

## Introduction to Theoretical Ecology

# Average lifetime of population

To estimate the average lifetime of a population, we may focus on a population that is only dying (i.e., isolating the mortality rate of a population). Suppose a population with a constant per capita mortality rate  $\delta$ , its population dynamics  $\frac{dN}{dt}$  can be written as follows:

$$\frac{dN}{dt} = -\delta N,$$

where  $\delta$  is a positive constant. This differential equation can be solved analytically (try this yourself using the technique “separation of variables”). The solution, with initial population size  $N(t = 0) = N_0$ , is as follows:

$$N(t) = N_0 e^{-\delta t}.$$

As mentioned, the average lifetime of the population is  $\frac{1}{\delta}$ . Below we provide two ways to derive this quantity. Note that the general concept is similar: the expected value of a continuous variable  $t$  is  $\int_0^\infty t p(t) dt$ , and the goal is to find the probability density function  $p(t)$  in order to perform the integration.

### Proof 1 - Using the cumulative distribution function

Assume that the lifetime of an individual in the population is a random variable  $\mathbf{T}$ . Since the population starts to die from a population size of  $N_0$  and reaches  $N(t)$  at time  $t$ , the ratio of the at-risk (alive) individuals in the population at time  $t$  is  $\frac{N(t)}{N_0}$ . From this, we can define a survival function  $S(t)$ , which represents the probability of an individual staying alive until time  $t$ :

$$S(t) = P(\mathbf{T} \geq t) = \frac{N(t)}{N_0}.$$

To calculate the average lifetime is to calculate the expected value of  $\mathbf{T}$ , i.e.,

$$E(T) = \int_{\mathbb{R}} t f(t) dt,$$

where  $f(t)$  is the probability density function, indicating the relative possibility that the individual died at time  $t$ . From the survival function, we know that the probability of an individual living less than time  $t$  (i.e., died before time  $t$ ) is  $1 - S(t)$ . Note that this is a cumulative distribution function and thus the probability density function can be derived as its derivative:

$$f(t) = \frac{d}{dt}(1 - S(t)) = -\frac{d}{dt} \frac{N(t)}{N_0} = -\frac{d}{dt} e^{-\delta t} = \delta e^{-\delta t}.$$

Then, we can derive the average lifetime by the technique “integration by parts” (for more detail on this technique please refer to the end of this document):

$$E(T) = \int_{\mathbb{R}} t f(t) dt = \int_{\mathbb{R}} t \delta e^{-\delta t} dt = \frac{1}{\delta}.$$

□

## Proof 2 - without random variable assumption

Here, we try to derive the probability density function directly. The probability that an individual dies within  $t_0$  to  $t_0 + \Delta t$ , i.e., the probability of an individual has lifetime within  $t_0$  to  $t_0 + \Delta t$ , can be estimated by:

$$\begin{aligned} \frac{N(t_0) - N(t_0 + \Delta t)}{N_0} &= e^{-\delta t_0} - e^{-\delta(t_0 + \Delta t)} \text{ (recall the Taylor series)} \\ &\approx \delta e^{-\delta t_0} \Delta t \text{ (when } \Delta t \text{ is small)} \\ &= \delta e^{-\delta t_0} dt \end{aligned}$$

Then, since the probability is the area under the probability density function, we recognize that  $\delta e^{-\delta t_0}$  is the probability density function. We can then calculate the average lifetime by the technique “integration by parts”:

$$E = \int_0^{\infty} t \delta e^{-\delta t} dt = \frac{1}{\delta}$$

□

## Details of integration by parts

Integration by parts can be thought of as an integral version of the product rule of differentiation. Consider two continuous functions  $u(t)$  and  $v(t)$ , the general form of integration by parts can be written as:

$$\int_a^b u(t)v'(t) dt = [u(t)v(t)]_a^b - \int_a^b v(t)u'(t) dt.$$

For our specific case, consider  $u(t) = t$  and  $v(t) = -e^{-\delta t}$ . What follows is  $du = u'(t) dt = dt$  and  $dv = v'(t) dt = \delta e^{-\delta t} dt$ , thereby giving the solution:

$$\begin{aligned}\int_0^\infty t\delta e^{-\delta t} dt &= t \cdot (-e^{-\delta t}) \Big|_{t=0}^\infty - \int_0^\infty -e^{-\delta t} dt \\ &= (0 - 0) + \int_0^\infty e^{-\delta t} dt \\ &= -\frac{1}{\delta} e^{-\delta t} \Big|_{t=0}^\infty \\ &= \frac{1}{\delta}\end{aligned}$$

□