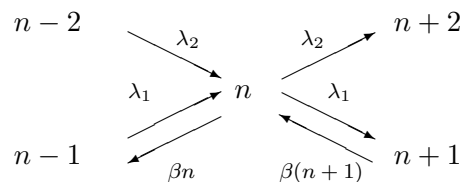


## Mathematical Biology – Examples Sheet 2

[Please communicate any errors in this sheet to [pjh@damtp.cam.ac.uk](mailto:pjh@damtp.cam.ac.uk). Some further material for this course is available at <http://www.damtp.cam.ac.uk/user/pjh/mathbio.html>.]

1. Consider a birth and death process in which births can give rise to either one or two offspring, with probability  $\lambda_1$  and  $\lambda_2$  respectively, while the probability of death per individual is  $\beta$ ; i.e. consider the system



Write down the master equation (or probability balance equation) for this system, and show that the generating function

$$\phi(s, t) = \sum_{n=0}^{\infty} s^n P(n, t) \quad \text{satisfies the equation:}$$

$$\frac{\partial \phi}{\partial t} = [\lambda_1(s-1) + \lambda_2(s^2-1)] \phi - \beta(s-1) \frac{\partial \phi}{\partial s}.$$

Use this equation in the steady state to show that

$$\langle n \rangle = \frac{1}{\beta}(\lambda_1 + 2\lambda_2)$$

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

2. Consider a birth-death process described by the following master equation:

$$\frac{\partial P}{\partial t} = \lambda(P(n-1) - P(n)) + \beta(f(n+1)P(n+1) - f(n)P(n)), \quad f(n) = n(n-1).$$

- (i) Give an explanation of the terms on the right hand side.  
 (ii) Show that the equation satisfied by the generating function  $\phi(s, t) \equiv \sum_{n \geq 0} s^n P(n, t)$  is

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

- (iii) Use the equation for  $\phi$  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  $\langle n \rangle$  and  $r = \lambda/\beta$  (do not try to evaluate  $\langle n \rangle$  itself).
- (iv) With  $\langle n \rangle$  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  $\langle n \rangle \leq (1 + \sqrt{1 + 4r})/2$ .

3. Consider the following Fokker-Planck equation (FPE) for a certain random process:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x}(x(1-x)P) + \frac{1}{\alpha} \frac{\partial^2}{\partial x^2}(x^2 P).$$

- (i) Show directly from the equation that

$$\frac{\partial}{\partial t} \langle x^k \rangle = k \left[ (1 + (k-1)\alpha^{-1}) \langle x^k \rangle - \langle x^{k+1} \rangle \right].$$

- (ii) Solve the FPE in the steady state, showing that  $P(x) = Cx^{\alpha-2}e^{-\alpha x}$  for some constant  $C$ . Give  $C$  in terms of an integral (which need not be evaluated). What restriction must be placed on  $\alpha$  for the solution to make sense?
- (iii) Use the steady-state solution for  $P(x)$  to verify that for  $k = 0, 1, 2, \dots$

$$\langle x^{k+1} \rangle = \frac{k + \alpha - 1}{\alpha} \langle x^k \rangle.$$

Use this result to determine  $\langle x^k \rangle$ ,  $k = 1, 2, 3$ .

4. A two-population dynamic model has the following transition probabilities:

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

- (i) Construct a master equation for  $P(m, n, t)$  and use it to derive equations for  $\langle m \rangle, \langle n \rangle$ . Show that, under appropriate conditions on the coefficients  $a, \lambda_i, \beta_i$ , there is a fixed point with  $\langle m \rangle, \langle n \rangle > 0$ , and give the conditions for this to be stable.
- (ii) Write down a Fokker-Planck equation describing small perturbations from this fixed point using the method in lectures, with the matrix  $A$  the jacobian at the fixed point and the matrix  $B$  evaluated at the fixed point. Write down the equation for the covariance matrix  $C$ .
- (iii) Show that the equation for  $C$  has a stable fixed point, satisfying  $AC + CA^T + fB = 0$ , and calculate  $C$  in this case.

5. For the one-dimensional random walk problem discussed in lectures, i.e. the process

$$n \xrightarrow{\lambda} n+1$$

use the master equation and the Fokker-Planck equation to calculate the time development of the fourth moment ( $\langle n^4 \rangle$  or  $\langle x^4 \rangle$ ). Explain carefully why the two answers are not the same, and why the ratio of the two answers tends to unity at large times.

6. (This question concerns a random walk in two dimensions.)

- (i) A particle starts at the origin  $(0, 0)$  at time  $t = 0$ . It moves (a) on a square grid from  $(m, n)$  with equal probability  $\lambda$  per unit time to one of the four adjacent points  $(m \pm 1, n \pm 1)$ , (b) on a triangular grid from  $X_{m,n} = (m + \frac{n}{2}, \frac{n\sqrt{3}}{2})$  with the same probability  $\lambda$  to one of the six adjacent points

$$X_{m\pm 1,n}, X_{m,n\pm 1}, X_{m-1,n+1}, X_{m+1,n-1}.$$

Write down the master equation for the probability distribution in each case and derive the corresponding Fokker-Planck equation in the  $x - y$  plane.

- (ii) For the square grid, the isotropy is broken due to the existence of an additional probability  $\lambda$  per unit time to jump from  $(m, n)$  to  $(m + 1, n + 1)$  and  $(m - 1, n - 1)$ . Find the Fokker-Planck equation in this case and calculate  $\langle m^2 + n^2 \rangle$  directly from the master equation and  $\langle x^2 + y^2 \rangle$  from the Fokker-Planck equation.