

## Math 592D. Homework 3. Due: 3/10/05

Do at least 2, 3, 4 (not 4(e)). Then 1 if possible. 5 and 6 are suggestions.

1. The approach to modeling age-structured populations in continuous time is similar to what we have done in discrete time. If  $u(a, t)$  is the age density of females of age  $a$  at time  $t$ , then  $u(a, t)\Delta a + O(\Delta a^2)$  is the number of females in the age interval from  $a$  to  $a + \Delta a$  at time  $t$ . Let  $m(a)$  denote the maternity function, so that  $m(a)\Delta a + O(\Delta a^2)$  is the probability that an individual who survives to age  $a$  gives birth in the time interval from  $a$  to  $a + \Delta a$ . Let  $\ell(a)$  be the survival function, that is, the probability that an individual survives to age  $a$ . Then  $f(a) = \ell(a)m(a)$  (called the net maternity function) is the probability that an individual both survives to age  $a$  and gives birth then.

(a) Suppose that the initial age density of the female population is given by  $u(a, 0) = u_0(a)$ . Then show that

$$u(a, t) = \begin{cases} u_0(a-t)\ell(a)/\ell(a-t), & a > t; \\ B(t-a)\ell(a), & a < t; \end{cases}$$

where  $B(t)$  denotes the female birth rate at time  $t$ .

(b) The birth rate  $B$  is unknown. Assume that  $m(a) = 0$  for  $a$  outside the interval  $(\alpha, \beta)$ . Show that

$$B(t) = \int_0^t B(t-a)f(a) da + G(t)$$

where  $G$  is a function such that  $G(t) = 0$  for  $t > \beta$ , and thus that

$$B(t) = \int_0^\infty B(t-a)f(a) da$$

(c) The last equation in part (b) is an integral equation linear in  $B$ , so as in the discrete case analogue we may try to find a solution of the form  $B(t) = B_0 e^{rt}$ . Show that this is a solution as long as

$$1 = \int_0^\infty e^{-ra} f(a) da$$

(d) The last equation in (c) is called the continuous Euler-Lotka equation for the growth rate  $r$ . Assume that  $f$  is continuous and positive on  $[0, \omega]$  and zero outside of this interval. Then show that the continuous Euler-Lotka equation for this  $f$  has a unique real root  $r_0$ , called the Lotka rate of natural increase.

(e) Show that the population almost always settles down to grow exponentially at this rate, that is  $B(t) \rightarrow B e^{r_0 t}$  and

$$u(a, t) \rightarrow \frac{A \ell(a) e^{r_0(t-a)}}{\int_0^\infty e^{-r_0 a} \ell(a) da},$$

as  $t \rightarrow \infty$

The other approach to age structure in continuous time is the McKendrick-von Foerster. Assume that the change in age is the same as the change in time (that is,  $\Delta a = \Delta t$ ), if  $u(a, t)$  is the density for females of age  $a$  at time  $t$ , then at a later time  $t + \Delta t$  all individual that are still alive will have age by  $\Delta a = \Delta t$ , so that we can write

$$u(a + \Delta a, t + \Delta t) = u(a, t) - \mu(a) u(a, t) \Delta t + O(\Delta t^2)$$

where  $\mu$  is the mortality rate function and  $\mu(a)\Delta t + O(\Delta t^2)$  is the probability that an individual of age  $a$  will die in the next interval of time  $\Delta t$ .

(f) Show that  $u$  satisfies the McKendrick partial differential equation

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu u$$

(g) Assume that  $\omega$  is the greatest possible age of the population, let  $u_0(a) = u(a, 0)$ , let  $B(t) = \int_{\alpha}^{\beta} u(a, t)m(a) da$  (where  $\alpha$  and  $\beta$  are the youngest and oldest ages for child bearing, and that  $\ell(a) = \exp - \int_0^a \mu(x) dx$ ). Then show that  $u(a, t)$  as given in (a) is a solution to the McKendrick PDE.

2. Crouse *et al.* (1987) constructed a Leslie-Usher model for the population of loggerhead sea turtles.

(a) Read their paper to find out the matrix for this model.

(b) Determine the stable age distribution for their model.

(c) What is the best course of action to avoid the disappearance of the population: to enhance juvenile survivorship or to protect eggs on nesting-beaches?

3. There are many instances where interaction of two or more species is to the advantage of all. Mutualism or symbiosis often plays the crucial role in promoting and even maintaining such species.

The simplest mutualism model equivalent to the Lotke-Volterra predator-prey one is

$$\frac{dN_1}{dt} = r_1 N_1 + a_1 N_1 N_2 \quad \frac{dN_2}{dt} = r_2 N_2 + a_2 N_2 N_1$$

where  $r_1, r_2, a_1, a_2$  are all positive constants. This model is not very realistic because since  $dN_1/dt > 0$  and  $dN_2/dt > 0$ ,  $N_1$  and  $N_2$  simply grow unboundedly in, as May (1981) puts it, an “orgy of mutual benefaction”.

A first step to designing a reasonable two-species model is to incorporate some carrying capacity for both species, that is:

$$\begin{aligned} \frac{dN_1}{dT} &= r_1 N_1 \left( 1 - \frac{N_1}{K_1} + \alpha \frac{N_2}{K_1} \right) \\ \frac{dN_2}{dT} &= r_2 N_2 \left( 1 - \frac{N_2}{K_2} + \beta \frac{N_1}{K_2} \right) \end{aligned}$$

where  $r_1, r_2, K_1, K_2, \alpha$  and  $\beta$  are all positive constants. Nondimensionalize this system by making the change of variables

$$x = \frac{N_1}{K_1}, \quad y = \frac{N_2}{K_2}, \quad t = r_1 T, \quad r = \frac{r_2}{r_1}, \quad a = \alpha \frac{K_2}{K_1}, \quad b = \beta \frac{K_1}{K_2},$$

(a) Determine the nature of the steady states of this model.

(b) Explain the following statement about this model: “if symbiosis of either species is too large, then both populations grow unboundedly.”

4. Flores (1998) proposed the following model for competition between Neandertal man ( $N$ ) and Early Modern man ( $E$ ):

$$\begin{aligned} \frac{dN}{dt} &= N(\alpha - \gamma(N + E) - \beta) \\ \frac{dE}{dt} &= E(\alpha - \gamma(N + E) - s\beta) \end{aligned}$$

where  $\alpha, \beta$  and  $\gamma$  are positive constants and  $0 < s < 1$  is a measure of the difference in mortality between the two species.

(a) Determine the nature of the steady states of this model.

(b) Show that the populations  $N$  and  $E$  are related by

$$N(t) = E(t) e^{a-\beta(1-s)t}$$

where  $a$  is a constant of integration.

(c) Use (a) to give the order of magnitude of the time for Neardenthal extinction.

(d) If the lifetime of an individual is roughly 30 to 40 years and the time to extinction is (from paleontological data) 5,000 to 10,000 years, determine the range of the mortality difference parameter.

(e\*) Construct a competition model for this situation using the model system discussed in class with equal carrying capacities and linear birth rates in the absence of competition but with slightly different competition efficiencies. Determine the conditions under which Neardenthal will become extinct and the conditions under which the two species could coexist.

5. Imagine a predator-prey interaction in which a certain number of the prey population cannot be eaten because of a refuge in their environment that the predator cannot enter. Construct a model for this predator-prey interaction.

6. Veilleux (1979) studies the interaction between the predator *Didinium masutum* and its prey *Paramecium aurelia* in the laboratory. Can you find a mathematical model that fits reasonably well his description of this interaction?\*

## References

May, R. M. 1981. *Theoretical Ecology: Principles and Applications*. Oxford: Blackwell Sci. Publ.

Flores, J. C. 1998. *A mathematical model for Neardenthal extinction*. *Journal of Theoretical Biology*, vol. **191**, pp. 295–298. (Available as E-journal from CSUN Library.)

Crouse, D. T., L. B. Crowder and H. Caswell. 1987. *A stage-based population model for loggerhead sea turtles and implications for conservation*. *Ecology*, vol. **68**, pp. 1412–1423. (Available from JSTOR.)

Veilleux, B.G. 1979. *An analysis of the predatory interaction between Paramecium and Didinium*. *The Journal of Animal Ecology*, vol. **48**, pp. 787–803. (Available from JSTOR.)