Math 19a - Midterm I, Readings Review

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This is intended to serve as a quick reference guide to remind you of the key points of the readings. It does not substitute the actual readings in preparation for the exams. Note that the purpose of the readings is to show real biological models which use the mathematics we discuss in lectures. The point is to understand the nature of these models (where they come from, what their terms mean biologically, etc), methods for solving or analyzing them have already been discussed in the lectures and chapters preceding the readings.

1 Reading 2.1: HIV-1 Dynamics in Vivo: Virion Clearance Rate, Infected Cell Life-Span, and Viral Generation Time

This was the first article to show us a system of differential equations representing a real biological phenomenon. The authors created two different models for the evolution of the virus with and without treatment with ritonavir. Ritonavir is a HIV protease inhibitor, which disables the protease from cleaving the single viral protein produced from the host cell's machinery and thus creating the viral enzymes.

In this article T denotes the total number of T-lymphocytes, which in this paper is assumed to be a constant, T^* - the number of infected cells, V - the total number of virions. In the first model, there is no ritonavir, so all viruses are infectious.

$$\frac{dT^*}{dt} = kVT - \delta T^* \tag{1}$$

$$\frac{dV}{dt} = N\delta T^* - cV \tag{2}$$

T^* cells are produced by the infection a healthy T-cell, the production rate is hence proportional to the total number of viruses (the more of them, the more likely it is a cell to get infected) and the number of $T-$cells, with a proportionality constant k, which gives the positive term kVT in equation (1). The death rate of infected cells is δ, which gives us the term $-\delta T^*$. Viruses are produced (born) from infected cells. Denote by N the average number of viruses that an infected cell produces over its lifetime. It can be shown (you don't need to know that for the exam), that the average lifetime of a T^* cell is $1/\delta$ (1/"death rate"), so the average number of newly produced non-infectious viruses per given time (dt) is "total number of produced"/"cell's lifetime" times the number of T^*-cells , i.e. $N/(1/\delta)T^* = N\delta T^*$. This is the production rate, the positive term in equation (2). We need to subtract the number of viruses that died (eaten by macrophages, or entered a host cell), which is an exponential decay with death rate c, i.e. the term $-cV$.

After the protease inhibitor (ritonavir) has taken effect, infected T-cells can produce only non-infectious virions. Here V_1 is the number of infectious virions and V_{NI} the number of non-infectious virions. The authors propose the following model for the dynamics of cells and viruses:

$$\frac{dT^*}{dt} = kV_1T - \delta T^* \tag{3}$$

$$\frac{dV_1}{dt} = -cV_1 \tag{4}$$

$$\frac{V_{NI}}{dt} = N\delta T^* - cV_{NI} \tag{5}$$

This system is a modified version of the previous, as you would notice equations (1) and (2) look very much like (3) and (5). Equation (3) is the same as equation (1), where we only changed V for V_1, since in this case V_1 are the only infectious viruses. Assuming that ritonavir is 100% effective means that every single T cell of the patient contains ritonavir and ritonavir itself always inhibits the viral protease, so the infected cell produces only non-infectious viruses (those without functional viral enzymes). Therefore nothing is producing infectious viruses anymore, hence V_1 follows an exponential decay with death rate c, giving equation (4). Equation (5) shows how the number of non-infectious viruses is changing and it follows the same logic as for equation (2): non-infectious viruses are produced exactly the same way the viruses in (2) were produced - from infected T^* cells with a rate of $N\delta$ per time per T^*-cell. We assume that non-infectious viruses do not appear any different than infectious ones, and so have the same death rate - c, giving us the second term $-cV_{NI}$.

Note that solving this systems is not difficult - you can readily solve equation (4), being just an exponential decay. After you found V_1, you can substitute it into equation (3) and use integrating factors to solve for T^*. Finally substitute your solution for T^* into equation (5) and again using integrating factors find V_{NI}.

2 Three Fisheries papers

Here the issue is to determine whether fish populations exhibit depensation. Depensation is the effect on a population (or stock) whereby, due to certain causes, a decrease in the number of mature individuals (or just total population) leads to reduced survival and production of eggs or offspring. The cause may be either predation levels rising per offspring (given the same level of overall predator pressure), or the Allee effect, which is the reduced likelihood of finding a mate in a big territory. Mathematically, if we are modeling a population p, we can find depensation if there is a certain positive value, denoted by D, such that if p becomes less than D, then p goes to 0 (dies out).

For this paper we first consider the logistic model with p denoting the fish population:

$$\frac{dp}{dt} = kp(1 - \frac{p}{N}),$$

which does not model depensation - N is the only stable steady state, no matter how low p falls (and is still positive), it will grow back to the carrying capacity N.

Then we consider the modified logistic model:

$$\frac{dp}{dt} = kp(1 - \frac{p}{N})(\frac{p}{M} - 1),$$

with $0 < M < N$. We analyze its behavior (following the "recipe" in Chapter 3) and see that the stable steady states are 0 and N and M is an unstable steady state. So if p falls bellow M, $p < M$, then p will approach the 0 steady state, meaning the population dies out. Here there is depensation with level $D = M$.

The third paper (reading 3.3) discusses a Beverton-Holt model, which is a discrete model. We measure time by the number of generations so far (denoted by n). Fish are divided into two groups - spawners (mature fish producing spawn) and recruits (fish which developed from the spawn). Denote by R_n the number of recruits and S_n - the abundance of spawners at generation n. So the recruits R_n will grow into spawners and the spawners will produce spawn and hence recruits. The n-th generation recruits will grow up (survive) with some probability, c, so

$$S_n = cR_n$$

.

On the other hand, the number of recruits which grow from the spawner's spawn is

$$R_{n+1} = \frac{\alpha S_n^{\delta}}{1 + \frac{S_n^{\delta}}{K}}.$$

Such model can be analyzed by graphing the functions $S = cR$ and the Beverton-Holt function $R = \frac{\alpha S^{\delta}}{1+\frac{S^{\delta}}{K}}$ in the $R-S$ plane and finding R_n and S_n successively (recursively) from each other by finding the intercept with the graphs. (Note that you are not responsible to know this technique) It is important to note that if $\delta = 1$ there is only one stable steady state at $R = (\alpha - 1/c)K$ and $S = (\alpha c - 1)K$, so no matter how low the spawner population drops it will still return to this positive stable steady state.

However, if $\delta > 1$, then we have 3 steady states, with (0,0) a stable one and the others positive (these are the 3 intersection points of the two graphs). The system then exhibits depensation. This is why the parameter δ controls the depensation.

3 Left Snails, Right Minds

The issue in this paper is that there are many more snails with right curling shells than snails with left curling ones. Even though the article does not analyze this issue, it is discussed in the commentaries (2.2 and 5.1).

The first commentary proposes a model for the ratio of left snails over the entire snails population. The model is based on very simplified assumptions: A pair of two left snails produces only left offspring, a pair of left and right produces left offspring with 50% probability, etc. It also appears that the choice of partner of a certain type is only proportional to the abundance of such type (Note that the implication in the first paragraph on page 23 is wrong). With this assumptions the left offspring will be proportional to the number of (left,left) pairs plus half the number of (left,right) pairs. If we denote the left population by L and the right by R, then by the assumptions $\frac{dL}{dt} = \beta(L^2 + 1/2RL) - \gamma L$ - the change in left population is equal to the new progeny minus the number of death snails ($-\gamma L$). We can write a similar equation for $\frac{dR}{dt}$ with the same constants (assuming no practical advantage of one type over the other). The ratio of left snails, p is by definition $p = \frac{L}{L+R}$, so we obtain an equation for $\frac{dp}{dt}$ by finding $\frac{d\frac{L}{R+L}}{dt}$ using the quotient rule (you are not responsible for this derivation). At the end we arrive at the equation

$$\frac{dp}{dt} = \alpha p(1-p)(p - \frac{1}{2}),$$

which is the first model. Analyzing its behavior using Chapter 2's techniques we notice that 0 and 1 are stable steady states and 1/2 is unstable. So if $p < 1/2$, then p will approach 0, i.e. the left snails population will become very small compared to the right snails' one, so this model does predict the phenomenon of too little left snails.

The second model that applies to this situation is the competing species model of chapter 5:

$$\frac{dR}{dt} = (R - R^2) - aRL \tag{1}$$

$$\frac{dL}{dt} = (L - L^2) - aRL. \tag{2}$$

Here, again, R and L are the populations of right and left snails. We assume this time that left and right snails do not interbreed, but compete for the same resources. The terms in parenthesis are the usual logistic growth equation of a population, i.e. if there was no competition between them, the right snails' population would follow the equation $\frac{dR}{dt} = R(1-R)$, and similarly for the left. The terms $-aRL$ indicate the interaction (in this case competition) between the species with the parameter a being a crude measure of relative interaction. This equation is analyzed in Chapter 5 using phase plane analysis.

It is important to note that there are two different cases depending on $a < 1$ or $a > 1$. If $a < 1$, analysis there is only one stable equilibrium at $(\frac{1}{a+1}, \frac{1}{a+1})$, so in this case the populations of left and right snails will both approach the same value of $\frac{1}{a+1}$ and so neither will prevail upon the other. This case does not model our situation. However, when $a > 1$ there are two stable equilibria, at $(1, 0)$ and $(0, 1)$, so depending on the initial conditions (R, L) will approach one of them, i.e. one kind of snails will go extinct while the other one prevails. This case is the one that models our situation.

4 Red grouse and their predators

This article considers the fact that the population of red grouse on the Langholm moor has been steadily decreasing since 1990, which coincides with the introduction of birds of prey (raptors, harriers and peregrines). Before that the grouse have been hunted only by hunters and have exhibited a cyclic (periodic) growth with period of 6 years, similar to the example of hares and lynx in our first lecture.

The model in this case is the Lotka-Volterra predator-prey model. Let x be the number of grouse and y the number of hunters. Before 1990 the model representing the situation is:

$$\begin{aligned}\frac{dx}{dt} &= (a - bx - cy)x = x(a - bx) - cyx \\ \frac{dy}{dt} &= (-d + ex)y = -dy + exy.\end{aligned}$$

Here, similarly to the competing species model, the term $x(a-bx)$ shows the logistic growth of the population if left on its own (without predators) and the term $-cyx$ reflects the portion of the population taken by predators. In the second equation $-dy$ shows that if there was no prey, the predators would die out, exy denotes their increase from the presence of food (prey). Since before 1990 the solutions were cyclic, we must have that $b = 0$. After 1990 other predators are introduced, who do not feed only on grouse, so for the purpose of this model are assumed constant. They take away a constant portion of the grouse population, a term $-hx$ to be added to the first equation, so our model becomes:

$$\begin{aligned}\frac{dx}{dt} &= (a - h)x - cyx \\ \frac{dy}{dt} &= (-d + ex)y.\end{aligned}$$

Analyzing this model using phase plane analysis, we see that if $h < a$, then the solution circles around the equilibrium at $(\frac{d}{e}, \frac{a-h}{c})$, the same picture as on Figure 6.3 on page 93. In this case x does not go to 0, so the grouse population doesn't die out and this case doesn't model our situation. In the case of $h > a$, however, using the same analysis one sees that $(0, 0)$ is the only non-negative stable equilibrium, so the grouse population dies out as is the case.

5 Better Protection of the Ozone Layer

This article develops a new model that asses how much damage (depletion) potential a chemical has. The way chemicals damage the ozone layer is by dissociating under solar radiation and realizing free atomic chlorine or bromine, which reacts with ozone molecules and destroys them

$$Cl + O_3 \to ClO + O_2$$

$$ClO + O \to Cl + O_2.$$

The damage (ozone depleting potential, ODP) is measured by the amount of chlorine released from the chemical. Formally, if $C(t)$ is the amount of free chlorine in the stratosphere at time t, the damage of chemical X is measured by its "integrated chlorine loading", i.e. $IC_X(t) = \int_0^t C(\tau)d\tau$, divided by the same thing for chlorofluorocarbon (F-11), i.e. ODP of X is $IC_X(t)/IC_{F-11}(t)$. In order to determine the amount of chlorine released, the authors propose the following model:

$$\begin{aligned}
\frac{dB_\tau}{dt} &= -\frac{B_\tau}{L_\tau} - \frac{B_\tau f - B_S}{\tau_t} \\
\frac{dB_S}{dt} &= -\frac{B_S}{L_S} - \frac{B_S - B_\tau f}{\tau_t} \\
\frac{dC}{dt} &= -\frac{C}{\tau_t} + \frac{B_S}{L_S}
\end{aligned}$$

Here B_T stands for the amount of the undissociated chemical (in other words, the bound chlorine) in the troposphere, B_S - the amount of undissociated chemical in the stratosphere and C - the free (dissociated, atomic) chlorine in the stratosphere. The terms $-\frac{B_T}{L_T}$ and $-\frac{B_S}{L_S}$ represent the dissociation of the chemicals under solar radiation in the specific part of the atmosphere. Similarly to the HIV paper, L_T and L_S turn out to be the average lifetimes of the chemicals in the troposphere, resp stratosphere.

The term $-\frac{B_\tau f - B_S}{\tau_t}$ represents the exchange of tropospheric and stratospheric chemicals due to air flowing from one part of atmosphere to the other. More specifically, $\frac{B_S}{\tau_t}$ is the amount of stratospheric chemical entering the troposphere due to air convection. Here τ_t is actually the average turnover (exchange) time for air to move from stratosphere to troposphere and vice versa. Then $-\frac{B_T f}{\tau_t}$ is the amount of tropospheric chemical leaving the troposphere to go into the stratosphere with the general air flow. The factor $f = 0.15/0.85$ denotes the proportion of total amount of air in stratosphere over the total amount of air in troposphere and it figures in the term in order to account for the difference of air density in the different parts of atmosphere. The same reasoning explains the second equation.

The third equation models the rate of change of free chlorine in the stratosphere - new chlorine in the stratosphere is obtained exactly from the dissociation of the chemical in the stratosphere, which is $\frac{B_S}{L_S}$. Chlorine is lost by moving down to the troposphere with the air flow, which accounts for $-\frac{C}{\tau_t}$. Note here that the rate at which any gas moves from stratosphere to troposphere is the same as the air flow rate in this direction, namely $\frac{1}{\tau_t}$. This system can be solved easily as a linear system by rewriting the first two equations in vector-matrix form:

$$\vec{v} = \begin{pmatrix} B_\tau \\ B_S \end{pmatrix} \text{ and } A = \begin{pmatrix} -\frac{1}{L_\tau} - \frac{f}{\tau_t} & \frac{1}{\tau_t} \\ \frac{f}{\tau_t} & -\frac{1}{L_S} - \frac{1}{\tau_t} \end{pmatrix}$$

and after solving for B_T and B_S, plug the solution for B_S in the third equation and use integrating factors to solve for C.

6 Hopes for the Future: Restoration Ecology and Conservation

This article discusses the issue of converting the natural habitats into agricultural and industrial areas and ultimately into degraded land. They propose solutions for restoring the abandoned (unused) land via restoration ecology. Proper application of these tools require understanding of how human population growth and land changes interact with natural recovery processes. They propose the following model:

$$\frac{dF}{dt} = sU - dPF \tag{1}$$

$$\frac{dA}{dt} = dPF + bU - aA \tag{2}$$

$$\frac{dU}{dt} = aA - (b+s)U \tag{3}$$

$$\frac{dP}{dt} = rP\left(\frac{A - hP}{A}\right). \tag{4}$$

Here F stand for the total area of pristine forest habitat, A is the total area of agricultural land, which after exploitation becomes unused land denoted by U, P denotes the human population. The more people there are, the bigger the need for new agricultural land created by destroying forests, and this accounts for the negative term $-dFP$ in equation (1). However, forest can grow back on unused land with a constant rate s, which gives the positive term sU in equation (1). Agricultural land is created from forests (the same term, $-dPF$ as in equation (1)), some of it could be restored from unused land (cU) and it becomes unused land at a rate of a, giving $-aA$. Equation (3) just accounts for the fact that unused land is created only when agricultural land becomes unused, aA, and is lost by becoming forests or agricultural land ($-(b+s)U$). The last equation is a logistic growth equation for the human population, with h being the land necessary to support one person and so the maximum (carrying capacity) number of people that can be supported by the total agricultural land is A/h.

Note that $1/a$ is again as in the HIV paper the average lifetime of the agricultural land. Similarly $1/s$ is the average time for unused land to turn into forest and $1/b$ - time to turn into agricultural land.

Notice that the total area (forests, agricultural land and unused land) is always the same, so $F+A+U = F_0$, where F_0 is the initial total area (at $t = 0$ everything is a forests) - constant. This is also visible from the equations - $\frac{dF}{dt} + \frac{dA}{dt} + \frac{dU}{dt} = 0$. So we actually have a 3-dimensional system, 3 variables (F, A and P). In order to find the equilibrium of this system, we just need to set all derivatives to 0, i.e. $\frac{dF}{dt} = 0$, $\frac{dA}{dt} = 0$ etc, and solve the 4 equations ($0 = sU - dPF$, $0 = dPF + bU - aA$, etc), using the fact that $F + A + U = F_0$.