Mathematical Biology: Example Sheet 4

David Tong, January 2026

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

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

Use this equation in the steady state to show that

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

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

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

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

$$\begin{aligned}
(m,n) &\to (m+1,n) : \mu + \lambda_1 n, \\
(m,n) &\to (m-1,n) : \beta_1 m, \\
(m,n) &\to (m,n+1) : \lambda_2 m, \\
(m,n) &\to (m,n-1) : \beta_2 n.
\end{aligned}$$

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.