Solution to An Introduction to Population Genetics Theory

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Chapter 1

Models of Population Growth

Problem 1.1. *In a population with discrete generations and with fitness w, how many generations are required to double the population number?*

Proof. By the definition of fitness in discrete generations, w is given by $w = \frac{N_{i+1}}{N_i}$. This gives $N_i = w^i N_0$. Since $N_i = 2N_0$ by the given condition, $i = \log 2 / \log w$. $\square$

Problem 1.2. *How long is required for the population to double with model 2?*

Proof. By the definition of fitness in continuous generations, w is given by $w = \frac{1}{N}\frac{dN}{dt}$. This gives $\frac{1}{N}dN = wdt$ followed by $\int_{N_0}^{N} \frac{1}{N}dN = \int_{t_0}^{t} wdt$. Therefore, $\log 2 = \log \frac{N}{N_0} = w(t - t_0)$. $\square$

Problem 1.3. *A population under model 3 has reached age stability. How long, in units of λ, will be required for the population to double? What is the effective generation length, defined as the unit that will give the same answer as problem 1?*

Proof. Assume that, like the textbook, every individual lives for 5 years.

Let $n_t = (n_{0t}, n_{1t}, \ldots, n_{4t})^T$, $(b_0, b_1, \ldots, b_4)$ and $(p_0, \ldots, p_3)$ denote the number of individuals in each age, reproduction rates of each age and probability of survival of each age respectively. Then the following matrix equation holds:

$$n_t = \begin{pmatrix} n_{0,t} \\ n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ n_{4,t} \end{pmatrix} = \begin{pmatrix} b_0 & b_1 & b_2 & b_3 & b_4 \\ p_0 & 0 & 0 & 0 & 0 \\ 0 & p_1 & 0 & 0 & 0 \\ 0 & 0 & p_2 & 0 & 0 \\ 0 & 0 & 0 & p_3 & 0 \end{pmatrix} \begin{pmatrix} n_{0,t-1} \\ n_{1,t-1} \\ n_{2,t-1} \\ n_{3,t-1} \\ n_{4,t-1} \end{pmatrix} = A \cdot n_{t-1}$$

Then, by induction, we obtain $n_t = A^t n_0$. To compute the power of the matrix A, we compute the characteristic polynomial and assume that it has at least one zero:

$$\det(A - \lambda I) = \lambda^5 - b_0\lambda^4 - p_0 b_1 \lambda^3 - p_0 p_1 b_2 \lambda^2 - p_0 p_1 p_2 b_3 \lambda - p_0 p_1 p_2 p_3 b_4$$

Under suitable conditions, the polynomial above has a single positive largest(in terms of absolute value) zero λ^* and a corresponding eigenvector l^*.

For a large t, $(l^*)^t$ dominates all other power of eigenvalues, so $M^t n_0$, which is expressed as a linear combination of power of eigenvalues, can be approximated by

$$M^t n_0 \approx CM^t l = C(\lambda^*)^t l$$

where C is a constant determined by the initial condition.

N_t, the size of the population at time t, is given as the sum of entries of n_t. Therefore, $N_t = n_0 + n_1 + \ldots + n_4 = C'(\lambda^*)^t$ by the above equation. Hence, using $N_t = 2N_0$, we get $t = \log 2/\log \lambda$. □

Problem 1.4. *Suppose you know the age-specific death rates (the probability that an individual of age x will die during the next time unit). What is the life expectancy, that is, the mean length of life? What is the median length of life?*

Proof. Let $\{p_i\}_{i\in\mathbb{Z}_{\geq 0}}$ be the probability that an individual will survive during age i. Then the probability of survival until age t is given as the product of p_i from 0 to $t-1$. Thus, the expectation is given by

$$E(X) = \sum_{k=0}^{\infty}\left(k \cdot \prod_{i=0}^{k} p_i\right)$$

The median value can also be computed in a similar manner using formulas from basic probability theory. □

Problem 1.5. *Show that equation* 1.6.8*a is correct for any number of strains.*

Proof. Suppose that there are k strains and $n_1, \ldots, n_k$ individuals for each strain. The Malthusian parameters of each strain is given as $r_1, \ldots, r_k$.

Now we use the same method in the textbook.

$$\begin{aligned}
\frac{d\ln(p_1/(1-p_1))}{dt} &= \frac{d\ln(n_1/(N-n_1)}{dt} \\
&= \frac{dn_1}{dt} - \frac{d(N-n_1)}{dt} \\
&= \frac{d\ln n_1}{n_1 dt} - \frac{d\ln(N-n_1)}{(N-n_1)dt} \\
&= r_1 - \bar{r}_1
\end{aligned}$$

Here, $\bar{r}_i$ denotes the mean parameter except for the i-th strain.

Notice also that

$$\begin{aligned}\frac{d\ln(p_1/(1-p_1))}{dt} &= \frac{\ln p_1}{dt} - \frac{\ln 1 - p_1}{dt} \\ &= \frac{dp_1}{p_1 dt} - \frac{d(1-p_1)}{(1-p_1)dt} \\ &= \frac{dp_1}{p_1(1-p_1)dt}\end{aligned}$$

Putting these two equations together gives

$$\begin{aligned}\frac{dp_1}{dt} &= (r_1 - \bar{r}_1)p_1(1-p_1) \\ &= ((N-n_1)r_1 - (n_2 r_2 + \ldots + n_k r_k)) \cdot p_1 \cdot \left(\frac{1}{N-n_1}\right) \cdot (1-p_1) \\ &= (Nr_1 - (n_1 r_1 + \ldots + n_k r_k)) \cdot p_1 \cdot \left(\frac{1}{N-n_1}\right) \cdot \left(\frac{N-n_1}{N}\right) \\ &= N(r_1 - \bar{r}) \cdot p_1 \cdot \left(\frac{1}{N-n_1}\right) \cdot \left(\frac{N-n_1}{N}\right) \\ &= p_1(r - \bar{r})\end{aligned}$$

$\square$