Problem Set 10 (70 points)

1 Neutral cycles in Lotka-Volterra model (10 points)

$$\frac{du}{dt} = u(1-v)$$
$$\frac{dv}{dt} = \alpha v(u-1)$$

Here we have the non-dimensionalized version of the Lotka-Volterra Model. In class, it was claimed that the oscillations were neutrally stable, but that in principle the non-linear terms could result in either a stable spiral or a limit cycle oscillation. In this problem you will prove that the oscillations are neutrally stable orbits.

a. Demonstrate that the fixed point in the (linearized) Lotka-Volterra Equation is neutrally stable.

b. Show that the function H is a constant of motion in this system

$$H = \alpha u + v - ln(u^{\alpha} v) = \alpha[u - ln(u)] + [v - ln(v)]$$

c. Solutions of the equations require that $H > H_{min}$. Find H_{min}.

d. Demonstrate that the prey size $u(t)$ is bounded by u_{min} and u_{max} for a fixed H.

e. Explain why the existence of a constant of motion, together with the bound, implies that the predator and prey undergo closed orbits.

f. On the phase plane (u, v) plot solutions for two different H_1 and $H_2 (H_1 < H_2)$, assuming $\alpha = 2$. Which direction (clockwise or counterclockwise) does the system follow?

2 Noise induced oscillations in predator-prey dynamics (24 points)

As we saw in class, the Lotka-Volterra predator-prey dynamics leads to neutral cycles. In this problem, we will see how, in a predator-prey system that has a stable fixed point, demographic fluctuations alone can cause sustained oscillations[1].

Consider a system of n predator and m prey individuals, with a total carrying capacity (prey + predator) N. We will denote the state of the system as $S(n, m)$. The following processes occur

[1]Predator-Prey Cycles from Resonant Amplification of Demographic Stochasticity, Phys. Rev. Lett. 94, 218102

in this population:

$$\begin{aligned}
S(n,m) &\xrightarrow{d_1 n} S(n-1,m) \\
S(n,m) &\xrightarrow{2b\frac{m}{N}(N-n-m)} S(n,m+1) \\
S(n,m) &\xrightarrow{2p_2\frac{nm}{N}+d_2 m} S(n,m-1) \\
S(n,m) &\xrightarrow{2p_1\frac{nm}{N}} S(n+1,m-1)
\end{aligned}$$

The expressions on top of the arrows are the rates at which these processes occur. We will call this the individual based model, as opposed to the deterministic model that you will derive below.

a. [3 points] What do each of the processes, and the parameters d_1, d_2, p_1, p_2, b represent?

b. [7 points] Master equation formulation:

1. Write down the master equation for this system.
2. Show that the normalized means, $f_1 = \frac{<n>}{N}$, $f_2 = \frac{<m>}{N}$, satisfy the equations shown below. You can do this by multipling $\frac{dP(n,m)}{dt}$ by n, m respectively, and then summing over all n, m for each case. Assume higher order correlations are negligible, i.e. $\langle nm \rangle = \langle n \rangle \langle m \rangle$. What are r, K, p in terms of the parameters defined above?

$$\begin{aligned}
\frac{df_1}{dt} &= 2p_1 f_1 f_2 - d_1 f_1 \\
\frac{df_2}{dt} &= r f_2 \left(1 - \frac{f_2}{K}\right) - 2p f_1 f_2
\end{aligned}$$

Notice that this equation is like the Lotka-Volterra equations incorporating an effective carrying capacity K for the prey. We will call this the deterministic model.

c. [6 points] Stability analysis:

1. What are the fixed points in the deterministic model? What is their stability?
2. Does the system oscillate (limit cycle or neutral) about any of the fixed points?
3. If the interior fixed point ($f_1, f_2 \neq 0$) is neutrally stable, what is the oscillation frequency? If not, what is the frequency of transient oscillations around the fixed point?

d. [10 points] **COMPUTATION** Stochastic simulations of the individual based model:

1. Set $d1 = 0.1, d2 = 0.05, b = 0.1, p1 = 0.25, p2 = 0.05, N = 3000$. Will the corresponding deterministic model show transient oscillations with these parameter values? If yes, what is their frequency?
2. The resonant frequencies from the deterministic model amplify demographic noise, so that the frequency of oscillations in the individual based model is close to the frequency of transients you see in the deterministic model. To see this, perform a Gillispie simulation of the individual based model. Plot the timeseries of the prey and predator number as a function of time. Do you see oscillations?

3. Plot the Fourier transform of either the predator or the prey population timeseries, and mark the resonant frequency. Does it agree with part (a) of this subquestion?
4. Now choose the parameters appropriately so that the interior fixed point has purely real eigenvalues and repeat the simulation. Plot the Fourier transform and comment on the result.
5. To see how the amplitude of oscillations scales with the population size, run the above simulations with parameters from part 1 for $N = 300, 3000, 30000$. Plot the amplitude against N on a log-log scale. The slope gives the powerlaw co-efficient β of the scaling relation $A \propto N^{\beta}$. What is β?

3 Critical Transitions: Allee effect and bifurcation diagram (15 points)

For some populations, the per capita growth rate $\frac{1}{N}\frac{d\dot{N}}{dt}$ is maximal at intermediate N. This phenomena is called the Allee effect. The situation may arise when it is difficult to find mates (thus an increase in per capita growth rate with N) when N is small, while competition for resources (thus a decrease in per capita growth rate with N) when N is large. In this problem, let's consider the following model:

$$\frac{1}{N}\frac{d\dot{N}}{dt} = r - a(N-b)^2$$

a. Show that this model captures the Allee effect. Assume $r > 0$, $a > 0$, $b > 0$. Note that we only consider $N \geqslant 0$.

b. Assume $r = 2ab^2$. How many fixed points does the system have? Are the fixed points stable?

c. Due to environmental deterioration, r decreases. Find $r_1^{critical}$ at which the system becomes bistable. Which type of bifurcation does this transition correspond to?

d. If r continues to decrease, find $r_2^{critical}$ at which the system becomes monostable again. What is this monostable state? Which type of bifurcation does this transition correspond to?

e. Find the eigenvalue of the nonzero stable fixed point as a function of r. How does it behave as r approaches $r_2^{critical}$? What does it mean for the recovery time after a small perturbation? How could this possibly be used as an early warning indicator of critical transitions, e.g. an impending population collapse in our system?

f. Plot a bifurcation diagram showing the position of fixed points as a function of r. Mark stable and unstable fixed points.

4 Time is Discrete: logistic map and chaos (9 points)

COMPUTATION The logistic map is a great example of how complex, chaotic dynamics can arise from simple nonlinear equations. The logistical model in population dynamics is a description of population growth in the presence of overcrowding. The differential equation for logistic growth is $\frac{dN}{dt} = rN(1 - \frac{N}{K})$, where N is the population size, r is the rate of reproduction and K is the carrying capacity. In this problem, we will explore its version in discrete time, i.e. a difference equation, the logistic map:

$$x_{t+1} = Rx_t(1 - x_t)$$

a. [2 points] Set $R = 2$, $x_0 = 0.2$. Plot x vs. t for 20 time steps. Then make a similar plot for $x_0 = 0.99$. What kind of behavior do you observe with different initial poplation size ($x_0$between 0 and 1)?

b. [1 point] Set $R = 3.1$, $x_0 = 0.2$. Plot x vs. t for 20 time steps. How is the trajectory different from the previous simulation?

c. [1 point] Set $R = 3.5$, $x_0 = 0.2$. Plot x vs. t for 20 time steps. What is the oscillation period now?

d. [2 points] Find a value of R which gives an oscillation period equal to 8.

e. [3 points] In dynamical systems theory, each of these transitions is called a period-doubling bifurcation. However, as we continue increasing R, deterministic chaos occurs.

   Set $R = 4$. Plot x vs. t for 80 time steps, with $x_0 = 0.2$ and $x_0 = 0.2000000001$. Plot the two trajectories on the same graph and compare them. Do you observe "sensitive dependence on initial conditions"?

5 SIS on a Network (10 points)

SIS (Susceptible-Infectious-Susceptible) is an epidemic model in which there are two species: Susceptible (S) and Infectious (I). Let's study this model on a network, where each node of the network is occupied by some individuals.

a. Let's define S_t and I_t as the population densities of susceptible and infectious individuals on the nodes of a random network, at time t. p_I is the probability for a susceptible individual to be infected by a neighboring infectious individual. Show that, on average, the probability P_t for a susceptible individual (randomly picked from the network) to be infected at time t is:

$$P_t = 1 - exp(-p_I I_t \langle d \rangle),$$

   where $\langle d \rangle$ is the average degree of a node, and we assume that the degree follows a Poisson distribution. (Hint: the probability of being infected is one minus the probability of not being infected.)

b. Assume that $I_t + S_t = \rho$ at any time t (in unit of generations). If p_R is the probability for an infectious individual to recover and become susceptible again in a generation, write down the expression for I_{t+1} as a function of I_t.

c. In the infinite-time limit, we can assume that $I_t = I_{t+1} = I_\infty$. Under what condition is $I_\infty = 0$ no longer stable? In this case, a nonzero fraction of the population are infected and the system is in the endemic state. What is the threshold value of ρ that leads to the transition? Comment on how the threshold depends on $\langle d \rangle$.

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8.591J / 7.81J / 7.32 Systems Biology
Fall 2014

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