Homework 5

Due Friday, August 4 2017

Problem 1 (10 points)

Suppose that we have a species whose population $N(t)$ is governed by a simple linear birth-death process. That is, in a small interval of time Δt, the probability that any one individual gives birth is approximately $\beta\Delta t$ and the probability that any one individual dies is $\delta\Delta t$.

$$\frac{\mathrm{d}P_n}{\mathrm{d}t} = \beta(n-1)P_{n-1} - (\beta+\delta)nP_n + \delta(n+1)P_{n+1}, \tag{1}$$

where

$$P_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0\right] \tag{2}$$

is the probability that $N(t) = n$ given the initial population N_0. We will always assume that $P_{-1} = 0$.

In class, we solved this problem using a probability generating function and then used that function to find the expected value

$$\langle N(t)\rangle = \sum_{n=0}^{\infty} nP_n(t). \tag{3}$$

If all we need is the expected value, then there is a much simpler way to find it.

(a) Use equation (1) to show that

$$\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} = (\beta-\delta)\langle N(t)\rangle. \tag{4}$$

(b) Solve equation (4) for $\langle N(t)\rangle$. (You should not have any arbitrary constants of integration in your solution.)

Problem 2 (10 points)

To incorporate density dependence into birth-death processes, we let the birth and death rates depend on the population N. That is, we replace the constant values β and δ with β_n and δ_n, which vary with n. One particularly simple version of density dependence arises if we assume that β_n decreases linearly with n, while δ_n is constant. That is, let

$$\beta_n = \beta - \frac{n}{K} \quad \text{and} \quad \delta_n = \delta, \tag{5}$$

where β and δ are constants and K is a constant positive integer.

The governing equations are otherwise identical to those of problem 1, so we find that

$$\frac{\mathrm{d}P_n}{\mathrm{d}t} = \beta_{n-1}(n-1)P_{n-1} - (\beta_n + \delta_n)nP_n + \delta_{n+1}(n+1)P_{n+1}, \tag{6}$$

where

$$P_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0\right] \tag{7}$$

for all $n \geq 0$ and $P_{-1}(t) = 0$.

(a) Using a similar technique to that in problem 1, show that

$$\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} = (\beta - \delta)\langle N(t)\rangle - \frac{\langle N(t)^2\rangle}{K}. \tag{8}$$

(b) Using the fact that the variance of $N(t)$ is

$$\mathrm{Var}\left[N(t)\right] = \langle N(t)^2\rangle - \langle N(t)\rangle^2, \tag{9}$$

show that

$$\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} = (\beta - \delta)\langle N(t)\rangle - \frac{\langle N(t)\rangle^2}{K} - \frac{\mathrm{Var}\left[N(t)\right]}{K}. \tag{10}$$

(c) If this were a deterministic problem, then $\mathrm{Var}\left[N(t)\right]$ would be zero. Find the two equilibria of (10) assuming that $\mathrm{Var}\left[N(t)\right] = 0$. (You may assume that $\beta > \delta > 0$.)

(d) Since this really isn't a deterministic problem, we should not expect the variance to be zero. Instead, we will assume that $\mathrm{Var}\left[N(t)\right] \approx \sigma^2$ is a small positive constant. Find the two equilibria of (10) under this assumption. (You may still assume that $\beta > \delta > 0$.)

Problem 3 (10 points)

Suppose that we have a birth-death process governed by

$$\frac{\mathrm{d}P_n}{\mathrm{d}t} = \beta_{n-1}(n-1)P_{n-1} - (\beta_n + \delta_n)nP_n + \delta_{n+1}(n+1)P_{n+1}, \tag{11}$$

where

$$P_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0\right] \tag{12}$$

for all $n \geq 0$ and $P_{-1}(t) = 0$. Instead of the formulas for β_n and δ_n from problem 2, suppose that β_n and δ_n are arbitrary functions of n with $\delta_n \neq 0$ for all $n \geq 0$.

Remember that $\pi = (\pi_0, \pi_1, \pi_2, \dots)$ is a stationary state if the constant functions $P_n(t) = \pi_n$ are solutions of (11). (Note, in particular, that $\sum_{n=0}^{\infty} \pi_n = 1$.)

Show that the only stationary solution to (11) is given by $\pi_0 = 1$ and $\pi_n = 0$ for all $n > 0$. This means that the only stationary state of any birth-death process corresponds to extinction.

Problem 4 (10 points)

The result of problem 3 suggests that stationary states are probably too restrictive a notion for birth-death processes. The problem is that $N(t) = 0$ is an absorbing state, and so the only two long term possibilities are that the population dies out or grows to infinity. Many populations, however, seem to reach "stable" levels for a very long time before eventually succumbing to extinction.

To make this new idea of stability rigorous, we will define the conditional probability

$$q_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0 \text{ and } N(t) \neq 0\right] = \frac{P_n(t)}{1 - P_0(t)}, \tag{13}$$

for all $n > 0$. This is the probability that $N(t) = n$ under the assumption that it has not yet gone extinct. Use equations (11) and (13) to show that

$$\frac{\mathrm{d}q_n}{\mathrm{d}t} = \beta_{n-1}(n-1)q_{n-1} - (\beta_n + \delta_n)nq_n + \delta_{n+1}(n+1)q_{n+1} + \delta_1 q_1 q_n, \tag{14}$$

for all $n > 0$. (We are assuming that $q_0 = 0$.)

Extra credit (5 points): Equation (14) often does have constant solutions. If $q_n(t) = \pi_n$ is constant for every $n > 0$, then we call π a *quasistationary state* of the birth-death process. Unfortunately, (14) is nonlinear, so it is generally very difficult to solve for π explicitly. However, there are several ways to approximate the quasistationary state numerically. For instance, you can

1. Guess a nonzero value for π_1.

2. Calculate π_2, π_3, π_4, etc. by repeatedly using (14) with $\mathrm{d}q_n/\mathrm{d}t = 0$. Stop at π_N, where N is chosen so that π_N is sufficiently small.

3. Find $Q = \sum_{n=1}^{N} \pi_n$ and replace each π_n with π_n/Q so that they all sum to 1.

4. If the new value of π_1 is substantially different from your previous guess, start again using the new π_1 as your starting guess.

For extra credit, implement this algorithm to find the quasistationary state of the birth-death process from problem 2 with $\beta = 0.1$, $\delta = 0.02$ and $K = 100$. Make a plot of π_n versus n. How does the peak of this plot compare to your solutions from parts c and d of problem 2? How big do you think the variance is?