## SOLUTION TO AN INTRODUCTION TO POPULATION GENETICS THEORY

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## Contents

1 Models of Population Growth

 $\mathbf{2}$ 

## 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,  $i = \log 2/\log w$ .

**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  $\frac{1}{N} dN = w dt$  followed by  $\int_{N_0}^N \frac{1}{N} dN = \int_{t_0}^t w dt$ . 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  $\lambda$ , 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  $n_t = (n_{0t}, n_{1t}, \dots, n_{4t})^T$ ,  $(b_0, b_1, \dots, b_4)$  and  $(p_0, \dots, p_3)$  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  $\lambda^*$  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

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

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.  $\Box$ 

**Problem 1.5.** Show that equation 1.6.8a 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.

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

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

Notice also that

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

Putting these two equations together gives

$$\frac{dp_1}{dt} = (r_1 - \bar{r}_1)p_1(1 - p_1) 
= ((N - n_1)r_1 - (n_2r_2 + \dots n_kr_k)) \cdot p_1 \cdot \left(\frac{1}{N - n_1}\right) \cdot (1 - p_1) 
= (Nr_1 - (n_1r_1 + \dots + n_kr_k)) \cdot p_1 \cdot \left(\frac{1}{N - n_1}\right) \cdot \left(\frac{N - n_1}{N}\right) 
= N(r_1 - \bar{r}) \cdot p_1 \cdot \left(\frac{1}{N - n_1}\right) \cdot \left(\frac{N - n_1}{N}\right) 
= p_1(r - \bar{r})$$