6 Continuous-Time Birth and Death Chains

Angela Peace

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Lecture notes follow: Allen, Linda JS. An introduction to stochastic processes with applications to biology. CRC Press, 2010.

General Birth and Death Processes

- Let $X(\Delta t)$ denote the change in the process from t to Δt:

$$\Delta X(t) = X(t + \Delta t) - X(t)$$

- Standard notation for birth and death rates for $X(t) = i$

$$\lambda_i = \text{ birth rate} \qquad \& \qquad \mu_i = \text{ death rate}$$

- The CTMC $\{X(t) : t \in [0, \infty)\}$ may have a finite or infinite state space: $\{0, 1, ..., N\}$, $\{0, 1, 2...\}$

General Birth and Death Processes

The transition probabilities:

$$p_{i+j,i}(\Delta t) = \text{Prob}\{\Delta x(t) = j | X(t) = i\}$$
$$= \begin{cases} \lambda_i \Delta t + o(\Delta t), & j = 1 \\ \mu_i \Delta t + o(\Delta t), & j = -1 \\ 1 - (\lambda_i + \mu_i)\Delta t + o(\Delta t), & j = 0 \\ o(\Delta t), & j \neq -1, 0, 1 \end{cases}$$

where $\lambda_i, \mu_i \geq 0$ for $i = 0, 1, 2, ...$ and $\mu_0 = 0$

- If $\lambda_0 > 0$ then there is immigration.
- Δt is sufficiently small so at most one change in state can occur in the time interval
  - a birth $i \to i + 1$
  - a death $i \to i = 1$

General Birth and Death Processes

- The forward Kolmogorov differential equations can be derived directly from the transition probabilities.
- Consider the transition probability $p_{ji}(t+\Delta t)$

$$\begin{aligned} p_{ji}(t+\Delta t) &= p_{j-1,i}(t)[\lambda_{j-1}\Delta t + o(\Delta t)] \\ &+ p_{j+1,i}(t)[\mu_{j+1}\Delta t + o(\Delta t)] \\ &+ P_{ji}(t)[1-(\lambda_j+\mu_j)\Delta t + o(\Delta t)] \\ &+ \sum_{k\neq -1,0,1}^{\infty} p_{j+k,i}(t)o(\Delta t) \end{aligned}$$

$$= p_{j-1,i}(t)\lambda_{j-1}\Delta t + p_{j+1,i}(t)\mu_{j+1}\Delta t + P_{ji}(t)[1-(\lambda_j+\mu_j)\Delta t] + o(\Delta t)$$

- If $j=0$ then $p_{0i}(t+\Delta t) = p_{1i}(t)\mu_1\Delta t + p_{0i}(t)[1-\lambda_0\Delta t] + o(\Delta t)$
- If $j=N$ and $\lambda_N = 0$, $p_{kN}(t) = 0$ for $K > N$ then $p_{Ni}(t+\Delta t) = p_{N-1,i}(t)\lambda_{N-1}\Delta t + p_{Ni}(t)[1-\mu_N\Delta t] + o(\Delta t)$

General Birth and Death Processes

Question

Given the transition probabilities of the finite general birth and death process

$$
\begin{aligned}
p_{ji}(t+\Delta t) &= p_{j-1,i}(t)\lambda_{j-1}\Delta t + p_{j+1,i}(t)\mu_{j+1}\Delta t + P_{ji}(t)[1-(\lambda_j+\mu_j)\Delta t] \\
p_{0i}(t+\Delta t) &= p_{1i}(t)\mu_1\Delta t + p_{0i}(t)[1-\lambda_0\Delta t] + o(\Delta t) \\
p_{Ni}(t+\Delta t) &= p_{N-1,i}(t)\lambda_{N-1}\Delta t + p_{Ni}(t)[1-\mu_N\Delta t] + o(\Delta t)
\end{aligned}
$$

1. Derive the forward Kolmogorov differential equations for

$$\frac{dp_{ji}(t)}{dt}, \qquad \frac{dp_{0i}(t)}{dt}, \qquad \& \qquad \frac{dp_{Ni}(t)}{dt}$$

2. What is the generator matrix Q?
3. What is the transition matrix T of the embedded DTMC?

Stationary Probability Distribution

π for general CTMC

Stationary probability distribution $\pi = (\pi_0, \pi_1, ...)^T$ of a CTMC with generator matrix Q satisfies

$$Q\pi = 0, \qquad \sum_{i=0}^{\infty} \pi_i = 1, \qquad \& \qquad \pi_i \geq 0$$

Stationary Probability Distribution

Theorem 6.1: π for birth and death processes

Let $\{X(t) : t \in [0, \infty)\}$, be a general birth and death chain. If the state space is infinite, $\{0, 1, 2, ...\}$, a unique positive stationary probability distribution exists iff $\mu_i > 0$ and $\lambda_{i-1} > 0$ for $i = 1, 2, ...$, and

$$\sum_{i=1}^{\infty} \frac{\lambda_0 \lambda_1 \cdots \lambda_{i-1}}{\mu_1 \mu_2 \cdots \mu_i} < \infty$$

- For $i = 1, 2, ...$, the stationary probability distribution equals

$$\pi_i = \frac{\lambda_0 \lambda_1 \cdots \lambda_{i-1}}{\mu_1 \mu_2 \cdots \mu_i} \pi_0 \qquad \& \qquad \pi_0 = \frac{1}{1 + \sum_{i=1}^{\infty} \frac{\lambda_0 \lambda_1 \cdots \lambda_{i-1}}{\mu_1 \mu_2 \cdots \mu_i}}$$

- If the state space is finite $\{0, 1, 2, ..., N\}$ a unique positive stationary probability distribution exists iff $\mu_i > 0$ and $\lambda_{i-1} > 0$ for $i = 1, 2, ..., N$. Here the above summations extend from $i = 1, 2, ..., N$
- If $\lambda_0 = 0$ and $\mu_i > 0$ for $i \geq 1$, then $\pi = (1, 0, 0, ...)^T$

Stationary Probability Distribution

Example

Suppose a continuous-time birth and death Markov chain had birth and death rates $\lambda_i = b$ and $\mu_i = id$ for $i = 0, 1, 2, ...$

1. Show that the unique stationary probability distribution is

$$\pi_i = \frac{(b/d)^i}{i!} e^{-b/d}$$

Simple Birth Process

- Let $X(t)$ represent the population size at time t
- Assume $X(0) = N$ so that $p_i(0) = \delta_{iN}$.
- The only event is a birth
- The population can only increase in size
- For Δt sufficiently small the transition probabilities are

$$
\begin{aligned}
p_{i+j,i}(\Delta t) &= \text{Prob}\{\Delta x(t) = j | X(t) = i\} \\
&= \begin{cases} \lambda i \Delta t + o(\Delta t), & j = 1 \\ 1 - \lambda i \Delta t + o(\Delta t), & j = 0 \\ o(\Delta t), & j \geq 2 \\ 0, & j < 0 \end{cases}
\end{aligned}
$$

Simple Birth Process

- The probabilities $p_i(t) = \text{Prob}\{X(t) = i\}$ are solutions of the forward Kolmogorov differential equations $\frac{dp}{dt} = Qp$ where

$$\frac{dp_i(t)}{dt} = \lambda(i-1)p_{i-1}(t) - \lambda i p_i(t), \qquad i = N, N+1, ...,$$
$$\frac{dp_i(t)}{dt} = 0, \qquad i = 0, 1, ..., N-1$$

- with initial conditions $p_i(0) = \delta_{iN}$.
- The state space is $\{N, N+1, ...\}$

Simple Birth Process

- The generating functions for the simple birth process correspond to a negative binomial distribution.
- We can see this by deriving a PDE for the p.g.f. and the m.g.f. and solving them using the method of characteristics.

Working through the details

1. Multiply the forward equations by z^i and sum over i to get the p.g.f.

$$\frac{\partial \mathcal{P}(z,t)}{\partial t} = \lambda z(z-1)\frac{\partial \mathcal{P}}{\partial z}$$

   with initial conditions $\mathcal{P}(z,0) = Z^N$.
2. Derive the PDE for the m.g.f. from the above PDE using the change of variables: $z = e^{\theta}$.
3. Use the method of characteristics to find the solutions $M(\theta, t)$
4. Write the solution for the p.g.f by changing the variables back: $\theta = \ln z$

Simple Birth Process

- The m.g.f. for the simple birth process is
$$M(\theta, t) = [1 - e^{\lambda t}(1 - e^{-\theta})]^{-N}$$
- The p.g.f. for the simple birth process is
$$\mathcal{P}(z, t) = \frac{(pz)^N}{(1 - zq)^N}$$
where $p = e^{-\lambda t}$ and $q = 1 - e^{-\lambda t}$.
- The probabilities can be written as
$$p_n(t) = \binom{n-1}{n-N} e^{-\lambda N t}(1 - e^{-\lambda t})^{n-N}, \qquad n = N, N+1, \ldots$$
- The mean and variance are
$$m(t) = Ne^{\lambda t} \qquad \& \qquad \sigma^2(t) = Ne^{2\lambda t}(1 - e^{-\lambda t})$$
- The mean corresponds to exponential growth
- The variance increases exponentially with time

Simple Death Process

- Let $X(t)$ represent the population size at time t
- Assume $X(0) = N$ so that $p_i(0) = \delta_{iN}$.
- The only event is a death
- The population can only decrease in size
- For Δt sufficiently small the transition probabilities are

$$p_{i+j,i}(\Delta t) = \text{Prob}\{\Delta x(t) = j | X(t) = i\}$$

$$= \begin{cases} \mu i \Delta t + o(\Delta t), & j = -1 \\ 1 - \mu i \Delta t + o(\Delta t), & j = 0 \\ o(\Delta t), & j \geq 2 \\ 0, & j < 0 \end{cases}$$

- The state space is $\{0, 1, 2, ..., N\}$

Simple Death Process

- The forward Kolmogorov equations are

$$\frac{dp_i(t)}{dt} = \mu(i+1)p_{i+1}(t) - \mu i p_i(t), \qquad i = 0, 1, ...N-1$$
$$\frac{dp_N(t)}{dt} = -\mu N p_N(t)$$

- Initial conditions: $p_{i0} = \delta_{iN}$
- Here 0 is an absorbing state
- The stationary probability distribution is $\pi_i = (1, 0, ...0)^T$.

Simple Death Process

- The generating function technique and method of characteristics are used to find the probability distribution
- The PDE for the p.g.f is

$$\frac{\partial \mathcal{P}(z,t)}{\partial t} = \mu(1-z)\frac{\partial \mathcal{P}}{\partial z}, \quad \mathcal{P}(z,0) = z^N$$

- The PDE for the m.g.f is

$$\frac{\partial M}{\partial t} = \mu(e^{-\theta} - 1)\frac{\partial M}{\partial \theta}, \quad M(\theta,0) = e^{N\theta}$$

- Applying the method of characteristics yields the solutions:

$$\mathcal{P}(z,t) = (1 - e^{-\mu t} + e^{-\mu t} z)^N \quad \& \quad M(\theta,t) = (1 - e^{-\mu t}(1 - e^{\theta}))^N$$

Simple Death Process

- The p.g.f had the form $\mathcal{P}(z,t) = (q + pz)^N$ where $p = e^{-\mu t}$ and $q = 1 - e^{-\mu t}$
- This corresponds to a binomial distribution $b(N,p)$
- For $i = 0, 1, ..., N$ the probabilities satisfy

$$p_i(t) = \binom{N}{i} p^i q^{N-i}$$

- The mean and variance for a binomial distribution $b(N,p)$ are $m(t) = Np$ and $\sigma^2(t) = Npq$:

$$m(t) = Ne^{-\mu t} \qquad \& \qquad \sigma^2(t) = Ne^{-\mu t}(1 - e^{-\mu t})$$

- The mean corresponds to exponential decay
- The variance decreases exponentially with time

Simple Birth and Death Process

- Let $X(t)$ represent the population size at time t
- Assume $X(0) = N$ so that $p_i(0) = \delta_{iN}$.
- An event can be a birth or a death
- The population can increase or decrease in size
- For Δt sufficiently small the transition probabilities are

$$p_{i+j,i}(\Delta t) = \text{Prob}\{\Delta x(t) = j | X(t) = i\}$$
$$= \begin{cases} \mu i \Delta t + o(\Delta t), & j = -1 \\ \lambda i \Delta t + o(\Delta t), & j = 1 \\ 1 - (\lambda + \mu) i \Delta t + o(\Delta t), & j = 0 \\ o(\Delta t), & j \neq -1, 0, 1 \end{cases}$$

- The state space is $\{0, 1, 2, ..., N\}$
- $\lambda_0 = 0$ and $\pi = (1, 0, ...,)^T$

Simple Birth and Death Process

- The forward Kolmogorov equations are

$$\frac{dp_i(t)}{dt} = \lambda(i-1)P_{i-1}(t) + \mu(i+1)p_{i+1}(t) - (\lambda+\mu)ip_i(t)$$
$$\frac{dp_0(t)}{dt} = \mu p_1(t)$$

for $i = 0, 1, ...$ with initial conditions $p_i(0) = \delta_{iN}$.

- An explicit solution to $P(t)$ is not possible but we can determine the moments of this distribution by using the generating function technique
- First-order partial differential equations can be derived for the p.g.f and m.g.f.

Simple Birth and Death Process

Generating function technique

- $\mathcal{P}(z,t) = \sum_{i=0}^{\infty} p_i(t) z^i$ is the p.g.f. and $M(\theta, t) = \mathcal{P}(e^\theta, t)$ the m.g.f.
- Multiply $P(t) = QP(t)$ by z^i and sum over i

$$\sum_{i=0}^{\infty} z^i \frac{dp_i(t)}{dt} = \sum_{i=0}^{\infty} z^i [\lambda(i-1)p_{i-1}(t) + \mu(i+1)p_{i+1}(t) - (\lambda+\mu) i p_i(t)]$$

- Interchange differentiation and integration, evaluate at $z = 1$ to obtain the PDE for the p.g.f.

$$\frac{\partial \mathcal{P}(z,t)}{\partial t} = [\mu(1-z) + \lambda z(z-1)] \frac{\partial \mathcal{P}}{\partial z}, \qquad \mathcal{P}(z,0) = z^N$$

- The change of variables $z = e^\theta$ leads to the m.g.f. equation

$$\frac{\partial M(\theta,t)}{\partial t} = [\mu(e^{-\theta} - 1) + \lambda(e^\theta - 1)] \frac{\partial M}{\partial \theta}, \qquad M(\theta, 0) = e^{\theta N}$$

Simple Birth and Death Process

Generating function technique

- Application of the method of characteristics to the m.g.f yields the ODES

$$\frac{dt}{d\tau} = 1, \quad \frac{d\theta}{\mu(e^{-\theta} - 1) + \lambda(e^{\theta} - 1)} = -d\tau, \quad \& \quad \frac{dM}{d\tau} = 0$$

- with initial conditions

$$t(s, 0) = 0, \quad \theta(s, 0) = s, \quad \& \quad M(s, 0) = e^{sN}$$

Simple Birth and Death Process

Generating function technique

- The m.g.f. is

$$M(\theta, t) = \begin{cases} \left(\frac{e^{t(\mu-\lambda)}(\lambda e^{\theta}-\mu)-\mu(e^{\theta}-1)}{e^{t(\mu-\lambda)}(\lambda e^{\theta}-\mu)-\lambda(e^{\theta}-1)} \right)^{N}, & \text{if } \lambda \neq \mu \\ \left(\frac{1-(\lambda t-1)(e^{\theta}-1)}{1-\lambda t(e^{\theta}-1)} \right)^{N}, & \text{if } \lambda = \mu \end{cases}$$

- Making the change of variables $\theta = \ln z$ yields the p.g.f

$$\mathcal{P}(z, t) = \begin{cases} \left(\frac{e^{t(\mu-\lambda)}(\lambda z-\mu)-\mu(z-1)}{e^{t(\mu-\lambda)}(\lambda z-\mu)-\lambda(z-1)} \right)^{N}, & \text{if } \lambda \neq \mu \\ \left(\frac{1-(\lambda t-1)(z-1)}{1-\lambda t(z-1)} \right)^{N}, & \text{if } \lambda = \mu \end{cases}$$

Simple Birth and Death Process

Generating function technique

- Unlike, the simple birth process and the simple death process, these generating functions can not be associated with a well known probability distribution.
- But, probabilities and moments associated with the process can be obtained directly from the generating functions.
- Recall that

$$\mathcal{P}(z,t) = \sum_{i=0}^{\infty} p_i(t) z^i, \qquad \& \qquad p_i(t) = \frac{1}{i!} \frac{\partial^i \mathcal{P}}{\partial z^i}\bigg|_{z=0}$$

- The first term in the series expansion of $\mathcal{P}(z,t)$ are $p_0(t) = \mathcal{P}(0,t)$:

$$p_0(t) = \begin{cases} \left(\frac{\mu - \mu e^{(\mu-\lambda)t}}{\lambda - \mu e^{(\mu-\lambda)t}}\right)^N, & \text{if } \lambda \neq \mu \\ \left(\frac{\lambda t}{1+\lambda t}\right)^N, & \text{if } \lambda = \mu \end{cases}$$

Simple Birth and Death Process

Generating function technique

- The probability of extinction has a simple expression when $t \to \infty$

$$p_0(\infty) = \lim_{t\to\infty} p_0(t) = \begin{cases} 1, & \text{if } \lambda \le \mu \\ \left(\frac{\mu}{\lambda}\right)^N, & \text{if } \lambda > \mu \end{cases}$$

- The mean and variance for $\lambda \neq \mu$ are

$$m(t) = Ne^{(\lambda-\mu)t} \quad \& \quad \sigma^2(t) = N\left(\frac{\lambda+\mu}{\lambda-\mu}\right) e^{(\lambda-\mu)t}(e^{(\lambda-\mu)t} - 1)$$

- The mean corresponds to exponential growth when $\lambda > \mu$ and exponential decay when $\lambda < \mu$
- The mean and variance for $\lambda = \mu$ are

$$m(t) = N \quad \& \quad \sigma^2(t) = 2N\lambda t$$

Simple Birth and Death Process

Population Extinction

- The probability of extinction has a simple expression with $t \to \infty$:

$$p_0(t) = \begin{cases} 1 & \text{if } \lambda \leq \mu \\ \left(\frac{\mu}{\lambda}\right)^N & \text{if } \lambda > \mu \end{cases}$$

- This is similar to the gambler's ruin problem, a semi-infinite random walk with an absorbing barrier at $x = 0$.
    - μ is probability of losing a game
    - λ is the probability of wining a game
    - If probability of losing (death) is greater than or equal to the probability of winning (birth), then, in the long run the probability of losing all of the initial capital N (probability of absorption) approaches 1.
    - If the probability of winning is greater than the probability of losing, then, in the long run, the probability of losing all of the initial capital is $(\mu/\lambda)^N$

Population Extinction Theorem

Let $\mu_0, \lambda_0 = 0$ in a general birth and death chain with $X(0) = m \geq 1$

1. Suppose $\mu_i > 0$ and $\lambda_i > 0$ for $i = 12, ...,$

$$\text{If } \sum_{i=1}^{\infty} \frac{\mu_1 \mu_2 \cdots \mu_i}{\lambda_1 \lambda_2 \cdots \lambda_i} = \infty \text{ then } \lim_{t \to \infty} p_0(t) = 1$$

$$\text{If } \sum_{i=1}^{\infty} \frac{\mu_1 \mu_2 \cdots \mu_i}{\lambda_1 \lambda_2 \cdots \lambda_i} < \infty \text{ and } p_0(t) \to 0 \text{ as } m \to \infty$$

$$\text{then } \lim_{t \to \infty} p_0(t) = \frac{\sum_{i=m}^{\infty} \frac{\mu_1 \mu_2 \cdots \mu_i}{\lambda_1 \lambda_2 \cdots \lambda_i}}{1 + \sum_{i=1}^{\infty} \frac{\mu_1 \mu_2 \cdots \mu_i}{\lambda_1 \lambda_2 \cdots \lambda_i}}$$

2. Suppose $\mu_i > 0$ for $i = 1, 2, ...$ and $\lambda_i > 0$ for $i = 1, 2, ..., N - 1$ and $\lambda_i = 0$ for $i = N, N + 1, ...$ Then

$$\lim_{t \to \infty} p_0(t) = 1$$

First Passage Time

- The time until the process reachers a certain stage for the first time is the **first passage time**.
- Suppose a population size is a and we want to find the time it takes until it reaches a size of b ($b < a$ or $b > a$).
- The first passage time problems are related to the **backward Kolmogorov equations**.
- We will see how to compute the expected time to extinction

First Passage Time

Time to Extinction

- Suppose $\lambda_0, \mu_0 = 0$ and $\lim_{t \to \infty} p_0(t) = 1$ in a finite MC.
- Define $\tau = (\tau_1, \tau_2, ..., \tau_n)$ as the expected time to extinction
- τ is the solution of the following system

$$\tau^T \tilde{Q} = -1^T$$

- where $\tilde{Q}$ is the $n \times n$ generator matrix with the first row and column deleted.
- These elements are deleted to correspond with $\tau_0 = 0$.

Logistic Growth Process

- Recall deterministic logistic model:

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right), \qquad n(0) = n_o > 0$$

- where r is the intrinsic growth rate and K is the carrying capacity
- $\lim_{t\to\infty} n(t) = K$
- The right hand side equals the birth minus the death rate

$$\lambda_n - \mu_n = rn - \frac{r}{k}n^2$$

- Similar to the case for DTMC there are ways to describe a stochastic logistic growth process

Logistic Growth Process

Recall the forumlation for DTMC

DTMC Stochastic Logistic Growth Model

Case a:

$$b_i = r\left(i - \frac{i^2}{2K}\right) \text{ and } d_i = r\frac{i^2}{2K}$$

for $i = 0, 1, 2, ..., 2K$

Case b:

$$b_i = \begin{cases} ri, & i = 0, 1, 2, ..., N \\ 0, & i \geq N \end{cases} \text{ and } d_i = r\frac{i^2}{K}$$

for $i = 0, 1, 2, ..., N$

Logistic Growth Process

Analogous forumlation for CTMC

CTMC Stochastic Logistic Growth Model

Case a:

$$\lambda_i = r\left(i - \frac{i^2}{2K}\right) \text{ and } \mu_i = r\frac{i^2}{2K}$$

for $i = 0, 1, 2, ..., 2K$

Case b:

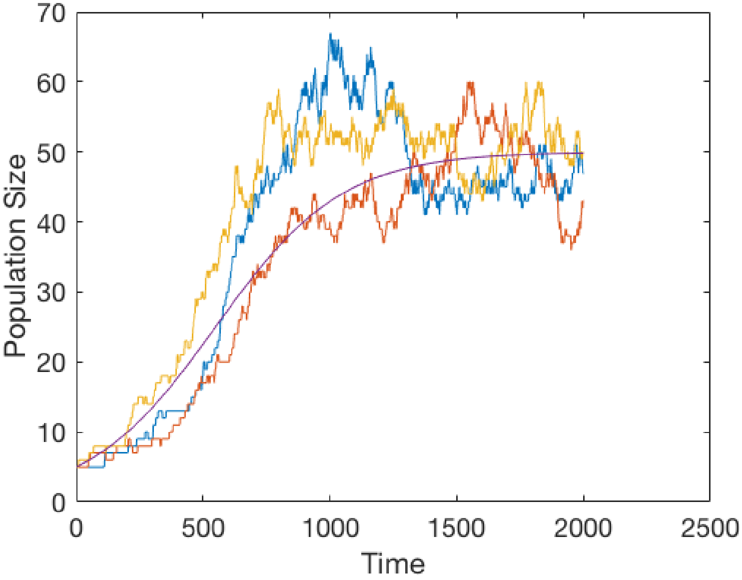
$$\lambda_i = \begin{cases} ri, & i = 0, 1, 2, ..., N \\ 0, & i \geq N \end{cases} \text{ and } d_i = r\frac{i^2}{K}$$

for $i = 0, 1, 2, ..., N$

Both cases correspond to the deterministic system

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

Logistic Growth Process



Logistic Growth Process

- Unlike the deterministic Logistic growth model, In the limit the stochastic logistic growth process does not approach K.
- Extinction is an absorbing state
- For large population size, the time to extinction is very large (but finite)