Exercise 2: The spruce budworm project – Resource dynamics with type 2 or 3 functional response

A famous application of bifurcation theory is the analysis of spruce budworm population dynamics [Ludwig et al. 1978, Qualitative analysis of insect outbreak systems: The spruce budworm and forest, Journal of Animal Ecology]. Spruce budworms are insects that feed on spruce and fir trees in North American forests. Most of the time, spruce budworms are present at low density and cause little damage. Apparently they are effectively held in check by their bird predators. Parasites and harsh weather conditions may also contribute to limiting their growth. But once every few decades there is an outbreak. Spruce budworm populations increase dramatically and substantially damage the forests.

The spruce budworm system consists of three trophic levels: the trees, the budworms, and the birds. However, trees and birds have a much longer generation time than budworm. To understand short-term budworm dynamics, we can therefore assume that tree biomass (related to the budworm's carrying capacity) and bird density are constant. A general model for spruce budworm densities N with logistic growth and bird predation is:

$$\dot{N} = rN\Big(1 - \frac{N}{K}\Big) - \frac{Ce(N)N}{1 + e(N)t_h N}, \tag{1}$$

where r is the intrinsic growth rate, K is the carrying capacity, C is bird density, $e(N)$ is the efficiency of bird predation, and t_h is the handling time. We will analyze this model both for a type 2 functional response and for a type 3 functional response and then compare the results. For all plots, rough hand drawings are fine, but if you like, you can also use mathematica, R, maple or some other software package.

Part 1: Nondimensionalization and Allee effect

- Show that model (1) with a type 2 functional response ($e(N) = e$) can be nondimensionalized as
$$\dot{x} = x(1 - x) - \frac{ax}{1 + bx}. \tag{2}$$
What are the underlying transformations?

- Show that model (1) with a type 3 functional response ($e(N) = e \cdot N$) can be nondimensionalized as
$$\dot{x} = x(1 - x) - \frac{ax^2}{x_0^2 + x^2}. \tag{3}$$
What are the underlying transformations?

- For what combinations of a, b, and x_0 do the population experience an Allee effect? Under what conditions is the Allee effect strong?

Part 2: Bifurcation analysis for type 2 functional response

- Plot logistic growth rate (first part of (2)) and consumption rate (second part of (2)) on the same axes. Sketch the various qualitatively different cases.
- Compute the equilibria and draw two bifurcation diagrams with a as bifurcation parameter, one for $b < 1$ and one for $b > 1$, e.g. 0.75 and 5. What kinds of bifurcations do you find?
- How do the bifurcation values of a depend on b? Plot these curves, but exclude branches that correspond to bifurcation points outside the biological state space. Label the different regions in the (a, b)-plane with the number of stable equilibria and their qualitative biological behavior.

Part 3: Bifurcation analysis for type 3 functional response

- Plot logistic per-capita growth rate ($g(x) = 1 - x$) and per-capita consumption rate ($h(x) = \frac{ax}{x_0^2+x^2}$) on the same axes. Sketch the various qualitatively different cases.
- Based on these curves, make a qualitative sketch of a bifurcation diagram with a as bifurcation parameter and $x_0 < 0.19$. (Actually computing the equilibria requires solving a cubic equation). Don't forget the equilibrium at 0.
- Compute the bifurcation values of a as a function of x_0. To do this, notice that at a bifurcation point $g(x) = h(x)$ and $dg/dx = dh/dx$. Combine these two equations to derive parametric equations $a(x)$ and $x_0(x)$. Plot the corresponding curves in the (a, x_0) plane.
- Label the different regions in the plane with the number of stable equilibria and their qualitative biological behavior.

Part 4: Comparison and biological interpretation

- Compare your results for parts 2 and 3. What are the qualitative differences between the two scenarios? Ludwig et al. (1978) used only one of the functional responses. Guess which one. Hint: Which one fits better to the dynamics described in the introduction?
- Discuss possible causes for an outbreak.
- After an outbreak, what could bring the spruce budworm population back to a lower density?