4.2 General birth and death dynamics of a single population

$$0 \underset{w_1}{\overset{u_0}{\rightleftharpoons}} 1 \ \cdots \underset{w_{n-1}}{\rightleftharpoons} n-1 \underset{w_n}{\overset{u_{n-1}}{\rightleftharpoons}} n \underset{w_{n+1}}{\overset{u_n}{\rightleftharpoons}} n+1 \overset{u_{n+1}}{\rightleftharpoons} \cdots \tag{59}$$

in which u_ℓ and w_ℓ are the birth and death rates with population ℓ. They are not rate per capita. They are the rates for increasing one individual and decrease one individual, respectively.

Let us consider the simplest case of with birth and death rates, per capita, b and d. Then one has $u_n = nb$ and $w_n = nd$. Let $X(t)$ be the population in numbers, and $p_n(t) = \Pr\{X(t) = n\}$ be the probability of having n individuals in the population at time t. Then

$$\frac{d}{dt}p_n(t) = (n-1)bp_{n-1} - (nb+nd)p_n + (n+1)dp_{n+1}, \ \ (n \geq 0). \tag{60}$$

$$\begin{aligned}
\frac{d}{dt}\langle X(t)\rangle &= \frac{d}{dt}\left(\sum_{n=0}^{\infty} np_n(t)\right) \\
&= \sum_{n=0}^{\infty}(n-1)^2bp_{n-1} - n^2(b+d)p_n + (n+1)^2dp_{n+1} \\
&\quad + \sum_{n=1}^{\infty}(n-1)bp_{n-1} - \sum_{n=0}^{\infty}(n+1)dp_{n+1} \\
&= \sum_{n=1}^{\infty}(n-1)bp_{n-1} - \sum_{n=0}^{\infty}(n+1)dp_{n+1} \\
&= (b-d)\langle X(t)\rangle. \qquad (61)
\end{aligned}$$

Indeed, the dynamics for the mean $\langle X(t)\rangle$ depends only one the difference of $b - d$. However, one can also compute the variance of $X(t)$:

$$Var[X(t)] = \langle X^2(t)\rangle - \langle X(t)\rangle^2, \tag{62}$$

in which

$$\langle X^2(t)\rangle = \sum_{n=0}^{\infty} n^2 p_n(t). \tag{63}$$

Then,

$$
\begin{aligned}
\frac{d}{dt}\langle X^2(t)\rangle &= \frac{d}{dt}\sum_{n=0}^{\infty} n^2 p_n(t) \\
&= \sum_{n=0}^{\infty} b\left[n^2(n-1)p_{n-1} - n^3 p_n\right] + d\left[n^2(n+1)p_{n+1} - n^2 p_n\right] \\
&= \sum_{n=0}^{\infty} b\left[n^2(n-1)p_{n-1} - n(n+1)^2 p_n + (2n+1)np_n\right] \\
&\qquad + d\left[n^2(n+1)p_{n+1} - n(n-1)^2 p_n - (2n-1)np_n\right] \\
&= \sum_{n=0}^{\infty} \left[b(2n+1)n - d(2n-1)n\right] p_n \\
&= 2b\langle X^2(t)\rangle + b\langle X(t)\rangle - 2d\langle X^2\rangle + d\langle X(t)\rangle. \qquad (64)
\end{aligned}
$$

$$
\begin{aligned}
\frac{d}{dt}Var[X(t)] &= \frac{d}{dt}\left[\langle X^2(t)\rangle - \langle X(t)\rangle^2\right] \\
&= 2(b-d)\langle X^2(t)\rangle + (b+d)\langle X(t)\rangle - 2\langle X(t)\rangle(b-d)\langle X(t)\rangle \\
&= 2(b-d)\; Var[X(t)] + (b+d)\langle X(t)\rangle. \qquad (65)
\end{aligned}
$$

The differential equation for $Var[X(t)]$,

$$\frac{d}{dt}Var[X(t)] = 2(b-d)Var[X(t)] + (b+d)\langle X(t)\rangle, \qquad (66)$$

is a linear, constant coefficient, inhomogeneous, first-order ordinary differential equation. Its solution can be obtained using the procedure in Sec. 4.4. Therefore, the mean and the variance of the population $X(t)$ are

$$\langle X(t)\rangle = X_o e^{(b-d)t}, \qquad (67)$$

$$Var[X(t)] = X_o\left(\frac{b+d}{b-d}\right)e^{(b-d)t}\left(e^{(b-d)t}-1\right). \qquad (68)$$

The relative variance

$$\frac{Var[X(t)]}{\langle X(t)\rangle^2} = \frac{1}{X_o}\left(\frac{b+d}{b-d}\right)\left(1-e^{-(b-d)t}\right). \qquad (69)$$

We see that for the same *net growth rate* $r = b-d$, larger the $b+d$, larger the variance. In a realistic population dynamics, the different rates of birth and death, b and d, matter; not just their difference $r = b-d$.

4.3 General nonlinear differential equation for a single population

For general birth and death rates u_n and w_n in (59), in the limit of population size goes to infinity, there is a single, deterministic differential equation that describes the dynamics of the stochastic model; the randomness will be gone!

Let us focus on the "state" when the population has precisely k individuals, with birth rate u_k and death rate w_k. Note they are not per capita birth and death rates; that would be $\frac{u_k}{k}$ and $\frac{w_k}{k}$. Because both birth event and death event have exponentially distributed waiting times, the waiting time for the next event, either birth or death, is $u_k + w_k$. But what are the relative probabilities for the two events? We shall show now that they are proportional to u_k and w_k.

To do this, we ask the following statistic question: T_1 and T_2 are two independent exponentially distributed waiting times, and $T^* = \min\{T_1, T_2\}$ is the wait time for the next event. For $T^* = t$, what is the probability that of $T_1 < T_2$? We have the joint probability density function for T_1 and T_2

$$f_{T_1T_2}(t_1, t_2) = f_{T_1}(t_1) f_{T_2}(t_2) = \lambda_1\lambda_2 e^{-(\lambda_1+\lambda_2)t}, \tag{70}$$

where λ_1 and λ_2 are the rates of T_1 and T_2, respectively. Then the probability

$$\begin{aligned}
& \Pr\{t < T^* \le t + \mathrm{d}t\} \\
= \;& \Pr\{t < T_1 \le t + \mathrm{d}t | T_1 < T_2\} + \Pr\{t < T_2 \le t + \mathrm{d}t | T_2 < T_1\} \\
= \;& \Pr\{t < T_1 \le t + \mathrm{d}t\} \times \Pr\{t \le T_2\} + \Pr\{t < T_2 \le t + \mathrm{d}t\} \times \Pr\{t \le T_1\} \\
= \;& \lambda_1 e^{-\lambda_1 t}\mathrm{d}t\, e^{-\lambda_2 t} + \lambda_2 e^{-\lambda_2 t}\mathrm{d}t\, e^{-\lambda_1 t}.
\end{aligned} \tag{71}$$

It is clear that the first term in (71) is when $T_1 < T_2$ and the second term is when $T_1 > T_2$. Therefore, given that $t < T^* \le t + \mathrm{d}t$, we have the probabilities for event 1 and event 2:

$$p_1 = \frac{\lambda_1 e^{-\lambda_1 t}\mathrm{d}t\, e^{-\lambda_2 t}}{\lambda_1 e^{-\lambda_1 t}\mathrm{d}t\, e^{-\lambda_2 t} + \lambda_2 e^{-\lambda_2 t}\mathrm{d}t\, e^{-\lambda_1 t}} = \frac{\lambda_1}{\lambda_1 + \lambda_2}, \tag{72a}$$

$$p_2 = \frac{\lambda_2 e^{-\lambda_2 t}\mathrm{d}t\, e^{-\lambda_1 t}}{\lambda_1 e^{-\lambda_1 t}\mathrm{d}t\, e^{-\lambda_2 t} + \lambda_2 e^{-\lambda_2 t}\mathrm{d}t\, e^{-\lambda_1 t}} = \frac{\lambda_2}{\lambda_1 + \lambda_2}. \tag{72b}$$

Therefore, using the result in (72), we have the waiting time for the next event being T^*, which is exponentially distributed with rate $u_k + w_k$, and the probability of increasing one individual with probability $\frac{u_k}{u_k+w_k}$, and decreasing one individual with probability $\frac{w_k}{u_k+w_k}$. Thus, the expected value for the change of the number of individual is

$$\frac{u_k}{u_k + w_k}(+1) + \frac{w_k}{u_k + w_k}(-1) = \frac{u_k - w_k}{u_k + w_k}. \tag{73}$$

And the rate of the mean population change :

$$\left(\frac{u_k - w_k}{u_k + w_k}\right)\big(u_k + w_k\big) = u_k - w_k. \tag{74}$$

For an infinitely large population, the randonness will be gone, and the rate of population change is the mean value. Therefore, $\frac{\mathrm{d}}{\mathrm{d}t}\langle k\rangle = u_k - w_k$.