Evolutionary Dynamics Homework 10

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Problem 2: Probability generating function

Let Z be a random variable such that $Z \in \mathbb{Z}^+$, and p_i is its distribution, *i.e.* $\text{Prob}[Z = i] = p_i$. The probability generating function (*pgf*) of Z is a function of a symbolic argument s, defined as the expected value

$$f_Z(s) = E[s^Z] = \sum_{i=0}^{\infty} p_i s^i \quad s \in [0, 1]$$

We assume that all probability generating functions are absolutely convergent on the interval $[0, 1]$. *Note: This is a technical requirement to ensure tht summand-wise operations are permitted.*

Prove the following statements

(a) $E[Z] = f'_Z(1)$

Proof. Compute the derivative of $f_Z(s)$ with respect to s:

$$f'_Z(s) = \sum_{i=1}^{\infty} i \cdot p_i \cdot s^{i-1} \tag{1}$$

Then we have

$$f'_Z(1) = \sum_{i=1}^{\infty} i \cdot p_i, \tag{2}$$

where i is the number of individuals in a generation (definition of Z), and p_i is the probability of $Z = i$, which is exactly the definition of $E[Z]$. Therefore, $E[Z] = f'_Z(1)$. □

(b) $Var[Z] = f'_Z(1) + f''_Z(1) - f'_Z(1)^2$

Proof. Compute the second derivative of $f_Z(s)$ with respect to s:

$$f''_Z(s) = \sum_{i=2}^{\infty} i(i-1) \cdot p_i \cdot s^{i-2} \tag{3}$$

Plug in $s = 1$:

$$
\begin{aligned}
f''_Z(1) &= \sum_{i=0}^{\infty} i(i-1) \cdot p_i \\
&= \sum_{i=0}^{\infty} i^2 \cdot p_i - \sum_{i=0}^{\infty} i \cdot p_i
\end{aligned} \tag{4}
$$

According to definition and (**a**),

$$
\begin{aligned}
Var[Z] &= E[Z^2] - E[Z]^2 \\
&= E[Z^2] - f'_Z(1)^2
\end{aligned} \tag{5}
$$

By definition of expectaion, we can rewrite:

$$
E[Z^2] = \sum_{i=0}^{\infty} i^2 \cdot p_i \tag{6}
$$

Combining (4), (5), and (6), we have:

$$
\begin{aligned}
Var[Z] &= E[Z^2] - E[Z]^2 \\
&= E[Z^2] - f'_Z(1)^2 \\
&= f''_Z(1) + f'_Z(1) - f'_Z(1)^2
\end{aligned}
$$

□

(c) $d^k f_Z / ds^k|_{s=0} = k! \cdot p_k$

Proof.

$$
\begin{aligned}
\frac{df}{ds} &= \sum_{k=0}^{\infty} k \cdot p_k \cdot s^{k-1} \\
\frac{d^2 f}{ds^2} &= \sum_{k=0}^{\infty} k(k-1) \cdot p_k \cdot s^{k-2} \\
&\vdots \\
\frac{d^k f}{ds^k} &= \sum_{k=0}^{\infty} k(k-1) \cdots 2 \cdot 1 \cdot p_k \cdot s^{k-k} \\
&= k! \cdot p_k
\end{aligned}
$$

Interestingly, any $k \in [0, k-1]$ will make the term $k(k-1) \cdots 2 \cdot 1 = 0$, which means the sum will be zero. Therefore, the only term left is $k! \cdot p_k$. Hence we can directly write:

$$
\frac{d^k f_Z}{ds^k} = k! \cdot p_k \cdot s^0 = k! \cdot p_k
$$

That is also true for $s = 0$ (actually since we have s^0 in the equation, the value of s does not matter). Therefore, $d^k f_Z / ds^k|_{s=0} = k! \cdot p_k$. □

(d) $f_{Z+Y}(s) = f_Z(s) f_Y(s)$, given that i.i.d. $Z, Y \in \mathbb{Z}^+$

Proof. Following the denotation of Z, we define Prob$[Y = k] = p_k$ and $f_Y(s) = \sum_{k=0}^{\infty} p_k s^k = E[s^Y]$

$$\begin{aligned}
f_{Z+Y}(s) &= E\left[s^{Z+Y}\right] \\
&= \sum_{k=0}^{\infty}\sum_{i=0}^{\infty} p_k p_i s^{k+i} \\
&= \sum_{k=0}^{\infty}\sum_{i=0}^{\infty} p_k s^k p_i s^i \\
&= \left(\sum_{k=0}^{\infty} p_k s^k\right)\left(\sum_{i=0}^{\infty} p_i s^i\right) \\
&= f_Y(s) f_Z(s)
\end{aligned}$$

□

(e) See below.

Given random variable $Y \in \mathbb{Z}^+$ and $\{Z^{(i)}, i \geq 1\}$ is a sequence of independent identically distributed random variables in $\mathbb{Z}^+$ independent of Y, then $V = \sum_{i=1}^{Y} Z^{(i)}$ has the pgf $f_V(s) = f_Y[f_{Z^{(1)}}(s)]$.

Hint: Use (d) and the law of total expectations

Proof. Expand the RHS:

$$\begin{aligned}
f_Y[f_{Z^{(1)}}(s)] &= f_Y\left[E\left[s^{Z^{(1)}}\right]\right] \\
&= E\left[E\left[s^{Z^{(1)}}\right]^Y\right] \\
&= E\,\underbrace{\left[E\left[s^{Z^{(1)}}\right]\cdots E\left[s^{Z^{(1)}}\right]\right]}_{\text{Y times}} \\
&= \underbrace{E\left[E\left[s^{Z^{(1)}}\right]\right]\cdots E\left[E\left[s^{Z^{(1)}}\right]\right]}_{\text{Y times}} && (E[XY] = E[X]E[Y]) \\
&= E\left[s^{Z^{(1)}}\right]^Y && (E[E[X]] = E[X])
\end{aligned}$$

Expand the LHS:

$$\begin{aligned}
f_V(s) &= f_{\sum_{i=1}^{Y} Z^{(i)}}(s) \\
&= f_{Z^{(1)}}(s) f_{Z^{(2)}}(s) \cdots f_{Z^{(Y)}}(s) && \text{(by (d))} \\
&= f_{Z^{(1)}}(s)^Y && Z^{(i)} \text{ are identically distributed}
\end{aligned}$$

By definition we know

$$f_{Z^{(1)}}(s) = E\left[s^{Z^{(1)}}\right]$$

Hence we have LHS = RHS, $f_V(s) = f_Y[f_{Z^{(1)}}(s)]$. □

Problem 3: The Luria-Delbrück experiment

(a) See below.

Compute the probability $P_0(t)$ that no mutations have occured at time t. Show that the mutation rate α can be estimated as

$$\alpha = \frac{\beta \ln \rho}{1 - e^{\beta t}},$$

where ρ is the ratio of experiments in which resistance was not found (estimator for $P_0(t)$). Assume $N(0) = 1$.

Hint: Assume that in a small time interval $[t, t+\Delta t]$ the number of mutants is Poisson distributed at rate $\alpha N(t)\Delta t$ to show that

$$\begin{aligned} P_0(t) &= P(0 \text{ mutants in } [0, \Delta t]) \cdot P(0 \text{ mutants in } [\Delta t, 2\Delta t]) \cdots P(0 \text{ mutants in } [t - \Delta t, t]) \\ &\approx \exp[-\alpha N(0)\Delta t] \cdots \exp[-\alpha N(t - \Delta t)\Delta t] \end{aligned}$$

and let $\Delta t \to 0$. Explain the assumptions made in this calculation.

(b)

(c)

(d)