AMATH 422/522
Problem set 1

**Working together is absolutely encouraged. Please do not refer to previous years' solutions.**

**For each problem: together with any analysis or explanations, turn in both all code and all relevant plots, labeled and with all line styles, marker sizes etc. adjusted for readability.**

Please note: EG stands for our book, by Ellner and Guckenheimer.

I Iterating Leslie Matrices and the Euler-Lotka Formula.

- Consider an age-structured population model as follows: maximum age $A = 3$. Also: $p_0 = 0.5$, $p_1 = .9$, $p_2 = .95$, $f_0 = 0$, $f_1 = 1$, $f_2 = 5$, $f_3 = .5$. Write a MATLAB model (feel free to modify any code from class) that simulates the state vector $\mathbf{n}(t)$ of individuals of each age $a = 0, 1, 2, 3$. Start with an initial population consisting of 100 individuals of each age. Plot as functions of time (1) the log of the total population size $N(t) = n_0(t) + n_1(t) + n_2(t) + n_3(t)$ and (2) the fraction of individuals in each age, $w_a(t) = n_a(t)/N(t)$, for $a = 0, 1, 2, 3$. Do this from $t = 1$ to $t = T_{\max}$, where $T_{\max} = 50$. Use the `polyfit` (MATLAB) function to fit a first order polynomial to the log $N(t)$ and report the growth rate $\lambda$. *Turn in the code you used for this, again OK if just modified from class.*
- Write down the Euler-Lotka formula for this example, and solve it numerically (use .m or .R files similar to those from class) for the population growth rate $\lambda$. How close are your predictions of $\lambda$ from the Euler-Lotka formulas and from the simulations above? *Turn in the code you used for this.*

II EG Exercise 2.4. Consider the Euler-Lotka equation:

$$G(\lambda) = \sum_{a=0}^{A} \lambda^{-(a+1)} I_a f_a - 1 = 0$$

- Show that $G(\lambda)$ has only one positive real root $\lambda^* \in (0, \infty)$. We outlined the proof in class, but now I want you to show your work. Hint: compute the derivative and the limits of $G(\lambda)$ as $\lambda \to 0^+$ and $\lambda \to \infty$, then make an argument to show that there is only one solution.
- Show that the eigenvector $(n_0, n_1, \ldots, n_A)^T$ associated with $\lambda^*$ has all positive entries.
- **Required only for graduate students. But undergrads are encouraged to try!** Consider the general Leslie matrix

$$L = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_A \\ p_0 & 0 & & \cdots & \\ & p_1 & 0 & & \\ \vdots & & \ddots & \ddots & \\ & & & p_{A-1} & 0 \end{bmatrix}.$$

Show that the Euler-Lotka formula is in fact the characteristic polynomial of $L$, i.e. $G(\lambda) = |L - \lambda I|$. Hint: one way to do this is using row-reduction. What does this imply about solutions to the difference equations $\mathbf{n}(t+1) = L\mathbf{n}(t)$?

III Taken with modifications from EG Ex 2.12. According to Lande (1988), females of the northern spotted owl begin breeding at age a=3 and are estimated to have an average of 0.24 female offspring until they die ($f_a = 0.24$ for $a \geq 3$). The survival probability from birth to age 3 is estimated to be 0.0722, and the annual survival probability of adults ($p_a$ for age $a = 3$ to $a = 49$) is 0.942. In our model we will take the maximum age $A = 50$. (These values refer to age-structured conventions, so newborns are age 0).

The owl has been controversial in our region, because of the conflict of interest between the need for old-growth forests as habitat, and the interest of logging companies in harvesting those forests.

- (a) We told you that $I_3 = p_0 p_1 p_2 = 0.0722$ but not the values of the individual $p$ values. That is because any choice of these individual $p$ values with the same product will yield the same long-term population growth rate ($\lambda$, from class). Why is this true?
- (b) Construct the projection matrix for the population.
- (c) Compute the long-term growth rate $\lambda$ for the population.
- (d) [Note, you'll probably want to save this problem for the very last of the whole HW, as it uses the final lecture from the unit.] Compute the matrix of elasticities for your projection matrix. Is the elasticity for fecundity values $f_a$ the same for all ages $a$? Is the elasticity for annual survival probabilities values $p_a$ the same for all ages $a$? Give an intuitive explanation for your findings in two to three sentences, and state one possible implication for management plans.

IV EG Exercise 2.15. HOWEVER: modify the rule they state there so that can never get a negative number of individuals: $n_a(t+1) = [An(t) - h]_a$ if $[An(t) - h]_a \geq 0$ and $n_a(t+1) = 0$ otherwise, where the subscript means take the $a^{th}$ element. Note, you'll need to look at Ex. 2.13 to get the $A$ matrix you need to get started.

One approach to this problem by numerical simulation of the stated dynamical rule and testing different $h$ values — one possibility is a for loop and logical operations to automate testing of a large number of values. Or you can try and find $h$ analytically.

V **MATLAB programming – tools and tips:** Read through, and practice where necessary, the provided sheet of MATLAB tools and tricks. Make sure you know how each one works. Write down, explain, and turn in two additional tips or tools that you have found helpful.

VI **What's the point of all of this / project warmup:** EG Exercise 1.1. finding a paper. Note: whatever paper you choose does NOT commit you to anything, project-wise. This is just to get us started in thinking about dynamical modeling in biology problems that we personally care about! NOTE – you need to turn in the writeup requested in this Exercise 1.1 of our book for this problem!

Some suggestions as example papers (OK to choose one of these, too):

- Li and Anderson 2009, The Vitality model: a way to understand population survival and demographic heterogeneity, Theoretical Population Biology.
- Ma, Trusina, El-Samad, Lim, Tang. Defining Network Topologies that can achieve biochemical adaptation. Cell 2009 138(4) 760-73. network topologies. Ordinary differential equation model with three nodes. Few assumptions, but seems to come to strong conclusions.)
- Pedraza and Paulsson, Effects of molecular memory and bursting on fluctuations in gene expression, Science 319(5681), 339-343.
- Wakamiya, Sarah, Roy, Charlotte 2009. Use of monitoring data and population vitality analysis to inform reintroduction decisions: perigrine falcons in the midwestern US. Biological conservation 142: 1767-1776.
- Prado, Kerr, 2008. Evolution of restraint in bacterial biofilm under nontransitive competition. Evolution 62-3, 538-548.
- J. C. Panetta. A Logistic Model of Periodic Chemotherapy. App. Math. Letters, Vol 8, 1995.
- Althaus, C. Estimating the Reproduction Number of Ebola Virus during the 2014 Outbreak in West Africa, PLOS Outbreaks, 2014.
- Your choice! The book and your fellow students will have more great options.