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.)

Part (a)

We have

$$\begin{aligned}
\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} &= \frac{\mathrm{d}}{\mathrm{d}t}\sum_{n=0}^{\infty} nP_n(t) \\
&= \sum_{n=0}^{\infty} n\frac{\mathrm{d}P_n}{\mathrm{d}t} \\
&= \sum_{n=0}^{\infty} n\left[\beta(n-1)P_{n-1}(t) - (\beta+\delta)nP_n(t) + \delta(n+1)P_{n+1}(t)\right] \\
&= \sum_{n=0}^{\infty} \beta n(n-1)P_{n-1}(t) - \sum_{n=0}^{\infty}(\beta+\delta)n^2P_n(t) + \sum_{n=0}^{\infty}\delta n(n+1)P_{n+1}(t).
\end{aligned}$$

If we let $i = n-1$ and $j = n+1$, we have

$$\begin{aligned}
\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} &= \sum_{i=-1}^{\infty} \beta(i+1)iP_i(t) - \sum_{n=0}^{\infty}(\beta+\delta)n^2P_n(t) + \sum_{j=1}^{\infty}\delta(j-1)jP_j(t) \\
&= \sum_{i=0}^{\infty} \beta(i^2+i)P_i(t) - \sum_{n=0}^{\infty}(\beta+\delta)n^2P_n(t) + \sum_{j=0}^{\infty}\delta(j^2-j)P_j(t).
\end{aligned}$$

Since i, j and n are just dummy variables, we can recombine these sums into

$$\begin{aligned}
\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} &= \sum_{n=0}^{\infty}\left[\beta(n^2+n) - (\beta+\delta)n^2 + \delta(n^2-n)\right]P_n(t) \\
&= \sum_{n=0}^{\infty}(\beta-\delta)nP_n(t) \\
&= (\beta-\delta)\sum_{n=0}^{\infty} nP_n(t) \\
&= (\beta-\delta)\langle N(t)\rangle,
\end{aligned}$$

as desired.

Part (b)

We have

$$\frac{\mathrm{d}}{\mathrm{d}t}\langle N(t)\rangle = (\beta-\delta)\langle N(t)\rangle. \tag{5}$$

This equation is separable, and we have solved it many times in this class. We get

$$\langle N(t)\rangle = Ce^{(\beta-\delta)t}.$$

From the definition of $P_n(t)$, we know that $P_{N_0}(0) = 1$ and $P_n(t) = 0$ for all $n \neq N_0$. Therefore,

$$\langle N(0)\rangle = \sum_{n=0}^{\infty} nP_n(0) = N_0. \tag{6}$$

(You don't really need to prove this. We know that $N(0) = N_0$, so it should be clear that $\langle N(0)\rangle = N_0$ as well.)

We can use this initial condition to find C, so we have

$$\langle N(t)\rangle = N_0 e^{(\beta-\delta)t}.$$

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

$$\beta_n = \beta - \frac{n}{K} \text{ and } \delta_n = \delta, \tag{7}$$

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

$$\frac{\mathrm{d}P_n}{\mathrm{d}t} = \beta_{n-1}(n-1)P_{n-1} - (\beta_n + \delta_n)nP_n + \delta_{n+1}(n+1)P_{n+1}, \tag{8}$$

where

$$P_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0\right] \tag{9}$$

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

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

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

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

$$\mathrm{Var}\left[N(t)\right] = \langle N(t)^2 \rangle - \langle N(t) \rangle^2, \tag{11}$$

show that

$$\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} = (\beta - \delta)\langle N(t)\rangle - \frac{\langle N(t)\rangle^2}{K} - \frac{\mathrm{Var}\left[N(t)\right]}{K}. \tag{12}$$

(c) If this were a deterministic problem, then $\mathrm{Var}\left[N(t)\right]$ would be zero. Find the two equilibria of (12) 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 (12) under this assumption. (You may still assume that $\beta > \delta > 0$.)

Part (a)

As above, we have that

$$\begin{aligned}
\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} &= \frac{\mathrm{d}}{\mathrm{d}t}\sum_{n=0}^{\infty} nP_n(t) \\
&= \sum_{n=0}^{\infty} n\frac{\mathrm{d}P_n}{\mathrm{d}t} \\
&= \sum_{n=0}^{\infty} n\left[\beta_{n-1}(n-1)P_{n-1}(t) - (\beta_n + \delta_n)nP_n(t) + \delta_{n+1}(n+1)P_{n+1}(t)\right] \\
&= \sum_{n=0}^{\infty} \beta_{n-1}n(n-1)P_{n-1}(t) - \sum_{n=0}^{\infty}(\beta_n + \delta_n)n^2P_n(t) + \sum_{n=0}^{\infty}\delta_{n+1}n(n+1)P_{n+1}(t).
\end{aligned}$$

As before, we can (temporarily) let $i = n - 1$ and $j = n + 1$. This gives

$$\begin{aligned}
\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} &= \sum_{i=-1}^{\infty} \beta_i (i+1) i P_i(t) - \sum_{n=0}^{\infty} (\beta_n + \delta_n) n^2 P_n(t) + \sum_{j=1} \delta_j (j-1) j P_j(t) \\
&= \sum_{i=0}^{\infty} \beta_i (i^2 + i) P_i(t) - \sum_{n=0}^{\infty} (\beta_n + \delta_n) n^2 P_n(t) + \sum_{j=0}^{\infty} \delta_j (j^2 - j) P_j(t) \\
&= \sum_{n=0}^{\infty} \left[\beta_n (n^2 + n) - (\beta_n + \delta_n) n^2 + \delta_n (n^2 - n) \right] P_n(t) \\
&= \sum_{n=0}^{\infty} (\beta_n - \delta_n) n P_n(t).
\end{aligned}$$

This is the same result as in the previous problem, but here β_n is not constant. We therefore have

$$\begin{aligned}
\frac{\mathrm{d}\langle N(t)\rangle}{\mathrm{d}t} &= \sum_{n=0}^{\infty} \left(\beta - \frac{n}{K} - \delta \right) n P_n(t) \\
&= \sum_{n=0}^{\infty} (\beta - \delta) n P_n(t) - \sum_{n=0}^{\infty} \frac{n^2}{K} P_n(t) \\
&= (\beta - \delta) \sum_{n=0}^{\infty} n P_n(t) - \frac{1}{K} \sum_{n=0}^{\infty} n^2 P_n(t) \\
&= (\beta - \delta) \langle N(t) \rangle - \frac{\langle N(t)^2 \rangle}{K},
\end{aligned}$$

as desired.

Part (b)

Rearranging equation (11), we obtain

$$\langle N(t)^2 \rangle = \mathrm{Var}\left[N(t)\right] + \langle N(t) \rangle^2.$$

Substituting this into our answer from the previous section, we get

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

as desired.

Part (c)

If we assume that $\mathrm{Var}[N(t)] = 0$, then equation (12) becomes

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

(Note that this is just the logistic equation from our second homework.) Equilibria of this equation are constant solutions $\langle N(t)\rangle = N^*$. This means

$$0 = (\beta - \delta)N^* - \frac{(N^*)^2}{K} = N^* \left((\beta - \delta) - \frac{N^*}{K} \right)$$

This means that either $N^* = 0$ or $N^* = K(\beta - \delta)$. (This means that if the equation were actually deterministic and $\beta > \delta > 0$, then the system would have an equilibrium population at 0, which corresponds to extinction, and at some positive population $K(\beta - \delta)$, which corresponds to an extant population.)

Part (d)

If we instead assume that $\mathrm{Var}[N(t)] = \sigma^2$ is some small positive constant, then we have

$$0 = (\beta - \delta)N^* - \frac{(N^*)^2}{K} - \frac{\sigma^2}{K},$$

so

$$(N^*)^2 - K(\beta - \delta)N^* + \sigma^2 = 0.$$

This is a quadratic equation, so we find that

$$N^* = \frac{1}{2}\left(K(\beta - \delta) \pm \sqrt{K^2(\beta - \delta)^2 - 4\sigma^2} \right).$$

Note that $\sqrt{K^2(\beta - \delta)^2 - 4\sigma^2} < K(\beta - \delta)$, but only slightly smaller. This means that one of the equilibria is almost zero (slightly positive, assuming $\beta > \delta$) and the other is slightly smaller than $K(\beta - \delta)$ (and positive, if $\beta > \delta$). It turns out that the variance really is almost constant when $N(t)$ is close to the larger equilibrium, but not when $N(t)$ is close to zero, so there really is a value of N slightly below $K(\beta - \delta)$ that is almost a fixed point.

Problem 3 (10 points)

Suppose that we have a birth-death process governed by

$$\frac{\mathrm{d}P_n}{\mathrm{d}t} = \beta_{n-1}(n-1)P_{n-1} - (\beta_n + \delta_n)nP_n + \delta_{n+1}(n+1)P_{n+1}, \tag{13}$$

where

$$P_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0\right] \tag{14}$$

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 (13). (Note, in particular, that $\sum_{n=0}^{\infty} \pi_n = 1$.)

Show that the only stationary solution to (13) 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.

Solution

If we assume that $P_n(t) = \pi_n$ is constant for all $n \geq 0$, then we also know that $P_n'(t) = 0$ for all $n \geq 0$. In particular, for $n = 0$ this means that

$$\begin{aligned} 0 &= \beta_{-1} \cdot (-1)P_{-1}(t) - (\beta_0 + \delta_0) \cdot 0P_0(t) + \delta_1 \cdot 1P_1(t) \\ &= \delta_1 \pi_1. \end{aligned}$$

(Here, we have used the fact that $P_{-1}(t) \equiv 0$ by definition.) Since $\delta_1 \neq 0$, we therefore know that $\pi_1 = 0$. Similarly, when $n = 1$ we get

$$\begin{aligned} 0 &= \beta_0 \cdot 0 \cdot P_0(t) - (\beta_1 + \delta_1) \cdot 1P_1(t) + \delta_2 \cdot 2P_2(t) \\ &= -(\beta_1 + \delta_1)\pi_1 + 2\delta_2\pi_2 \\ &= 2\delta_2\pi_2. \end{aligned}$$

As before, we know that $\delta_2 \neq 0$, so we must have $\pi_2 = 0$. We can continue this argument ad infinitum. To prove this, suppose that $\pi_k = \pi_{k-1} = 0$ for some $k \geq 2$. We therefore have

$$\begin{aligned} 0 &= \beta_{k-1}(k-1)P_{k-1}(t) - (\beta_k + \delta_k)kP_k(t) + \delta_{k+1}(k+1)P_{k+1}(t) \\ &= (k+1)\beta_{k+1}\pi_{k+1} - k(\beta_k + \delta_k)\pi_k + (k+1)\delta_{k+1}\pi_{k+1} \\ &= (k+1)\delta_{k+1}\pi_{k+1}. \end{aligned}$$

Since $\delta_{k+1} \neq 0$, we must have $\pi_{k+1} = 0$ as well. Since we already proved that $\pi_1 = \pi_2 = 0$, this completes the proof that $\pi_n = 0$ for all $n \geq 0$. To find π_0, note that

$$\sum_{n=0}^{\infty} \pi_n = 1.$$

All the terms in this sum are zero except for π_0, so we must have $\pi_0 = 1$, as desired.

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

$$q_n(t) = \Pr\left[N(t) = n \mid N(0) = N_0 \text{ and } N(t) \neq 0\right] = \frac{P_n(t)}{1 - P_0(t)}, \tag{15}$$

for all $n > 0$. This is the probability that $N(t) = n$ under the assumption that it has not yet gone extinct. Use equations (13) and (15) to show that

$$\frac{\mathrm{d}q_n}{\mathrm{d}t} = \beta_{n-1}(n-1)q_{n-1} - (\beta_n + \delta_n)nq_n + \delta_{n+1}(n+1)q_{n+1} + \delta_1 q_1 q_n, \tag{16}$$

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

Extra credit (5 points): Equation (16) 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, (16) 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 (16) 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?

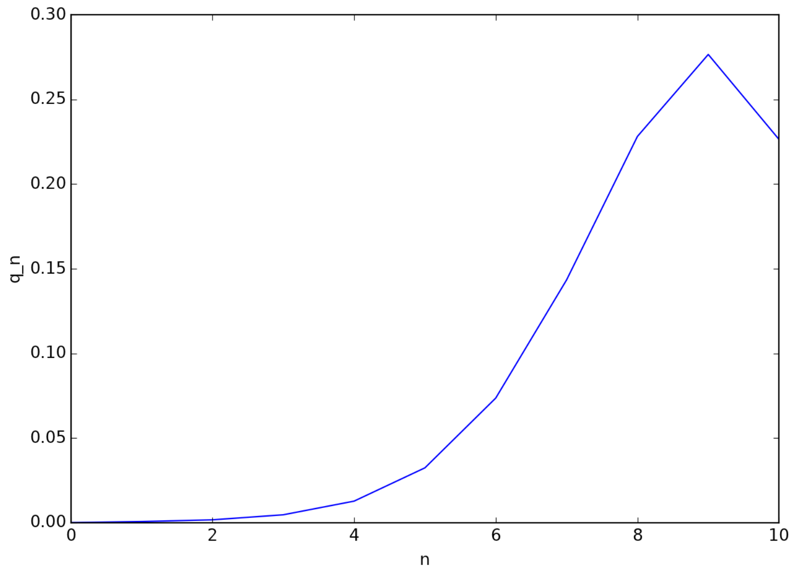
Solution

Since $q_n(t) = P_n(t)/(1 - P_0(t))$, we have

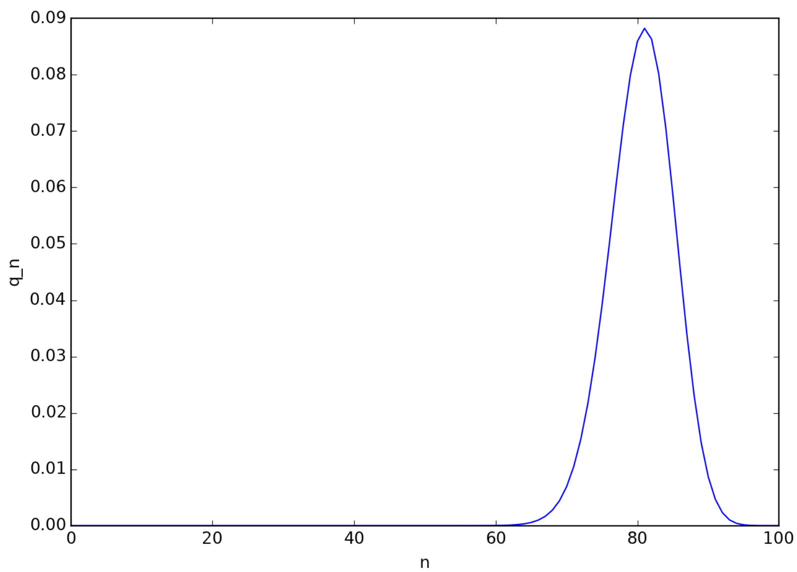
$$\begin{aligned}
\frac{\mathrm{d}q_n}{\mathrm{d}t} &= \frac{P_n'(t)(1-P_0) + P_0'(t)P_n(t)}{(1-P_0(t))^2} \\
&= \frac{P_n'(t)}{1-P_0(t)} + \frac{P_0'(t)}{1-P_0(t)} \cdot \frac{P_n(t)}{1-P_0(t)} \\
&= \frac{\beta_{n-1}(n-1)P_{n-1}(t) - (\beta_n + \delta_n)nP_n(t) + \delta_{n+1}(n+1)P_{n+1}(t)}{1-P_0(t)} \\
&\quad + \frac{\delta_1 P_1(t)}{1-P_0(t)} \cdot \frac{P_n(t)}{1-P_0(t)} \\
&= \beta_{n-1}(n-1)\frac{P_{n-1}(t)}{1-P_0(t)} - (\beta_n+\delta_n)n\frac{P_n(t)}{1-P_0(t)} + \delta_{n+1}(n+1)\frac{P_{n+1}(t)}{1-P_0(t)} \\
&\quad + \delta_1 \frac{P_1(t)}{1-P_0(t)} \cdot \frac{P_n(t)}{1-P_0(t)} \\
&= \beta_{n-1}(n-1)q_{n-1}(t) - (\beta_n+\delta_n)nq_n(t) + \delta_{n+1}(n+1)q_{n+1}(t) + \delta_1 q_q(t) q_n(t),
\end{aligned}$$

as desired.

If you implement the algorithm in the extra credit, you should obtain a graph like:



Note that $K(\beta - \delta) = 8$, so the peak of the quasistationary distribution roughly corresponds to the equilibrium of the deterministic problem. This is probably a little easier to see if we choose a larger K. When $K = 1000$, we get the graph:



Again, the peak roughly corresponds to $K(\beta - \delta) = 80$.