Math 4MB, winter 2021, midterm

- due in the Dropbox on Avenue to Learn at midnight (11:59) on **Monday March 15**
- please feel free to ask for clarifications from me, but do not discuss the test with anyone else
- open book, open web, open notes, but you **must** indicate all sources (other than class materials) used
- please submit as source (Python notebook or Rmarkdown or Sweave file) + rendered PDF.
- all state variables can be assumed to be ≥ 0, and all parameters can be assumed to be > 0.

The *Lotka-Volterra predator-prey equations* (Figure 1)

$$\frac{dV}{dt} = rV - aPV$$
$$\frac{dP}{dt} = caPV - dP$$

represent the (simplest possible) dynamics of a predator species P eating prey ("victim") species V. For positive parameters they are well known to have a trivial solution ($V = P = 0$) in addition to a *neutrally stable* equilibrium with a surrounding limit cycle. The parameters should be reasonably self-explanatory (c is a unitless *efficiency* parameter that determines how much of the energy from consuming prey can be used by the predators to increase reproduction/decrease mortality).

1. Consider the **L-V equations with prey self-regulation**, where the prey's exponential growth rate is replaced by a logistic term $rV(1 - V/K)$, where K is a carrying capacity.

a. Find all of the equilibria of the system, with their associated stability; show the Jacobian computations; you do **not** need to distinguish saddles from sources/sinks from stable/unstable spirals. (Hint: when evaluating the Jacobian for the non-trivial case, evaluate $\partial g_P/\partial P|_{P=P^*}$ first!)

b. Draw the phase space/nullclines of the system for parameter values in the range that include a non-trivial equilibrium (i.e., all state variables>0). Label all features of interest (equilibria and intersections of nullclines with axes) with their symbolically computed values.

c. Draw the bifurcation diagram of the system, showing the values of P^* and V^* on the y-axis as a function of K on the x-axis.

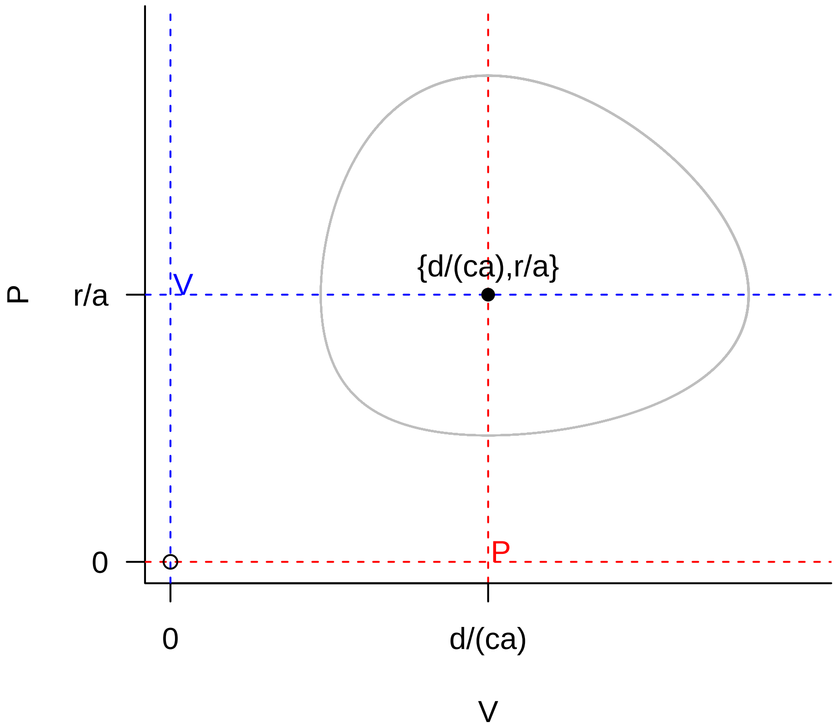

Figure 1: Lotka-Volterra phase plane; example of what is meant by a 'labeled phase plane with nullclines and trajectory'. If necessary you can give information in the caption or in legends, e.g. 'blue dashed line=V-nullcline; intersection of V-nullcline and P axis at $P = r/a$' etc..

d. What are the units of all of the parameters? Write the non-dimensionalized form of the system (hint: pick one parameter with units of time^{-1} and one that has units involving the density of prey).

e. How does this model differ qualitatively from the base Lotka-Volterra model? Can you explain why in terms that would make sense to an ecologist?

2. A **functional response** is a (usually) nonlinear function that describes the rate of prey consumption as a function of prey density. The **Holling type 2 functional response** is the most commonly used functional response: $\Phi(V) = K = aV/(1 + ahV)$, where K is the rate of consumption, V is the initial density/number of prey, a is the *attack rate*, and h is the *handling time*.

a. The data here are from an experiment on the predation of reed-frog tadpoles by dragonfly larvae. `Killed` is the number of tadpoles killed by a fixed number of predators (3) in a fixed time period (14 days); `Initial` is the initial number (equivalent to density) of tadpoles. Plot the data (number killed as a function of initial number) and fit a and h by eye by plotting curves that go through the data. (It may be useful to derive expressions for the initial slope, $d(\Phi(V))/dV|_{V=0}$, and the asymptote, $\lim_{V\to\infty} \Phi(V)$, and use these to get initial estimates of a and h.)

b. Incorporate a Holling type 2 functional response into the Lotka-Volterra predator-prey model (i.e., substitute $\Phi(V)$ above for aV, the per-predator prey consumption rate in the model). Find the conditions for the non-trivial equilibrium to be positive and draw (and label) the nullclines of the system for these conditions.

c. Write down the Jacobian and evaluate the stability of the non-trivial equilibrium (see hint from question 1a).

d. How does this model differ qualitatively from the base Lotka-Volterra model? Can you explain why in terms that would make sense to an ecologist?

3. Combining the two phenomena above (prey self-regulation and predator functional response) gives the **MacArthur-Rosenzweig model**.

a. Write a gradient function in Python/R for the MacArthur-Rosenzweig model.

Check your work by testing it for the parameter values $\{r = 1, a = 1, c = 1, d = 0.5, h = 1, K = 2\}$ and $\{V = 1.1, P = 2.1\}$: you should get the gradient vector `[V=-0.605, P=0.05]`

b. Write down the Jacobian of the MacArthur-Rosenzweig model and write a Python/R function to evaluate it numerically. Write a function to compute the non-trivial equilibrium of the model numerically for specified parameters (first compute the value of V^*, then use that to calculate the value of P^*).

Check that you get a zero (or nearly zero) gradient when you evaluate your gradient function from the previous step at the equilibrium. Make sure you get the following results (or nearly) for the parameters/state combination listed above.

```
##            [,1]       [,2]
## [1,] -0.5761905  0.5238095
## [2,]  0.4761905 -0.5000000
```

c. Find conditions such that the non-trivial equilibrium is positive **or** that the prey-only equilibrium is unstable.

d. Given a specified set of parameters (and limits on the V and P axes), write a function to compute and plot the nullclines. Your function should take three arguments, `p` (a vector/list/tuple of parameter values: if you are working in Python you will have to be careful about the ordering), `xlim` (a two-element vector/list/tuple) and `ylim` (ditto). (Don't worry about the trivial $[P = 0, V = 0]$ nullclines.)

e. Find parameter sets such that the non-trivial equilibrium is (i) stable (ii) unstable (hint: K has a strong effect on stability and won't drive any of the equilibria negative). Draw the phase space (nullclines + a computed trajectory) for each case. Use your functions from above to compute the equilibrium numerically for each parameter set. Check that the result is close to the ending point of the numerical integration for the stable case. Plug the numerical equilibrium values into your Jacobian function and compute the eigenvalues numerically to confirm the stability.

f. Create a numerical bifurcation diagram for the MacArthur-Rosenzweig model by starting from your parameter set that gives a stable equilibrium and gradually increasing the K parameter. For each value of K:

- integrate the differential equations from some starting point for a *transient period*; throw these dynamics away
- integrate the model for another (say) 100 time units, sampling frequently. Find the minimum and maximum values of P over this time.
- store each of these values in a vector/1-D array/list.

Now plot each of these vectors (min and max P) against K, on the same graph.

(the code here may be useful: `sapply()` is a shortcut for running a `for` loop)