Mathematical Biology: Example Sheet 4

David Tong, January 2025

1. Consider a birth and death process in which births can give rise to either one or two offspring, with probability λ_1 and λ_2 respectively, while the probability of death per individual is β .

Write down the master equation for the probability $p_n(t)$.

Show that the generating function $\phi(s,t) = \sum_{n=0}^{\infty} s^n p_n$ satisfies the equation

$$\frac{\partial \phi}{\partial t} = (s-1) \left[\left(\lambda_1 + \lambda_2 \left(s + 1 \right) \right) \phi - \beta \frac{\partial \phi}{\partial s} \right]$$

Use this equation in the steady state to show that

$$\langle n \rangle = \frac{1}{\beta} (\lambda_1 + 2\lambda_2) \text{ and } \sigma^2 = \frac{1}{\beta} (\lambda_1 + 3\lambda_2).$$

2. Consider an experiment where two or three individuals are added to a population with probability λ_2 and λ_3 respectively per unit time. The death rate in the population is a constant β per individual per unit time.

Write down the master equation and derive an equation for $\partial \phi / \partial t$, where ϕ is the generating function (as above). Find the solution for ϕ in steady state.

Show that for given target mean but otherwise a free choice of λ_2 and λ_3 , the experimenter can minimise the variance by only adding two individuals at a time. Find this minimum variance in terms of the mean.

3. Consider a birth-death process described by the master equation

$$\frac{dp_n}{dt} = \lambda(p_{n-1} - p_n) + \beta [f(n+1) p_{n+1} - f(n) p_n]$$

with f(n) = n(n-1)

- i) Give an explanation of the terms on the right hand side.
- ii) Show that the generating function $\phi(s,t)$ satisfies

$$\frac{\partial \phi}{\partial t} = \lambda(s-1)\phi + \beta s(1-s)\frac{\partial^2 \phi}{\partial s^2}$$

- iii) Use the equation for ϕ in the steady state, or the master equation directly, to obtain equations for $\langle n^2 \rangle$ and $\langle n^3 \rangle$, in terms of $\mu = \langle n \rangle$ and $r = \lambda/\beta$ (do not try to evaluate μ itself).
- iv) With the mean μ unknown this system of equations is not closed. Nonetheless show that the variance $\sigma^2 = \langle n^2 \rangle \langle n \rangle^2 \leq r + \frac{1}{4}$. Show also, using the inequality $\langle n^2 \rangle \geq \langle n \rangle^2$, that $\langle n \rangle \leq (1 + \sqrt{1 + 4r})/2$.

4. Consider a stochastic model of a population where the death rate is β per capita (so total rate βn), and M individuals are added at the same time at rate λ (where M is a positive integer).

- i) Give the master equation and find the mean and variance of the population size at steady state.
- ii) Write down the Fokker-Planck equation for this system. Use this to find the mean and variance of the population.

5. A particle starts at the origin (0,0) at time t = 0. In each of the cases below, derive the corresponding Fokker-Planck equation (in x, y). The particle moves in a random walk, where it takes steps with the step sizes below, each with probability rate λ .

- i) A square grid: (-1,0), (+1,0), (0,-1) and (0,+1)
- ii) A triangular grid: (+1,0), (-1,0), $(\frac{1}{2}, \frac{\sqrt{3}}{2})$, $(\frac{1}{2}, -\frac{\sqrt{3}}{2})$, $(-\frac{1}{2}, +\frac{\sqrt{3}}{2})$ and $(-\frac{1}{2}, -\frac{\sqrt{3}}{2})$
- iii) Square grid with bonus diagonal steps (breaking isotropy): (-1,0), (+1,0), (0,-1), (0,+1), (+1,+1) and (-1,-1)

For case iii), write down the master equation for the probability $P_{m,n}$ (where m, n are the discretised x, y) and use it to find $\langle m^2 + n^2 \rangle$. Also calculate $\langle x^2 + y^2 \rangle$ from the Fokker-Planck equation.

6. A two-population dynamic model has the transition probability rates

$$(m,n) \rightarrow (m+1,n) : \mu + \lambda_1 n,$$

$$(m,n) \rightarrow (m-1,n) : \beta_1 m,$$

$$(m,n) \rightarrow (m,n+1) : \lambda_2 m,$$

$$(m,n) \rightarrow (m,n-1) : \beta_2 n.$$

- i) Construct a master equation for $P_{m,n}$ and use it to derive equations for the time evolution of $\langle m \rangle$, $\langle n \rangle$. Find conditions on the parameters μ , λ_1 , λ_2 , β_1 and β_2 for there to be a *stable* fixed point with $\langle m \rangle$, $\langle n \rangle > 0$.
- ii) Write down the Fokker-Planck equation. Now consider small fluctuations near the fixed point found above, and approximate u as linear in x and D as constant. Show that the covariance matrix C satisfies

$$\frac{dC}{dt} = a C + C a^T + b$$

where a and b are matrices which should be given.

- iii) For the special case when $\lambda_1 = \lambda_2 = \lambda$ and $\beta_1 = \beta_2 = \beta$ consider the equation for dC/dt in components. Show that there is a fixed point for C (which need not be explicitly found) and that it is stable. Explain what this means for this model.
- * iv) As in iii), but with general λ_1 , λ_2 , β_1 and β_2 .