INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

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Exercise 1.1

(i) Probability of being alive after one hour is $e^{-\mu}$. Probability of dying within one hour: $p = 1 - e^{-\mu}$.

(ii) Since this is a Poisson process, the events are independent. Hence the probability that it survives the first hour but decays in the second hour is given by their product:

$$e^{-\mu}(1 - e^{-\mu})$$

Exercise 1.2

$L(a)$ = expected remaining lifetime at age a.

$l(a)$ = fraction of individuals alive at age a = probability of being alive at age a.

From the definition of $l(t)$, we get that the death rate is $\mu(t) = -l'(t)$. Hence, by using the formula of the conditional probability,

$$P(\text{dying at } t \geq a \mid \text{alive at } a) = \frac{P(\text{dying at } t \geq a)}{P(\text{being alive at } a)} = \frac{-l'(t)\,\mathrm{d}t}{l(a)}$$

We compute the expected value of the remaining lifetime:

$$\begin{aligned}
L(a) &= \int_a^\omega (t-a)\frac{-l'(t)}{l(a)}\,\mathrm{d}t \\
&= -\int_a^\omega t\frac{l'(t)}{l(a)}\,\mathrm{d}t + a\int_a^\omega \frac{l'(t)}{l(a)}\,\mathrm{d}t \\
&= \frac{1}{l(a)}\left(-[l(t)t]_a^\omega + \int_a^\omega l(t)\,\mathrm{d}t + a[l(t)]_a^\omega\right) \\
&= \frac{1}{l(a)}\left(l(a)a + \int_a^\omega l(t)\,\mathrm{d}t - al(a)\right) = \frac{1}{l(a)}\int_a^\omega l(t)\,\mathrm{d}t
\end{aligned}$$

(obtained by integrating by parts and using $l(\omega) = 0$)

Exercise 1.3

(i) Probability of dying exactly at t equals the probability of being alive at time t and then dying in $\mathrm{d}t$, i.e.,

$$P(\text{dying at } t) = e^{-\mu t}\mu\,\mathrm{d}t.$$

Hence, by taking the expected value and integrating by parts,

$$\begin{aligned} L(0) = \text{Expected lifetime at birth} &= \int_0^\infty te^{-\mu t}\mu \, \mathrm{d}t \\ &= [-te^{-\mu t}]_0^\infty + \int_0^\infty e^{-\mu t} = \frac{1}{\mu}. \end{aligned}$$

(ii) In this case with constant death rate, the fraction of individuals alive at age a is given by $l(a) = e^{-\mu a}$. Hence, from Exercise 1.2, we can calculate

$$L(a) = \frac{1}{e^{-\mu a}} \int_a^\omega e^{-\mu t} \, \mathrm{d}t = e^{\mu a} \frac{e^{-\mu a}}{\mu} = \frac{1}{\mu} = L(0)$$

(this comes from the assumption of the Poisson process: the past history of the individual is forgotten)

Exercise 1.4

As already remarked, for exponential decay we have $l(a) = e^{-\mu a}$. Hence

$$\begin{aligned} l(t_{1/2}) = \frac{1}{2} &\Leftrightarrow e^{-\mu t_{1/2}} = \frac{1}{2} \\ &\Leftrightarrow t_{1/2} = \frac{1}{\mu} \log 2 < \frac{1}{\mu} \end{aligned}$$

Exercise 1.5

$$\boxed{D} \overset{\mu}{\leftarrow} \boxed{N} \overset{\nu}{\rightarrow} \boxed{R}$$

The probability that you eventually recover equals the sum of all contributions of probability that you recover at time t given that you have not died nor recovered up to t.

$$\begin{aligned} P(\text{recover exactly in } [t, t + \mathrm{d}t]) &= P(\text{still infected at time } t) P(\text{recover in } \mathrm{d}t) \\ &= e^{-(\mu+\nu)t} \nu \, \mathrm{d}t. \end{aligned}$$

To obtain the probability that you eventually recover rather than die, we integrate over all possible recovery times:

$$\begin{aligned} P(\text{eventual recover}) &= \int_0^\infty P(\text{recover exactly in } [t, t + \mathrm{d}t]) \\ &= \int_0^\infty e^{-(\mu+\nu)t} \nu \, \mathrm{d}t = \frac{\nu}{\mu + \nu}. \end{aligned}$$

Notice that

$$1 = P(\text{eventual recover}) + P(\text{eventual death}) = \frac{\nu}{\mu + \nu} + \frac{\mu}{\mu + \nu}.$$

Consider the ODE model (1–3). The ODE system is linear homogeneous, so the solutions are exponential and can be obtained by ordinary methods. The solution is

$$\begin{aligned} N(t) &= e^{-(\mu+\nu)t} N_0, \\ R(t) &= \int_0^t \nu e^{-(\mu+\nu)s} N_0 \, \mathrm{d}s = N_0 \frac{\nu}{\mu+\nu}(1 - e^{-(\mu+\nu)t}), \\ D(t) &= \int_0^t \mu e^{-(\mu+\nu)s} N_0 \, \mathrm{d}s = N_0 \frac{\mu}{\mu+\nu}(1 - e^{-(\mu+\nu)t}) \end{aligned}$$

The probability that an individually eventually recovers equals the fraction of recovered individuals at $t \to \infty$, i.e.,

$$\lim_{t\to\infty} \frac{R(t)}{N(t) + R(t) + D(t)} = \frac{\lim_{t\to\infty} R(t)}{N_0} = \lim_{t\to\infty} \frac{\nu}{\mu+\nu}(1 - e^{-(\mu+\nu)t}) = \frac{\nu}{(\mu+\nu)}$$

Extra Exercise

Expected lifetime with multiple modes of decay. Suppose that individuals contract a disease at a constant rate $\lambda > 0$ and recover from the disease at a constant rate $\nu > 0$. Healthy individuals die at a constant rate $\mu > 0$ whereas sick individuals die at a potentially higher rate, $\mu + \alpha$, where $\alpha \geq 0$ is called the virulence of the disease. Calculate the expected lifetime of a healthy newborn (a) if individuals who recovered from the disease have acquired immunity such that they cannot contract the disease for a second time; and (b) if there is no immunity such that recovered individuals are susceptible to the disease.

For any transition from one state to the other, we have to sum up the expected time spent in the state given that we exit from a certain "path", times the probability of exiting the state from that specific path.

(a) In the presence of immunity the expected lifetime T of a susceptible is

$$T = \frac{1}{\mu+\lambda} + \frac{\lambda}{\mu+\lambda}\left[\frac{1}{\mu+\alpha+\nu} + \frac{\nu}{\mu+\alpha+\nu}\frac{1}{\mu}\right]$$

where the first term is the expected time spent in the susceptible class, and the term in square brackets is the expected time in the infected and recovered class (multiplied by the probability that you actually got infected, $\lambda/(\mu+\lambda)$).

(b) If there is no immunity, the expected lifetime of a recovered individual equals the expected lifetime of a susceptible individual, hence

$$T = \frac{1}{\mu+\lambda} + \frac{\lambda}{\mu+\lambda}\left[\frac{1}{\mu+\alpha+\nu} + \frac{\nu}{\mu+\alpha+\nu}T\right]$$

Then we can solve the equation to get the explicit value of T.