta)}{(h(x,\delta))^2} & \gamma\left[1 - \frac{y}{h(x,\delta)}\right] + \gamma y\left[-\frac{1}{h(x,\delta)}\right] \end{bmatrix}$$

Notice that $f(0) = 0, f'(0) = 1, g(0, \alpha) = 1, h(0, \delta) = 1$, and $h'(0, \delta) = \delta$ so

$$J(0, 1) = \begin{bmatrix} (1 - \beta) & 0 \\ \gamma\delta & -\gamma \end{bmatrix}$$

which has characteristic polynomial $p(\lambda) = ([1 - \beta] - \lambda)(-\gamma - \lambda)$. So we have eigenvalues,

$$\lambda_1 = 1 - \beta$$

$$\lambda_2 = -\gamma$$

which gives two real valued eigenvalues. Since $\gamma > 0$ then $\lambda_2 < 0$ so the stability of this equilibrium comes down to if $1 > \beta$, in which case λ_1 is positive and we have a saddle point, or if $1 < \beta$, which means λ_1 is negative and we have a stable sink.

∎

d) (Coexistence) The original analysis for this model made two interesting claims regarding equilibria where predators and prey coexist.

1. Any equilibrium where the predator zero-growth isocline intersects a descending part of the prey zero-growth isocline is stable.

2. Any equilibrium where the (ascending) prey zero-growth isocline is steeper than the predator zero-growth isocline is unstable.

Prove one or the other (or both) of these claims. Keep analysis lean and clean and avoid ugly algebra.

Proof. We will show claim 1 for this system. The major aspect of this proof is the fact that we are along our isoclines so when we plug the equilibrium point into our Jacobian we get massive simplifications. Our Jacobian at the intersection of the isoclines is

$$J(x^*, y^*) = \begin{bmatrix} g'(x^*, \alpha) f(x^*) & -\beta f(x^*) \\ \gamma h'(x^*, \delta) & -\gamma \end{bmatrix}.$$

Let $\frac{\mathrm{d}x}{\mathrm{d}t} = F$, $\frac{\mathrm{d}y}{\mathrm{d}t} = G$, and the corresponding Jacobian be J. We would like to make a statement about stability so we will refer to the Routh-Hurwitz criterion. We want to show that

$$\operatorname{Tr}(J(x^*, y^*)) = \left.\frac{\partial F}{\partial x} + \frac{\partial G}{\partial y}\right|_{(x^*, y^*)} < 0 \text{ and } \det(J(x^*, y^*)) = \left.\left(\frac{\partial F}{\partial x}\frac{\partial G}{\partial y} - \frac{\partial F}{\partial y}\frac{\partial G}{\partial x}\right)\right|_{(x^*, y^*)} > 0.$$

where (x^*, y^*) is the equilibrium point. We are given $\frac{\partial F}{\partial x} < 0$ at (x^*, y^*). Since we are at the intersection of the isoclines, we have that $y^* = h(x^*, \delta)$ so

$$\left.\frac{\partial G}{\partial y}\right|_{(x^*, y^*)} = -\gamma < 0$$

hence $\operatorname{Tr}(J(x^*, y^*)) < 0$. Now we will play the same game with the determinant. Since we are given $\frac{\partial F(x^*, y^*)}{\partial x} < 0$ and by the above we have $\frac{\partial G(x^*, y^*)}{\partial y} < 0$, then

$$\left.\frac{\partial F}{\partial x}\frac{\partial G}{\partial y}\right|_{(x^*, y^*)} > 0.$$

Since $\frac{\partial F}{\partial y} = -\beta f(x)$ and $f(x) > 0$ in the first quadrant then $\frac{\partial F(x^*, y^*)}{\partial y} < 0$. If we can show that $\frac{\partial G(x^*, y^*)}{\partial x} > 0$ then the determinant is positive and we win. Since we are at the intersection of our isoclines we again have that $y^* = h(x^*, \delta)$ so

$$\frac{\partial G(x^*, y^*)}{\partial x} = \gamma h'(x^*, \delta) = \gamma\delta > 0.$$

∎