Math 361 Winter 2001/2002
Assignment 7 (Quiz on Monday, November 19)

1. *Metapopulations and spatial structure I.* Suppose a population lives in an area in which there are a number of discrete, suitable habitat patches. In other words, the total habitat of the population is subdivided into local patches of habitat. In any one local habitat or site, it is assumed that the population colonizes the empty local habitat and at some later time goes extinct again in that local patch. This cycle can repeat, with the colonizers coming from other occupied sites. In the simplest model description of this situation, the rate at which populations go extinct from local sites (e.g. as the result of random processes) is assumed to be proportional to the fraction of all sites that are occupied. That is, if $p(t)$ is the fraction of local habitats occupied at time t, then the chance of extinction for a local population is $ep(t)$, where is some constant. (This simply corresponds to the intuitively obvious notion that, the more sites are occupied, the higher the chance that one of them becomes empty.) Similarly, the rate at which empty sites are colonized is assumed to be proportional to the number of empty sites (opportunity for colonizing) as well as to the number of occupied sites (supplying the colonizers), that is, this rate is assumed to be equal to $mp(t)(1-p(t))$, where m is a constant. The total rate of change of the fraction of occupied sites will then be

$$\frac{dp}{dt} = mp(1-p) - ep.$$

(a) Find the equilibria of this model.
(b) What is the condition required for the model to have an equilibrium $p^* > 0$? Does this condition make biological sense?
(c) Determine the stability of the equilibria of this model.
(d) How is this model related to the logistic model?
Note: This model makes the point that populations can survive in spatially structured habitats even though local extinction is certain.

2. *Metapopulations and spatial structure II.* Now assume that in addition to the situation described in problem 1, there is a second species, and assume that this second species is always outcompeted by the first one locally (i.e. whenever a local habitat patch happens to be colonized by species 1, then it will be occupied by species 1, regardless of whether the patch was empty or occupied by species 2). We further assume that extinction probabilities are the same for both species, but that colonization abilities are different. The point will be to see that even though species 2 always loses out to species 1 locally, species 2 can survive in the spatially structured situation if its colonization ability is higher than that of species 1.
Let $p_1(t)$ be the fraction of local habitats occupied by species 1, and let $p_2(t)$ be the fraction of local habitats occupied by species 2, at time t. Then, because species 1 always outcompetes species 2 locally, the dynamics of species 1 is given by the same equation as in problem 1, i.e. by

$$\frac{dp_1}{dt} = m_1 p_1(1-p_1) - ep_1,$$

where e describes extinction in the two species, and m_1 describes colonization ability in species 1. The dynamics of species 2 is similar, except that species 32 cannot colonize a patch occupied by species 1 and that some patches occupied by species 2 are lost as a result of colonization by species 1. Thus, those patches available for colonization by species 2 are the empty patches, with frequency $1 - p_1(t) - p_2(t)$ at time t. Al;so, we need to add a loss term accounting for the colonization by species 1 of patches that are occupied by species 2. This leads to the following equation for the dynamics of patches occupied by species 2:

$$\frac{dp_2}{dt} = m_2 p_2 (1 - p_1 - p_2) - m_1 p_1 p_2 - e p_2.$$

(a) Find the non-zero equilibrium for species 1. What conditions on the parameters are required for this equilibrium to be positive? Give an ecological interpretation.
(b) Assuming that species 1 can survive, determine the resulting non-zero equilibrium for species 2. What must be true about the colonization rate m_2, relative to the colonization rate m_1, for both species to survive? Does this make ecological sense?
(c) Start with colonization rates and an extinction rate that allow both species to survive at equilibrium. Which species would go extinct first (at equilibrium) if the extinction rate was slowly increased? (I.e., for which species will the equilibrium value first become negative as e is increased?
(d) If both species have positive equilibrium levels, what happens to the equilibrium level of species 2 as the extinction rate is increased.? Does this make ecological sense?
(e) Assume that colonization rates and an extinction rate allow both species to survive at equilibrium. Perform a linear stability analysis of this equilibrium.

3. Consider two competing populations $N_1(t)$ and $N_2(t)$ described by the Lotka-Volterra competition equations, and assume that in addition to competition, a fraction $m_i N_i(t)$ of each population is constantly removed (e.g. by removing part of the medium in which the populations are growing). Thus, the two equations describing this new system are

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 (1 - a_{11} N_1 - a_{12} N_2) - m_1 N_1 \\ \frac{dN_2}{dt} &= r_2 N_2 (1 - a_{21} N_1 - a_{22} N_2) - m_2 N_2\end{aligned}$$

Assume that without removal (i.e. with $m_1 = m_2 = 0$) species 1 always outcompetes species 2. Show that it is possible to have coexistence if $m_1, m_2 \neq 0$. Do this graphically by starting with 0-isoclines arranged so that coexistence is impossible with $m_1 = m_2 = 0$, and showing that the additional terms could produce equations with isoclines allowing for coexistence.

4. Read sections 4.2. to 4.6 in the textbook.

5. Solve problem 7 on p. 153 in the textbook.

6. Solve problem 14 on p. 154 in the textbook.

7. Solve problem 15 on p. 155 in the textbook (read the relevant material in Chapter 4 if necessary).

8. Solve problem 16 on p. 155 in the textbook.
9. Solve problem 20 on p. 156 in the textbook.
10. Solve problem 22 on p. 157 in the textbook.
11. Solve problem 29 on p. 160 in the textbook.