Example Sheet 2

1. A simple model of two competing populations eating the same food takes the form

$$\dot{N}_1 = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_2}\right),$$

$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_1}\right).$$

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   (a) Rescale the equations to simplify them, and show that the solutions depend only on $\rho = r_2/r_1, b_{12}$ and b_{21}.

   (b) Now assume that $\rho, b_{12}, b_{21} > 0$. Find all the physically relevant fixed points and determine their stability. Give conditions on the coefficients such that there is a stable state of *coexistence*, with $N_1, N_2 > 0$.

2. Consider this ‘harvesting’ model:

$$\dot{u} = u(1-v) - \epsilon u^2 - f$$

$$\dot{v} = -\alpha v(1-u),$$

   with constants $\alpha > 0, f > 0$ and $0 < \epsilon < 1/2$.

   (a) Find all the biologically relevant fixed points of this system, and investigate their stability, distinguishing between different ranges of f:

      i. $0 < f < \epsilon$,

      ii. $\epsilon < f < 1-\epsilon$

      iii. $1-\epsilon < f < 1/(4\epsilon)$

      iv. $1/(4\epsilon) < f$.

   (b) In each case, sketch trajectories in the $u - v$ phase-plane, and discuss what would happen to the predator and prey populations in practice.

   (c) Note that for this model something odd happens at $u = 0$. Comment on this, and discuss how the model might be improved in this respect.

3. Consider the difference equation $x_{n+1} = rx_n(1-x_{n-1})$. Show that the fixed point $x^* = 1-r^{-1}$ is unstable if r is sufficiently large. Show that when r takes its marginal value for instability, the linearised stability problem has a periodic solution and determine the solution.

4. A discrete-time model for breathing is given by

$$\begin{aligned} V_{n+1} &= \alpha\, C_{n-k} \\ C_{n+1} - C_n &= \gamma - \beta\, V_{n+1} \end{aligned}$$

   where V_n is the volume of each breath at time step n and C_n is the concentration of carbon dioxide in the blood at the end of time step n. This model was presented in lectures and we found and analysed the stability of the steady state when $k = 0$ and $k = 1$.

(a) For general (integer)$k > 1$, by seeking parameter values when the modulus of a perturbation to the steady state is constant, show that the range of parameters where the solution is stable is

$$0 < \alpha\beta < 2\sin\left(\frac{\pi}{4k+2}\right).$$

(b) Notice how this range shrinks as the time lag k increases. What is the periodicity of the constant-modulus solution at the upper end of this range?

5. Consider a birth-death process in which births can give rise to either one or *two* offspring, with rates λ_1 and λ_2 respectively, while the rate of death per individual is β. This means that transitions from $n \to n+1$ and $n \to n+2$ are allowed in the births.

(a) Write down the master equation for this system and show that the generating function $G(s,t) = \sum_{n=0}^{\infty} s^n\, p_n$ satisfies the equation

$$\partial_t G = (s-1)\left[\left(\lambda_1 + \lambda_2\,(s+1)\right)G - \beta\partial_s G\right]$$

(b) Use this equation to show that in the steady state, that is as $t \to \infty$, the mean and variance of the population are given by

$$\langle n \rangle = \frac{1}{\beta}(\lambda_1 + 2\lambda_2), \qquad \langle n^2 \rangle - \langle n \rangle^2 = \frac{1}{\beta}(\lambda_1 + 3\lambda_2).$$

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

(a) Write down the master equation, derive an equation for the generating function, and find the solution of the latter in the steady state.

(b) Show that for a fixed value of the mean but otherwise free choice of λ_2 and λ_3, the experimenter can minimise the variance by only adding two individuals at a time. Find the minimum variance in terms of the mean.

7. Consider a stochastic model of a population where the death rate is βn and M individuals, where M is a positive integer, are added at the same time at rate λ.

(a) Write down the master equation and find the mean and variance of the population size at steady state.

(b) Write down the diffusion limit, that is, the Fokker-Planck equation for this system. Use this to find the mean and variance of the population.

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

$$\dot{p_n} = \lambda(p_{n-1} - p_n) + \beta\left[f(n+1)\,p_{n+1} - f(n)\,p_n\right], \quad f(n) = n(n-1).$$

(a) Give an explanation of the terms on the right hand side.

(b) Show that the equation satisfied by the generating function $G(s,t)$ is

$$\partial_t G = \lambda(s-1)\phi + \beta\left((s-s^2)\partial_s^2 G\right).$$

(c) Use the equation for G 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).

(d) With the mean μ unknown this system of equations is not closed. Nonetheless show that the variance $\sigma^2 = \langle n^2 \rangle - \langle n \rangle^2 \le r + \frac{1}{4}$. Show also, using the inequality $\langle n^2 \rangle \ge \langle n \rangle^2$, that $\langle n \rangle \le (1 + \sqrt{1+4r})/2$.