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Spring, 1997
There are 140 points. Answer all questions. Be sure to supply adequate explanation for your answers. In most of the problems the later parts do not depend heavily on the earlier parts, so don't give up on (c) if you didn't get (a) or (b)!

1. (20 points) Give brief definitions (one well-formulated sentence will do, maybe a little more for the last one) of the following terms. Illustrative pictures might also be appropriate.
a. sensitivity or elasticity (your choice)
b. $\quad r$ and $K$-selection
c. Jacobian matrix
d. chaos (in what sense predictable behavior, in what sense unpredictable)
2. (20 points) A population $N(t)$ of turtles has a per capita growth rate $(0.2)(1-(5 / N)-(N / 40))$ in units of (turtles/year)/turtle.
a. Write the equation for the net growth rate $\frac{d N}{d t}$. What are the units?
b. This system is found to have two non-trivial equilibrium values: $N=5.9$ and $N=34.1$. Analyze the stability of these equilibria by selecting initial values close to them and using the differential equation. Sketch $N$ as a function of $t$ for each case (all on one graph).
3. (10 points) In this compartment model $X_{1}$ and $X_{2}$ represent uninjured and injured subpopulations of a prey population, and $Y$ is the predator population that only injures but does not kill the prey (e.g., flatfish consumption of bivalve siphon tips). The labels on the arrows from one box (the source) to another box (the target, or out of the system entirely) give per capita loss rates from the source population (i.e., the fraction of the source population that is lost). This simultaneously represents gain to the target population. Arrows from a box to itself represent net gain as a fraction of current population. Give the equations for $d X_{1} / d t, d X_{2} / d t$, and $d Y / d t$.
4. (20 points) Consider a population in which there are two types of individuals $S$ and $T$ which may come into conflict. The fitness of an individual is its baseline fitness $W_{0}$ plus the fitness change resulting from an encounter with another individual weighted by the probability of such an encounter.

$$
\begin{aligned}
& W(S)=W_{0}+p E_{S S}+(1-p) E_{S T} \\
& W(T)=W_{0}+p E_{T S}+(1-p) E_{T T}
\end{aligned}
$$

At time $t$ the proportion of $S$ type individuals is $p_{t}$, and of $T$ type individuals $1-p_{t}$. The proportion of type $S$ individuals in the next generation is dependent upon the proportion in the current generation and the ratio of fitness of type $S$ individuals to average fitness. We have the following fitness changes (payoffs): $E_{S S}=2, E_{S T}=0.5, E_{T S}=-0.5, E_{T T}=1$, where $E_{A B}$ denotes the fitness change for $A$ in an encounter with $B$ (taking $A$ to be the invader of the territory occupied by $B$ ). Under these conditions the system is in equilibrium if $p=0.5$. If, however, at time $t=0$ we have $p_{0}=0.4$, then $p_{5}=0.32$, $p_{10}=0.21$, and $p_{20}=0.03$; on the other hand, if $p_{0}=0.6$, then $p_{5}=0.67$, $p_{10}=0.78$, and $p_{20}=0.96$.
a. What gain or loss in fitness does type $S$ have if $p_{0}=0.6$ ? What gain or loss in fitness does type $T$ have under the same initial condition?
b. Is the mixed equilibrium strategy $(50 \% S$ and $50 \% T)$ stable to invasion by a different strategy? Explain. Is this equilibrium an ESS?
c. What are the ESS strategies, if any, in this population? Give some intuitive justification for your answer.
5. (40 points) In this problem we investigate a vegetation-herbivore interaction given by

$$
\begin{aligned}
\frac{d V}{d t} & =a V\left(1-\frac{V}{K}\right)-\frac{b V}{e+V} H \\
\frac{d H}{d t} & =\frac{c V}{e+V} H-d H
\end{aligned}
$$

Here $V$ is measure in units of mass, say, Kg , and $H$ is a population count. All parameter values are positive. In parts (a), (b), and (c) it may be helpful to relate this model to standard models.
a. What happens to the vegetation in the absence of the herbivores? What happens to the herbivores in the absence of vegetation?
b. If $V$ is small in comparison to $e$, what can you conclude about the growth term of the herbivore population?
c. If $V$ is large compared to $e$, what can you conclude about the growth term of the herbivore population?
e. There is a non-trivial steady state $(\bar{V}, \bar{H})$. Calculate just $\bar{V}$ (suggestion: use the second equation to solve for $\bar{V}$ in terms of the parameters).
d. What further restriction must be imposed on the parameter values to be sure the steady state is actually feasible?
e. We have sketched the nullclines of the system using parameter values $a=0.5, b=0.001, c=0.5, d=0.4, K=500$, and $e=100$. The equilibrium values are $\bar{V}=400$ and $\bar{H}=50,000$. Determine which nullcline corresponds to $\frac{d V}{d t}=0$ and which to $\frac{d H}{d t}=0$. Then determine what happens to $H$ if you start a trajectory in each of the four regions; do the same for $V$. Use arrows to indicate the direction of net change.
f. At the equilibrium the Jacobian matrix has eigenvalues $\lambda_{1}=-0.027$ and $\lambda_{2}=-0.292$. Is the equilibrium stable or not? Sketch a plausible trajectory on the graph above, if the initial state is $V=450$ and very small $H$ (a new infestation). What do you expect to happen in the long term?
g. If we only change the parameter $e$ to 25 , then the new equilibrium values become $\bar{V}=100$ and $\bar{H}=50,000$, and the new eigenvalues become $\lambda=0.11 \pm 0.14 i$. Now is the equilibrium stable or not? Sketch a plausible
trajectory on the graph below, if the initial condition is $V=120$, and $H=50,000$. What do you expect to happen in the long term?
6. (15 points) Hitchcock and Gratto-Trevor (1997, Ecology 78:522-534) discuss the dynamics of a population of semipalmated sandpipers in Manitoba. They report the following population projection matrix.

$$
A=\left[\begin{array}{ccc}
0.021 & 0.074 & 0.085 \\
0.563 & 0 & 0 \\
0 & 0.563 & 0.563
\end{array}\right]
$$

The dominant eigenvalue is $\lambda=0.639$ and the stable age distribution vector is [0.119, 0.105, 0.776].
a. What does the model predict about the long term for this population?
b. The authors propose the following model for this population: $\mathbf{N}_{t+1}=$ $A \mathbf{N}_{t}+\mathbf{I}_{t}$, where $\mathbf{I}$ is a vector of immigrant birds not hatched at the site. In 1985 they observed 80 breeding pairs. Assuming the population was at its stable age distribution, how many breeding pairs should have been observed in 1986? In fact 57 breeding pairs were observed, including 5 immigrant pairs. On the basis of this evidence do you think the model is worth further investigation?
d. Can you identify a possible flaw in the model if you observe that the immigrant pairs are all fully mature adults?
7. (15 points) Match the time plots (A, B, C) with the corresponding phase plots (I, II, III) and regions of parameter space (1, 2, 3, 4) for the Nicholson-Bailey density dependent host-parasitoid model. As usual, $\lambda$ denote the dominant eigenvalue of the linearization at a steady state. All initial conditions are taken within 0.1 of the steady state values. Explain the features that enable you to make the matches.
A. $\qquad$ B. $\qquad$ C. $\qquad$

