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Biological Physics II

Problem Set 2

Solutions were to be handed in before 12:00 noon on Wedenesday, May 5, 2021.

2. Predator-prey Dynamics

3+8+5+7+5+2=30 points

Consider a prey population of size N and a predator population of size P, with the dynamics given by

$$\begin{aligned} \frac{dN}{dt} &= N\big(r(1-\frac{N}{k}) - k\frac{P}{N+p}\big) \\ \frac{dP}{dt} &= sP(1-k\frac{P}{N}), \end{aligned} \tag{2.1}$$

where all parameters are positive.[0]

a) Find a transformation that allows us to rewrite the above equation in terms of dimensionless variables and parameters as

$$\frac{du}{d\tau} = u(1-u) - \frac{auv}{u+d}; \quad \frac{dv}{d\tau} = bv(1-\frac{v}{u}). \tag{2.2}$$

Solution: The transformation is

$$\tau = rt, u = \frac{N}{k}, v = P$$

and

$$a = \frac{1}{r}, b = \frac{s}{r}, d = \frac{p}{k}.$$

b) Find the fixed points of Eq (2.2) with positive u, v. You should find only one. Write down the condition involving a, b, d that makes the fixed point stable[1]. Using this, show that the fixed point is always stable for $a < \frac{1}{2}$.

Solution: The only such solution (u^*, v^*) is

$$u^* = v^* = \frac{1-a-d+\sqrt{(1-a-d)^2+4d}}{2}$$

[0]You may have noticed that the dimension of k is inconsistent in these equations. Originally, I had intended to use N/K instead of N/k in the first term in the first equation, and h instead of k in the second equation. With these, one would have $u = \frac{N}{K}$, $v = \frac{hP}{K}$, $a = \frac{k}{hr}$ in part a). Erroneously, both K and h were denoted k in the problem. However, it is still possible to arrive at eq (2.2) from eqs (2.1) with the transformations given in the solution.

[1]From this exercise onwards, we will reserve the word *stable* for fixed points where all eigenvalues of the Jacobian have negative real parts, consistent with the lecture notes.

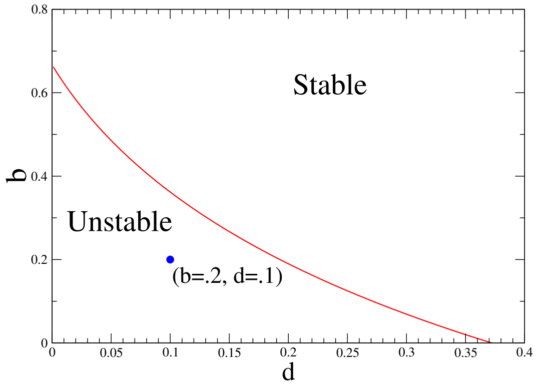

Figure 1: The boundary in the $b-d$ plane for $a = 1.5$.

The Jacobian matrix can be shown to be

$$J = \begin{bmatrix} u^*\left(\frac{au^*}{(u^*+d)^2} - 1\right) & -\frac{au^*}{u^*+d} \\ b & -b \end{bmatrix}.$$

Stability requires the real parts of the eigenvalues to be negative, which for a two-dimensional system is equivalent to the conditions $trJ < 0$, $det\ J > 0$. Here, these imply

$$u^*\left(\frac{au^*}{(u^*+d)^2} - 1\right) - b < 0; \quad 1 + \frac{a}{u^*+d} - \frac{au^*}{(u^*+d)^2} > 0.$$

These conditions, together with the expression for u^* derived above, give the complete stability condition. In fact, using the expression for u^* and the fact that u^* is a zero of the right hand side of the first equation in (2.2), it is easily shown that $det\ J > 0$. Therefore the stability condition reduces to only the first inequality above. Again using the expression for u^* and its aforementioned mentioned property in the first inequality, the final stability condition is found to be

$$b > \left(a - \sqrt{(1-a-d)^2 + 4d}\right) \frac{\left(1 + a + d - \sqrt{(1-a-d)^2 + 4d}\right)}{2a}.$$

c) For $a = 1.5$, numerically plot the boundary line in the $b-d$ plane that separates the regions of stability and instability of the fixed point. Indicate the two regions. What is the value of d in this case above which the fixed point is always stable? Find it analytically and check it with your numerical plot.

Solution: See fig 1. The required threshold for d is found by setting the first factor on the right hand side of the above inequality to zero with $a = \frac{3}{2}$. This leads to the equation

$$d^2 + 5d - 2 = 0,$$

with the positive solution $d = \frac{\sqrt{33}-5}{2} \simeq 0.372$.

d) For $a = 1.5, b = 0.2, d = 0.1$, use the numerical result in the previous part to show that the fixed point is not stable. Numerically find the (approximate) fixed point (u^*, v^*). Sketch with pen and paper the nullclines of the system (2.2) for these parameters. Mark the fixed point, and draw arrows on the nullclines to indicate the local direction of flow. This system has a limit cycle with the fixed point lying within it. Using the arrows on the nullclines, determine whether the cycle is traversed in the anticlockwise or clockwise direction.

Solution: From the solution for the fixed point, the numerical value for the fixed point is approximately $u^* = v^* \simeq 0.136$. Fig 1 shows that the fixed point must lie in the unstable region. Fig 2 shows the nullclines of the system corresponding to $h = 0$ and $g = 0$, where

$$h = u(1-u) - \frac{auv}{u+d}; \quad g = bv\left(1 - \frac{v}{u}\right).$$

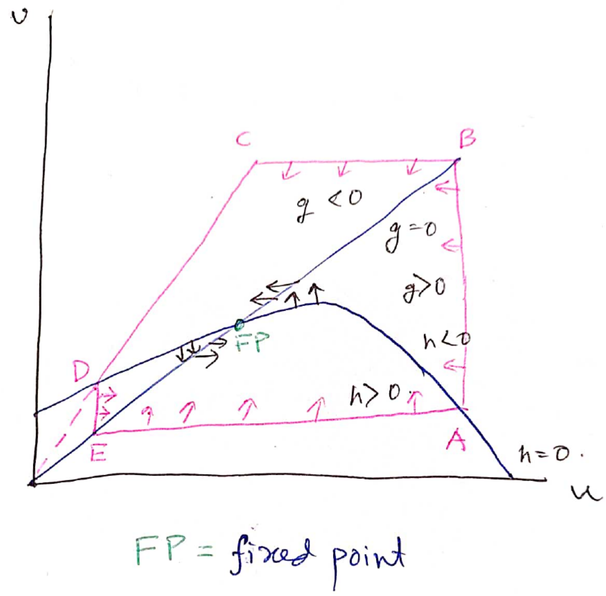

Figure 2: The nullclines of the system, and the boundary Ω containing the attractor in red.

The cycle is in the anticlockwise direction, as shown by the black arrows.

e) For the parameters in the above part, numerically integrate (2.2) with any initial condition (where $u, v > 0$) and for sufficient time such that convergence to the limit cycle can be observed. Plot $u(\tau)$, $v(\tau)$ as well as the orbit in the $u-v$ plane. Numerically average the values of u and v on the limit cycle, and compare the values to the numerically obtained value of the fixed point. Do they agree?

Solution: See fig 3. The numerical averages for u and v on the limit cycle are approximately 0.33 and 0.15 respectively. They do not agree with the value of the fixed point.

f) Based on the above observations, do you expect the system (2.2) to have an underlying integrable structure like the Lotka-Volterra equation? Explain in words.

Solution: It is not expected. A Hamiltonian system cannot have attracting fixed points or limit cycles. It is precluded by the property of phase-space volume conservation (a finite volume around a fixed point or a limit cycle has to shrink to zero volume asymptotically).

g) **Bonus problem:** In part d), you were told that the system has a limit cycle in some parameter range. Here we *prove* its existence. The first step is to find a confined region in the $u-v$ space with a boundary Ω such that the flow everywhere on Ω points inwards into the region. This indicates that there must be an attractor inside the region. The Poincaré-Bendixson theorem[2] states that in two dimensions, such an attractor can only be a fixed point or a limit cycle. Since the fixed point in this case is unstable, there must be a limit cycle attractor within the region. The problem then boils down to constructing an appropriate closed curve Ω. Formally, you need to show that $\hat{n} \cdot \hat{f} > 0$ on your chosen Ω, where $\hat{n}$ is the inward normal vector to the curve Ω, and $\hat{f} = (\frac{du}{d\tau}, \frac{dv}{d\tau})$.
Hint: The region enclosed by Ω must contain the fixed point. In this problem, it helps if Ω is a polygon. Moreover, choose as many of its sides to be horizontal or vertical as possible such that the direction of flow can be checked easily from the sign of the right hand side of the equations in (2.2).

Solution: Refer to fig 2. The curve Ω is the polygon marked in red. The flows on the horizontal segments CB and EA are easily checked to be inward from the signs of g, whereas those at the vertical segments ED and AB are checked to be inward from the signs of h, as given in the figure. The difficult bit is the

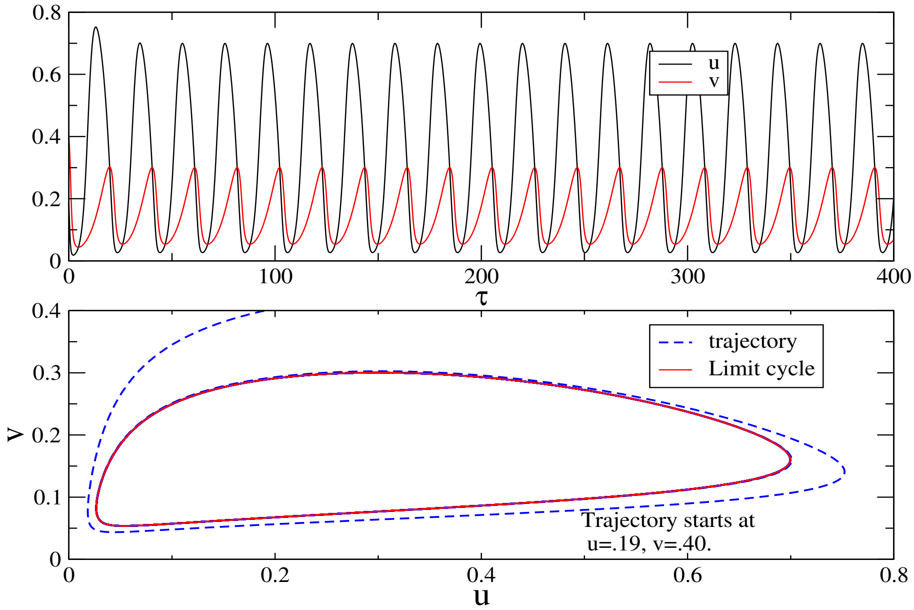

Figure 3: The trajectory leading to the limit cycle attractor.

segment DC. The segment lies on the line $v = cu$, where the slope $c > 1$. The inward vector normal to DC is $\hat{n} = (\frac{c}{\sqrt{1+c^2}}, -\frac{1}{\sqrt{1+c^2}})$. Then, on DC,

$$\hat{n} \cdot \hat{f} = \frac{1}{\sqrt{1+c^2}}\left[uc(1-u) - \frac{au^2c^2}{u+d} + buc(c-1)\right].$$

Now we can make c very large, with the consequence that the segment DC approaches the v axis (the flows on the horizontal and vertical segments remain inward). For large c, we have $u \sim O(\frac{1}{c})$ on DC, and $uc \sim O(1)$. Thus, for large c, the last term in the square brackets above dominates, and it has a positive sign. This shows that for sufficiently large c, the flow on DC is inward.

[2]Look into the books by Strogatz or Hofbauer and Sigmund for more details on the theorem. For the present exercise, however, the information given in the question should be sufficient.