ST2302/MA8002 Exercises chapter 1

1.14

Let J be the indicator of survival, i.e. $J = 1$ if the female survives and 0 otherwise, hence $J \sim \text{Bin}(1, p)$. Let B be the number of offspring per female. According to the text, $B|J = 1 \sim \text{Poisson}(\nu)$. The unconditional expecation of B is (by the law of total expectation)

$$\begin{aligned}
\mathrm{E}[B] &= \mathrm{E}[B|J=1]\mathrm{P}(J=1) + \mathrm{E}[B|J=0]\mathrm{P}(J=0) \\
&= \nu \cdot p + 0 \cdot (1-p) \\
&= \nu p.
\end{aligned}$$

The female's contribution to the next time step is given by $J + B$. The growth rate λ is the expected contribution, i.e.

$$\lambda = \mathrm{E}[J + B] = (1 + \nu)\, p.$$

Since there is no environmental variance, the demographic variance is given by

$$\sigma_d^2 = \mathrm{Var}(J + B) = \mathrm{Var}(J) + \mathrm{Var}(B) + 2\mathrm{Cov}(B, J).$$

First consider $\mathrm{Var}(B)$ which is given by $\mathrm{Var}(B) = \mathrm{E}[B^2] - \mathrm{E}[B]^2$. In order to find $\mathrm{E}[B^2]$, we derivate the moment-generating function of $B|J = 1$, then use the law of total expectation:

$$\begin{aligned}
M_{B|J=1}(t) &= e^{\nu(e^t-1)} \\
M'_{B|J=1}(t) &= \nu e^{t+\nu(e^t-1)} \\
M''_{B|J=1}(t) &= \nu e^t[e^{\nu(e^t-1)}(\nu e^t + 1)] \\
M''_{B|J=1}(0) &= \mathrm{E}[B^2|J=1] = \nu(\nu+1),
\end{aligned}$$

$$\begin{aligned}
\mathrm{E}[B^2] &= \mathrm{E}[B^2|J=1]\mathrm{P}(J=1) + \mathrm{E}[B^2|J=0]\mathrm{P}(J=0) \\
&= \nu p\,(\nu + 1).
\end{aligned}$$

This gives $\mathrm{Var}(B) = \nu p + \nu^2 p\,(1-p)$.

Now consider the term $\mathrm{Cov}(B, J)$, which is given by $\mathrm{Cov}(B, J) = \mathrm{E}[BJ] - \mathrm{E}[B]\mathrm{E}[J]$. To find $\mathrm{E}[BJ]$ we again use the law of total expectation, i.e.

$$\mathrm{E}[BJ] = \mathrm{E}[BJ|J=1]\mathrm{P}(J=1) + \mathrm{E}[BJ|J=0]\mathrm{P}(J=0) = \nu p.$$

This gives $\mathrm{Cov}(B, J) = \nu p\,(1-p)$. Finally, the demographic variance is given by

$$\begin{aligned}\sigma_d^2 &= \mathrm{Var}(B) + \mathrm{Var}(J) + 2\mathrm{Cov}(B, J) \\ &= \nu p + \nu^2 p(1-p) + p\,(1-p) + 2\,\nu p\,(1-p) \\ &= \nu p + (\nu+1)^2 p\,(1-p).\end{aligned}$$

1.15

In contrast to the previous exercise, ν is now a stochastic parameter. This means that all expectations, variances and covariances involving B in the previous exercise must be conditioned on ν. Using the hint, the environmental variance is given by

$$\begin{aligned}\sigma_e^2 &= \mathrm{Var}(\mathrm{E}[w|z]) \\ &= \mathrm{Var}(\mathrm{E}[B+J|\nu]) \\ &= \mathrm{Var}(\mathrm{E}[B|\nu] + \mathrm{E}[J|\nu]) \\ &= \mathrm{Var}(\nu p + p) \\ &= p^2 \mathrm{Var}(\nu) + 0 \\ &= p^2\sigma^2.\end{aligned}$$

The demographic variance is given by

$$\begin{aligned}\sigma_d^2 &= \mathrm{E}[\mathrm{Var}(w|z)] \\ &= \mathrm{E}[\mathrm{Var}(B+J|\nu)] \\ &= \mathrm{E}[\mathrm{Var}(B|\nu) + \mathrm{Var}(J|\nu) + 2\mathrm{Cov}(B, J|\nu)] \\ &= \mathrm{E}[\nu p + \nu^2 p\,(1-p) + p\,(1-p) + 2\nu\, p\,(1-p)] \\ &= \mu p + p\,(1-p)\,\mathrm{E}[\nu^2] + p\,(1-p) + 2\mu\, p\,(1-p) \\ &= \mu p + p\,(1-p)\,(\mu^2 + \sigma^2) + p\,(1-p) + 2\mu\, p\,(1-p) \\ &= \mu p + p\,(1-p)\,[\sigma^2 + \mu^2 + 2\mu + 1].\end{aligned}$$

1.16

1. The deterministic growth rates λ and r are given by

$$\lambda = \mathrm{E}[\Lambda] = \frac{\theta}{2},$$

and

$$r = \ln \lambda = \ln \left(\frac{\theta}{2}\right).$$

The environmental variance σ_e^2 is the variance of Λ, given by

$$\sigma_e^2 = \mathrm{Var}(\Lambda) = \frac{\theta^2}{12}.$$

Using the relationship between the uniform and exponential distribution, we have

$$-\ln \left(\frac{\Lambda}{\theta}\right) \sim \mathrm{Exp}(1).$$

This is used to find the stochastic growth rate s as well as σ_s^2, i.e.

$$s = \mathrm{E}[\ln \Lambda] = \ln \theta - 1,$$

and

$$\sigma_s^2 = \mathrm{Var}(\ln \Lambda) = 1.$$

2. The approximations break down because the variance in Λ is too large.
3. The expected population size is given by

$$\begin{aligned} \mathrm{E}[N_t] &= N_0 \mathrm{E}[\prod_{i=0}^{t-1} \Lambda_i] \\ &= N_0 \lambda^t \\ &= N_0 \left(\frac{\theta}{2}\right)^t. \end{aligned}$$

Since $\ln N_t$ is approximately normally distributed with mean $\ln N_0 + st$, and the median is equal to the mean in the normal distribution, the median M_t is given by

$$\begin{aligned}\ln M_t &= \ln N_0 + st \\ M_t &= N_0 e^{(\ln\theta - 1)t} \\ &= N_0 \left(\frac{\theta}{e}\right)^t .\end{aligned}$$

For $\theta = 2.2$ we have $\frac{\theta}{2} > 1$ whereas $\frac{\theta}{e} < 1$, i.e. $\mathrm{E}[N_t] \to \infty$ whereas $M_t \to 0$.

4. The above result for $\theta = 2.2$ is valid for $2 < \theta < e$, i.e. for large t the probability that $N < a$ becomes approximately 1, even if the expectation approaches infinity.

1.17

From exercise 1.14 we have

$$\begin{aligned}\mathrm{Var}(\Lambda) &= \mathrm{Var}(W) = \mathrm{Var}(B+J) \\ &= \mathrm{Var}(B) + \mathrm{Var}(J) + 2\mathrm{Cov}(B,J).\end{aligned}$$

The variance in individual fitness is the sum of the environmental variance and demographic variance, assuming the demographic covariance (not to be confused with the covariance of B and J) is zero, i.e.

$$\begin{aligned}\mathrm{Var}(W) &= \sigma_e^2 + \sigma_d^2 \\ &= \mathrm{Var}(B) + \mathrm{Var}(J) + 2\mathrm{Cov}(B,J).\end{aligned}$$

Hence, both σ_e^2 and σ_d^2 may be affected by the covariance of J and B. This will depend on how the parameters vary with the environment.

The variance of the individual contribution W increases if $\mathrm{Cov}(B,J)$ is positive and decreases if it is negative. Biologically both scenarios are possible. If the covariance is positive, individuals contribute with more offspring if they survive and fewer if they die. Such a covariance may arise for instance in species with parental care. A negative covariance can indicate a trade-off between survival and reproduction. It can also arise for instance if parents and offspring compete for the same resources.

1.18

We assume that $\Delta \ln N$ is normally distributed with mean s and variance σ_s^2. Then $\Lambda = e^{\Delta \ln N}$ is lognormally distributed with the same parameters, giving

$$
\begin{aligned}
\lambda &= \mathrm{E}[\Lambda] = e^{s+\frac{1}{2}\sigma_s^2} \\
r &= \ln \lambda = s + \frac{1}{2}\sigma_s^2 \\
\mathrm{Var}(\Lambda) &= e^{2s+\sigma_s^2}\left(e^{\sigma_s^2} - 1\right) = \lambda^2\left(e^{\sigma_s^2} - 1\right).
\end{aligned}
$$

The factor Λ may be written as

$$
\begin{aligned}
\Lambda &= \frac{1}{N}\sum_{i=1}^{N} w_i \\
&= \frac{1}{N}\sum_{i=1}^{N}(E[w] + e + d_i) \\
&= E[w] + e + \bar{d} \\
&= \lambda + e + \bar{d}.
\end{aligned}
$$

Hence

$$
\begin{aligned}
\mathrm{Var}(\Lambda) &= \sigma_e^2 + \frac{1}{N^2}\sum_{i=1}^{N}\sigma_d^2 \\
&= \sigma_e^2 + \frac{1}{N}\,\sigma_d^2.
\end{aligned}
$$

Putting together the two expressions for $\mathrm{Var}(\Lambda)$, and using a first order Taylor expansion, we find

$$
\begin{aligned}
\mathrm{Var}(\Lambda) &= \sigma_e^2 + \frac{1}{N}\,\sigma_d^2 \\
&= \lambda^2\left(e^{\sigma_s^2} - 1\right) \\
1 + \frac{1}{\lambda^2}\,\sigma_e^2 + \frac{1}{\lambda^2 N}\,\sigma_d^2 &= e^{\sigma_s^2} \\
\sigma_s^2 &= \ln\left(1 + \frac{1}{\lambda^2}\,\sigma_e^2 + \frac{1}{\lambda^2 N}\,\sigma_d^2\right) \\
\sigma_s^2 &\approx \frac{1}{\lambda^2}\,\sigma_e^2 + \frac{1}{\lambda^2 N}\,\sigma_d^2.
\end{aligned}
$$

This is inserted in the expression of s, and using the approximation $\lambda \approx 1$ we obtain

$$
\begin{aligned}
s &= r - \frac{1}{2}\sigma_s^2 \\
&\approx r - \frac{1}{2\lambda^2}\sigma_e^2 + \frac{1}{2\lambda^2 N}\,\sigma_d^2 \\
&\approx r - \frac{1}{2}\sigma_e^2 + \frac{1}{2N}\,\sigma_d^2.
\end{aligned}
$$