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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

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STOCHASTIC POPULATION THEORY
BIRTH AND DEATH PROCESSES

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The simple birth process

$X(t) = \#$ of individuals at time t

$p_n(t) = P\{X(t) = n\}$

$\lambda \Delta t$ = chance of a given individual producing a new one in time Δt

Time elapsing between birth and division into two daughter cells has negative exponential distribution:

$$f(u) = \lambda e^{-\lambda u} \qquad , \quad 0 \le u < \infty$$

Probability that the whole population $X(t)$ gives rise to a birth in Δt is then (to first order): $\lambda X(t) \Delta t$

$$p_n(t+\Delta t) = p_{n-1}(t)\,\lambda(n-1)\Delta t + p_n(t)(1-\lambda\Delta t)^n$$

$$\simeq p_{n-1}(t)\,\lambda(n-1)\Delta t + p_n(t)(1-\lambda n \Delta t)$$

$\therefore$

$$\frac{p_n(t+\Delta t) - p_n(t)}{\Delta t} = p_{n-1}(t)\,\lambda(n-1) - p_n(t)\,\lambda n$$

$\therefore$

$$\begin{cases} \dfrac{dp_n}{dt} = \lambda(n-1)p_{n-1} - \lambda n p_n \\ X(0) = a > 0 \quad , \quad n = a, a+1, a+2, \ldots \end{cases}$$

$p_{a-1} = 0$ in the first equation.

$$\frac{dp_a}{dt} = -\lambda a p_a$$

$\therefore$

$$p_a(t) = \text{const}\cdot e^{-\lambda a t}$$

Set $p_a(0) = 1$

$\therefore$

$$\boxed{p_a(t) = e^{-\lambda a t}}$$

Next:

$$\begin{cases} \dfrac{dp_{a+1}(t)}{dt} = \lambda a \underbrace{p_a(t)}_{= e^{-\lambda a t}} - \lambda(a+1)p_{a+1}(t) \\ p_{a+1}(0) = 0 \end{cases}$$

$\therefore$

$$\boxed{p_{a+1}(t) = a e^{-\lambda a t}}$$

In general:

$$p_{a+k}(t) = \binom{a+k-1}{a-1} e^{-\lambda a t}\left(1 - e^{-\lambda t}\right)^k \qquad k = 0, 1, 2 \ldots$$

$$p_n(t) = \binom{n-1}{a-1} e^{-\lambda a t}\left(1 - e^{-\lambda t}\right)^{n-a} \qquad (n = a, a+1, \ldots)$$

$\langle X(t)\rangle = a e^{\lambda t}$ (Malthusian growth)

$\mathrm{Var}[X(t)] = a e^{\lambda t}(e^{\lambda t}-1)$

coefficient of variation :

$$\frac{\sqrt{\mathrm{Var}[X(t)]}}{\langle X(t)\rangle} = \frac{\sqrt{a e^{\lambda t}(e^{\lambda t}-1)}}{a e^{\lambda t}} \sim \frac{1}{\sqrt{a}} \quad \text{as } t\to\infty$$

Yule, U. (1924) A mathematical theory of evolution based on the conclusion of Dr. J. C. Willis, F.R.S. Phil. Trans. B 213, 21

Furry, W.H. (1937) On fluctuation phenomena in the passage of high energy electrons through lead, Phys. Rev. 52, 569

The simple death process

Random death with chance $\mu\Delta t$ for the probability of a single individual dying in time Δt.
Individual life times u have negative exponential distribution:

$$f(u) = \mu e^{-\mu u} \qquad 0\le u<\infty$$

$$p_n(t) = \binom{a}{n} e^{-n\mu t}(1-e^{-\mu t})^{a-n} \quad , \ 0\le n\le a$$

The simple birth and death process

$$\begin{cases} P\{\Delta X(t,t+\Delta t)=1 \mid X(t)=n\} = \lambda n\Delta t + o(\Delta t) \\ P\{\Delta X(t,t+\Delta t)=-1 \mid X(t)=n\} = \mu n\Delta t + o(\Delta t) \\ P\{|\Delta X(t,t+\Delta t)|>1 \mid X(t)=n\} = o(\Delta t) \end{cases}$$

$\therefore$

$$P\{\Delta X(t,t+\Delta t)=0 \mid X(t)=n\} = 1-\lambda n\Delta t-\mu n\Delta t+o(\Delta t)$$

$$P_n(t+\Delta t) = P_n(t)(1-\lambda n\Delta t)(1-\mu n\Delta t) + P_{n-1}(t)(n-1)\lambda\Delta t[1-(n-1)\mu\Delta t] + P_{n+1}(t)[1-(n+1)\lambda\Delta t]\mu(n+1)\Delta t$$

$\therefore$

$$\begin{cases} \dfrac{dP_n}{dt} = -n(\mu+\lambda)P_n + \lambda(n-1)P_{n-1} + \mu(n+1)P_{n+1} \quad (n=0,1,2\dots) \\ P_n(0) = \delta_{nj} \end{cases}$$

Moments of $X(t)$

$$\langle X(t)\rangle = \sum_{n=0}^{\infty} n P_n(t)$$

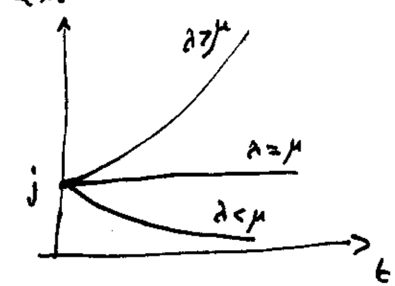
$$\begin{cases} \dfrac{d\langle X(t)\rangle}{dt} = (\lambda-\mu)\langle X(t)\rangle \\ \langle X(0)\rangle = j \end{cases}$$

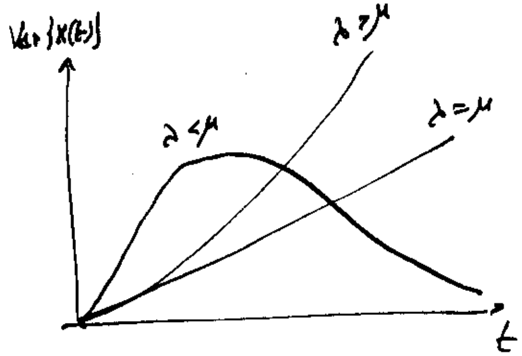
$$\langle X(t)\rangle = j\, e^{+(\lambda-\mu)t}$$

Similarly, writing an equation for $Var\{X(t)\} = \langle X^2(t)\rangle - \{\langle X(t)\rangle\}^2$ and solving it with the condition $Var\{X(0)\} = 0$ one obtains:

$$Var\{X(t)\} = \frac{j(\lambda+\mu)}{\lambda-\mu}\, e^{(\lambda-\mu)t}\left[e^{(\lambda-\mu)t} - 1\right], \quad \lambda \neq \mu$$

$$= 2j\mu t, \quad \lambda = \mu$$





Assume initially there is only one individual ($a=j=1$).
We must solve

$$\begin{cases} \dfrac{dP_n}{dt} = -(\mu+\lambda)\, n\, P_n + \lambda(n-1)P_{n-1} + \mu(n+1)P_{n+1} & (n=0,1,\dots) \\ P_n(0) = \delta_{n,1} \end{cases}$$

Probability generating function

$$F(s,t) = \sum_{n=0}^{\infty} s^n P_n(t)$$

$$\frac{\partial F(s,t)}{\partial t} = \sum_{n=0}^{\infty} s^n \left\{-(\mu+\lambda)\, n P_n + \lambda(n-1)P_{n-1} + \mu(n+1)P_{n+1}\right\}$$

$\therefore$

$$\frac{\partial F(s,t)}{\partial t} = \left[\lambda s^2 - (\mu+\lambda)s + \mu\right]\frac{\partial F(s,t)}{\partial s}$$

$$F(s,0) \equiv \sum_{n=0}^{\infty} s^n \delta_{n,1} = s$$

$$\underset{①}{\frac{ds}{\lambda s^2 - (\mu+\lambda)s + \mu}} = \underset{②}{\frac{dt}{-1}} = \underset{③}{\frac{dF}{0}}$$

From ② and ③ we get:

$\boxed{F = c_1}$, c_1 a constant

From ① and ②:

$$\frac{ds}{\lambda s^2 - (\mu+\lambda)s + \mu} \equiv \left[\frac{1}{(\lambda-\mu)(s-1)} - \frac{\lambda}{(\lambda-\mu)(\lambda s-\mu)}\right] ds = -dt$$

$$-\frac{1}{\lambda-\mu} \ln \frac{\lambda s-\mu}{s-1} = -t + \text{const}$$

$$\boxed{\frac{\lambda s-\mu}{s-1}\, e^{-(\lambda-\mu)t} = c_2}$$

c_2 a constant

$c_1 = H(c_2)$ H arbitrary function

$$F(s,t) = H\left(\frac{\lambda s-\mu}{s-1}\, e^{-(\lambda-\mu)t}\right)$$

Using initial condition $F(s,0)=s$ we find:

$$H\left(\frac{\lambda s-\mu}{s-1}\right) = s$$

or:

$$H(z) = \frac{\mu - z}{\lambda - z}$$

∴

$$F(s,t) = \frac{\mu(1-\alpha)-(\lambda-\mu\alpha)s}{\mu-\lambda\alpha - \lambda(1-\alpha)s} \qquad \alpha \equiv e^{(\lambda-\mu)t}$$

∴

$$F(s,t) = \frac{\mu(1-\alpha)-(\lambda-\mu\alpha)s}{\mu-\lambda\alpha} \times \frac{1}{1-\frac{\lambda(1-\alpha)}{\mu-\lambda\alpha}\, s}$$

Set: $\rho = \dfrac{1-\alpha}{\mu-\lambda\alpha}$

∴

$$F(s,t) = \frac{\mu(1-\alpha)-(\lambda-\mu\alpha)s}{\mu-\lambda\alpha} \sum_{n=0}^{\infty} (\lambda\rho)^n s^n$$

$$= \mu\rho \sum_{n=0}^{\infty} (\lambda\rho)^n s^n - \frac{(\lambda-\mu\alpha)s}{\mu-\lambda\alpha} \sum_{n=0}^{\infty} (\lambda\rho)^n s^n$$

∴

$$F(s,t) = (\mu\rho)\cdot s^0 + \sum_{n=1}^{\infty} \left\{\mu\rho(\lambda\rho)^n - \frac{\lambda-\mu\alpha}{(\mu-\lambda\alpha)\lambda\rho}(\lambda\rho)^n\right\}\cdot s^n$$

<u>Hence</u>, having started from <u>one</u> individual, we get:

$$P_0(t) \equiv \mu\rho = \frac{\mu\left[1-e^{(\lambda-\mu)t}\right]}{\mu-\lambda e^{(\lambda-\mu)t}}$$

$$P_n(t) = (\lambda\rho)^n\left[\mu\rho - \frac{\lambda-\mu\alpha}{(\mu-\lambda\alpha)\lambda\rho}\right] \quad (n=1,2,\ldots)$$

$$\left(\rho \equiv \frac{1-e^{(\lambda-\mu)t}}{\mu-\lambda e^{(\lambda-\mu)t}}\right)$$

If we started from $a>1$ individuals we would have obtained the more cumbersome expressions:

$$P_0(t) = (\mu\rho)^a$$

$$P_n(t) = \sum_{j=0}^{\min(a,n)} \binom{a}{j}\binom{a+n-j-1}{a-1}(\mu\rho)^{a-j}\beta^{n-j}(1-\alpha-\beta)^j \quad (n=1,2,\ldots)$$

$$\beta \equiv \frac{\lambda\left[e^{(\lambda-\mu)t}-1\right]}{\lambda e^{(\lambda-\mu)t}-\mu}$$

<u>Extinction</u>

Initially a individuals. Then:

$$P_0(t) = \frac{[\mu(1-e^{(\lambda-\mu)t})]^a}{[\mu-\lambda e^{(\lambda-\mu)t}]^a}$$

and:

$$\lim_{t\to\infty} P_0(t) = 1, \quad \lambda \le \mu.$$

Take now $\lambda > \mu$. Then:

$$\lim_{t\to\infty} P_0(t) = \left\{\lim_{t\to\infty}\left[\frac{\mu e^{-(\lambda-\mu)t}}{\mu e^{-(\lambda-\mu)t}-\lambda} - \frac{\mu}{\mu e^{-(\lambda-\mu)t}-\lambda}\right]\right\}^a$$

$$= \left(\frac{\mu}{\lambda}\right)^a$$

Even in the case when $\langle X(t)\rangle = a$ (constant) one has $P_0(t) \to 1$ as $t\to\infty$. Mean values are not good indicators of population's behavior.

Moment generating function

r.v. X:

$$M(\theta) = \langle e^{\theta X}\rangle$$

a. X discrete with values j:

$$M(\theta) = \sum_j p_j e^{\theta j} \equiv F(e^\theta) \qquad F\text{: probab. gen. funct.}$$

b. X continuous with density $f(u)$:

$$M(\theta) = \int_{-\infty}^{\infty} du\, e^{+\theta u} f(u)$$

In both cases, we see that:

$$M(\theta) = 1 + \sum_{r=1}^{\infty} \frac{\mu_r' \theta^r}{r!}, \quad \mu_r' = \langle X^r\rangle$$

Moment generating functions do not always exist.

Cumulant generating function:

$$K(\theta) = \ln M(\theta)$$

Then:

$$K(\theta) = \sum_{r=1}^{\infty} k_r \frac{\theta^r}{r!}$$

with

$$k_1 = \langle X\rangle$$
$$k_2 = \langle X^2\rangle - [\langle X\rangle]^2 = \mathrm{var}(X) = \langle (X-\langle x\rangle)^2\rangle$$
$$k_3 = \langle (X-\langle x\rangle)^3\rangle$$
$$k_4 = \langle X^4\rangle - 3[\langle X^2\rangle]^2 - 4\langle x\rangle\langle X^3\rangle + 12\langle X\rangle^2\langle X^2\rangle - 6\langle X\rangle^4$$

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Effects of immigration

Immigration occurs according to a Poisson process of parameter ν.

For simple birth and death process the probability g.f. is such that

$$\frac{\partial F(s,t)}{\partial t} = \left[\lambda s^2-(\mu+\lambda)s+\mu\right]\frac{\partial F(s,t)}{\partial s}$$

$F(s,0)=s$.

For $s=e^{\theta}$ we get:

$$\begin{cases}\dfrac{\partial M}{\partial t} = \left\{\lambda(e^{\theta}-1)+\mu(e^{-\theta}-1)\right\}\dfrac{\partial M}{\partial\theta}\\ M(\theta,0)=e^{\theta}\end{cases}$$

yielding:

$$M(\theta,t)=\left[\frac{\mu v(\theta,t)-1}{\lambda v(\theta,t)-1}\right]^{a}, \quad v(\theta,t)=\frac{(e^{\theta}-1)e^{(\lambda-\mu)t}}{\lambda e^{\theta}-\mu}$$

Due to the immigration phenomenon we now have:

$$\begin{cases}\dfrac{\partial M}{\partial t} = \left[\lambda(e^{\theta}-1)+\mu(e^{-\theta}-1)\right]\dfrac{\partial M}{\partial\theta} + \underbrace{\nu(e^{\theta}-1)M}_{\text{Poisson term}}\\ M(\theta,0)=e^{\theta}\end{cases}$$

$$\underset{①}{\frac{dt}{1}} = \underset{②}{\frac{-d\theta}{\lambda(e^{\theta}-1)+\mu(e^{-\theta}-1)}} = \underset{③}{\frac{dM}{\nu(e^{\theta}-1)M}}$$

From ① and ② we obtain:

$$\frac{(e^{\theta}-1)e^{(\lambda-\mu)t}}{\lambda e^{\theta}-\mu} = \text{constant}$$

whereas from ② and ③ we get:

$$(\lambda e^{\theta}-\mu)^{\nu/\lambda}M = \text{constant}$$

The general solution is then:

$$(\lambda e^{\theta}-\mu)^{\nu/\lambda}M = \Psi\left\{\frac{(e^{\theta}-1)e^{(\lambda-\mu)t}}{\lambda e^{\theta}-\mu}\right\}$$

Set:

$X(0)=a$, i.e. $M(\theta,0)=e^{a\theta}$;

$$(\lambda e^{\theta}-\mu)^{\nu/\lambda}e^{a\theta} = \Psi\left(\frac{e^{\theta}-1}{\lambda e^{\theta}-\mu}\right)$$

or:

$$\Psi(x)=\left(\frac{\mu x-1}{\lambda x-1}\right)^{a}\left(\frac{\mu-\lambda}{\lambda x-1}\right)^{\nu/\lambda} \qquad x\equiv\frac{e^{\theta}-1}{\lambda e^{\theta}-\mu}$$

In conclusion:

$$M(\theta,t)=\frac{(\lambda-\mu)^{\nu/\lambda}\left\{\mu\left[e^{(\lambda-\mu)t}-1\right]-\left[\mu e^{(\lambda-\mu)t}-\lambda\right]e^{\theta}\right\}^{a}}{\left\{\left[\lambda e^{(\lambda-\mu)t}-\mu\right]-\lambda\left[e^{(\lambda-\mu)t}-1\right]e^{\theta}\right\}^{a+\frac{\nu}{\lambda}}}$$

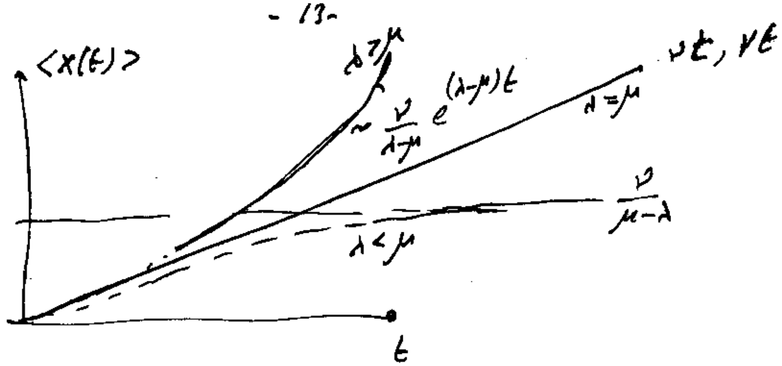
Special cases

$a=0$. Setting $e^{\theta}=s$ we get the probab. gen. funct.:

$$F(s,t)=\left[\frac{\lambda-\mu}{\lambda e^{(\lambda-\mu)t}-\mu}\right]^{\frac{\nu}{\lambda}}\left\{1-\frac{\lambda\left[e^{(\lambda-\mu)t}-1\right]}{\lambda e^{(\lambda-\mu)t}-\mu}s\right\}^{-\frac{\nu}{\lambda}}$$

Negative binomial distribution with mean

$$\langle X(t)\rangle = \frac{\nu}{\lambda-\mu}\left[e^{(\lambda-\mu)t}-1\right]$$



For the case $\lambda<\mu$ we obtain

$$F(s,\infty)=\left(\frac{\mu-\lambda s}{\mu-\lambda}\right)^{-\nu/\lambda} \quad , \lambda<\mu$$

When the birth rate is zero $(\lambda=0)$ this yields:

$$\lim_{\lambda\to 0} F(s,\infty) = \lim_{\lambda\to 0} \exp\left\{-\frac{\nu}{\lambda}\ln\left[1+\frac{\lambda(1-s)}{\mu-\lambda}\right]\right\}$$

$$=\lim_{\lambda\to 0}\exp\left\{-\frac{\nu}{\lambda}\left[\frac{\lambda(1-s)}{\mu-\lambda}-\left(\frac{\lambda(1-s)}{\mu-\lambda}\right)^2+\dots\right]\right\}$$

$$=e^{\frac{\nu}{\mu}(s-1)}$$

which is the prob. g.f. of a Poisson process of parameter $\frac{\nu}{\mu}$.

General birth and death process

Consider a deterministic process in which the birth rate per individual is proportional to the population size:

$$\begin{cases}\dfrac{dn}{dt}=\lambda n^2\\ n(0)=a\end{cases}$$

Then:

$$n(t)=\frac{a}{1-\lambda a t}$$

showing that:

$$\lim_{t\to\frac{1}{\lambda a}} n(t)=\infty$$

Infinite growth in finite time. Divergent or explosive growth.

For a birth process one may assume:

$$P\{\Delta X(t,t+\Delta t)=1 \mid X(t)=n\}=\lambda_n\Delta t+o(\Delta t)$$

$$P\{\Delta X(t,t+\Delta t)>1 \mid X(t)=n\}=1-\lambda_n\Delta t+o(\Delta t)$$

with $\lambda_1, \lambda_2, \dots$ arbitrary.

Then:

$$\begin{cases}\dfrac{dp_n}{dt}=\lambda_{n-1}p_{n-1}-\lambda_n p_n \quad , n\geq 1\\ \dfrac{dp_0}{dt}=-\lambda_0 p_0\end{cases}$$

In general the process may be explosive, in the sense that:

$$\sum_j p_{ij}(s,t) < 1$$

This means that there is a non-zero probability

$$1-\sum_j p_{ij}(s,t)$$

that the process undergoes an infinite number of transitions from state i in time $(t-s)$.

Set:

$$P_{jk}(\Delta t) = P\{X(t)=k \mid X(t-\Delta t)=j\}, \quad \forall j,k \in \mathcal{R}$$

and assume:

$$P_{jk}(\Delta t) = \begin{cases} \lambda_j \Delta t + o(\Delta t), & \text{if } k=j+1 \\ \mu_j \Delta t + o(\Delta t), & \text{if } k=j-1 \\ o(\Delta t), & \text{if } k\neq j, \neq j-1, \neq j+1 \end{cases}$$

$$P_{jj}(\Delta t) = 1-(\lambda_j+\mu_j)\Delta t + o(\Delta t)$$

We can then write the pair of equations:

$$P_{jk}(t+\Delta t) = P_{jk}(t)\left[1-(\lambda_k+\mu_k)\Delta t\right] + P_{j,k-1}(t)\,\lambda_{k-1}\Delta t(1-\mu_{k-1}\Delta t) + P_{j,k+1}(\Delta t)(1-\lambda_{k+1}\Delta t)\mu_{k+1}\Delta t$$

FORWARD

and:

$$P_{jk}(t+\Delta t) = (1-\lambda_j\Delta t-\mu_j\Delta t)P_{jk}(t) + P_{j+1,k}(t)\,\lambda_j\Delta t(1-\mu_j\Delta t) + P_{j-1,k}(t)\,\mu_j\Delta t(1-\lambda_j\Delta t)$$

BACKWARD

Pure birth process

Forward and backward equations read:

$$\begin{cases} \dfrac{d}{dt}P_{jk}(t) = -(\lambda_k+\mu_k)P_{jk}(t) + \lambda_{k-1}P_{j,k-1}(t) + \mu_{k+1}P_{j,k+1}(t) & k\geq 0 \\ \dfrac{d}{dt}P_{jk}(t) = -(\lambda_j+\mu_j)P_{jk}(t) + \mu_j P_{j-1,k}(t) + \lambda_j P_{j+1,k}(t) & j\geq 0 \end{cases}$$

Set now $\mu_j = 0$ $(j\geq 0)$ (pure birth). Then:

$$\frac{dP_{jk}(t)}{dt} = -\lambda_k P_{jk}(t) + \lambda_{k-1}P_{j,k-1}(t) \qquad (k\geq 0)$$

$$\frac{dP_{jk}(t)}{dt} = -\lambda_j P_{jk}(t) + \lambda_j P_{j+1,k}(t) \qquad (j\geq 0)$$

We shall assume $\lambda_j \geq 0$ $(j\geq 0)$.

Theorem

The forward equations of the pure birth process with the λ_j all distinct have the unique solution given by

$$P_{jk}(t) = \begin{cases} 0 & (k<j) \\ \sum_{\nu=j}^{k} A_{jk}^{(\nu)} e^{-\lambda_\nu t} & (k\geq j) \end{cases}$$

where

$$A_{jk}^{(\nu)} = \frac{\lambda_j\lambda_{j+1}\cdots\lambda_{k-1}}{(\lambda_j-\lambda_\nu)(\lambda_{j+1}-\lambda_\nu)\cdots(\lambda_{\nu-1}-\lambda_\nu)(\lambda_{\nu+1}-\lambda_\nu)\cdots(\lambda_k-\lambda_\nu)}$$

Further, one has $\sum_k P_{jk}(t) = 1$ if and only if

$$\frac{1}{\lambda_j} + \frac{1}{\lambda_{j+1}} + \cdots = \infty$$

<u>Proof</u>. Set

$$P^*_{jk}(\theta) = \int_0^\infty e^{-\theta t} P_{jk}(t)\,dt , \qquad \theta > 0$$

Since

$$\int_0^\infty e^{-\theta t} \frac{dP_{jk}(t)}{dt}\,dt = \left[e^{-\theta t} P_{jk}(t) \right]_0^\infty + \theta\, P^*_{jk}(\theta)$$
$$= -\delta_{jk} + \theta\, P^*_{jk}(\theta)$$

taking the $\mathcal{L}$-transform of the forward equations we get:

$$(\theta + \lambda_k) P^*_{jk}(\theta) = \delta_{jk} + \lambda_{k-1} P^*_{j,k-1}(\theta) \qquad (k \geq 0).$$

Solving this successively for $k = 0, 1, \ldots$ we obtain:

$$P^*_{jk}(\theta) = 0 \quad \text{for } k < j$$

and:

$$P^*_{jk}(\theta) = \frac{\lambda_j \lambda_{j+1} \cdots \lambda_{k-1}}{(\theta+\lambda_j)(\theta+\lambda_{j+1})\cdots(\theta+\lambda_k)} \quad \text{for } k \geq j$$

Expressing the r.h.s. in partial fractions we obtain:

$$P^*_{jk}(\theta) = \sum_{\nu=j}^{k} \frac{A^{(\nu)}_{jk}}{\theta + \lambda_\nu} , \quad A^{(\nu)}_{jk} = \lim_{\theta \to -\lambda_\nu} (\theta + \lambda_\nu) P^*_{jk}(\theta)$$

or:

$$P^*_{jk}(\theta) = \sum_{\nu=j}^{k} \frac{\lambda_j \lambda_{j+1} \cdots \lambda_{k-1}}{(\lambda_j - \lambda_\nu)(\lambda_{j+1} - \lambda_\nu)\cdots(\lambda_{\nu-1} - \lambda_\nu)(\lambda_{\nu+1} - \lambda_\nu)\cdots(\lambda_k - \lambda_\nu)} \left(\frac{1}{\theta + \lambda_\nu} \right)$$

Since the inverse $\mathcal{L}$-transform of $\frac{1}{\theta + \lambda_\nu}$ is $e^{-\lambda_\nu t}$ the first part of the theorem is proved.

To prove the second part we add the forward equations over $k = j, j+1, \ldots, k$. Then, for $k \geq j$ we obtain:

$$\frac{d S_{jk}(t)}{dt} = -\lambda_k P_{jk}(t)$$

with

$$S_{jk}(t) = P_{jj}(t) + P_{j,j+1}(t) + \cdots + P_{j,k}(t).$$

Setting

$$S^*_{jk}(\theta) = \int_0^\infty e^{-\theta t} S_{jk}(t)\,dt$$

we then have:

$$\theta S^*_{jk}(\theta) = 1 - \lambda_k P^*_{jk}(\theta)$$

From the previous expression of $P^*_{jk}(\theta)$ we have:

$$\lambda_k P^*_{jk}(\theta) = \frac{\lambda_j \lambda_{j+1} \cdots \lambda_{k-1} \lambda_k}{(\theta+\lambda_j)(\theta+\lambda_{j+1})\cdots(\theta+\lambda_k)} = \frac{1}{\left(1+\frac{\theta}{\lambda_j}\right)\left(1+\frac{\theta}{\lambda_{j+1}}\right)\cdots\left(1+\frac{\theta}{\lambda_k}\right)}$$

Hence:

$$\lim_{k \to \infty} \lambda_k P^*_{jk}(\theta) = \begin{cases} 0 , & \text{if } \sum \frac{1}{\lambda_\nu} = \infty \\ \prod_j^\infty \left(1 + \frac{\theta}{\lambda_\nu}\right)^{-1} , & \text{if } \sum \frac{1}{\lambda_\nu} < \infty \end{cases}$$

Therefore, from

$$\theta S^*_{jk}(\theta) = 1 - \lambda_k P^*_{jk}(\theta)$$

it follows that $\lim_{k\to\infty} \theta S^*_{jk}(\theta) = 1$ or < 1 according as the series $\sum \frac{1}{\lambda_\nu}$ diverges or not. In the first case we have

$$\lim_{k\to\infty} S_{jk}(t) \equiv \sum_k P_{jk}(t) = 1$$

and in the second case

$$\lim_{k\to\infty} S_{jk}(t) \equiv \sum_k P_{jk}(t) < 1 \quad , \forall \text{ finite } t.$$

Theorem The solutions of the forward equation also satisfies the backward equations.

Theorem If the series $\sum \frac{1}{\lambda_\nu}$ diverges, the forward and the backward equations have the unique solution written down in the foregoing.

In the case of a general birth and death process the following special conditions insure the uniqueness of the solutions of forward and backward equations:

a. $\lambda_n = 0$ for some $n \geq 1$.

(i.e. an upper limit of n is placed on the population size

b. $\lambda_n > 0$ for $n \geq a$ and $\sum_{n=a}^{\infty} \frac{1}{\lambda_n} = \infty$

(essentially this prohibits an infinity of births to take place in finite time)

c. $\lambda_n > 0$ for $n \geq a$ and

$$\sum_{n=a}^{\infty} \frac{\mu_n \mu_{n-1} \cdots \mu_a}{\lambda_n \lambda_{n-1} \cdots \lambda_a} = \infty$$

(finiteness of the population is achieved by a suitable balance of birth and death rates).

d. $\lambda_n > 0$ for $n \geq a$ and

$$\sum_{n=a}^{\infty} \left[\frac{1}{\lambda_n} + \frac{\mu_n}{\lambda_n \lambda_{n-1}} + \cdots + \frac{\mu_n \cdots \mu_{a+1}}{\lambda_n \cdots \lambda_a} + \frac{\mu_n \cdots \mu_a}{\lambda_n \cdots \lambda_a} \right] = \infty$$

in which both kind of conditions b. and c. are combined.

In the simple birth and death process for which

$$\lambda_n = \lambda n$$
$$\mu_n = \mu n$$

we have:

$$\sum \frac{1}{\lambda_n} = \frac{1}{\lambda} \sum \frac{1}{n} = \infty$$

and the solution for finite t is unique.

Non Homogeneous Processes

Time-dependent birth and death rates : $\lambda(t), \mu(t)$

Pólya process

$X(t)$ = number of individuals present at time t.

Non homogeneous birth process : — 2 parameters

$$P\{\Delta X(t) = 1 \mid X(t)\} = \frac{\lambda[1+\mu X(t)]}{1+\lambda\mu t}\,\Delta t \quad , \lambda>0, \mu>0$$

Differential equation for the moment g. f. is:

$$\frac{\partial M}{\partial t} = \frac{\lambda(e^\theta-1)}{1+\lambda\mu t}\left(M+\mu\frac{\partial M}{\partial\theta}\right)$$

[for simple birth and death with immigration we had
$$\frac{\partial M}{\partial t} = \{\lambda(e^\theta-1)+\mu(e^{-\theta}-1)\}\frac{\partial M}{\partial\theta} + \nu(e^\theta-1)M$$]

Setting $k = \ln M$:

$$\frac{\partial K}{\partial t} = \frac{\lambda(e^\theta-1)}{1+\lambda\mu t}\left(1+\mu\frac{\partial K}{\partial\theta}\right)$$

Set :
$\lambda\mu t = T$, $e^\theta - 1 = \varphi$ $\quad \mu k = L$

$$(1+T)\frac{\partial L}{\partial T} - \varphi(1+\varphi)\frac{\partial L}{\partial\varphi} = \varphi$$

$$\frac{dT}{1+T} = \frac{d\varphi}{\varphi(1+\varphi)} = \frac{dL}{\varphi}$$

(1) (2) (3)

From (1) and (2) :

$$\frac{(1+T)\varphi}{1+\varphi} = \text{constant}$$

From (2) and (3) :

$$e^L(1+\varphi) = \text{constant}$$

$\therefore$

$$e^L(1+\varphi) = f\left[\frac{(1+T)\varphi}{1+\varphi}\right]$$

Assume:

$X(0) = 0$.

Then, since at $t=0$ we have $T=0$ and:

$$K(\theta,0) \equiv \ln M(\theta,0) = 0 = L(\varphi,0)$$

we get:

$$1+\varphi = f\left(\frac{\varphi}{1+\varphi}\right)$$

or

$$f(u) = \frac{1}{1-u} \quad , \quad u = \frac{\varphi}{1+\varphi}$$

Therefore:

$$e^{L}(1+\varphi) = \frac{1+\varphi}{1-T\varphi}$$

or:

$$L = -\ln(1-T\varphi)$$

Returning to the old variables, we get

$$K(\theta,t) = -\mu^{-1}\ln\left[1-\lambda\mu t(e^{\theta}-1)\right]$$

and:

$$M(\theta,t) = \left\{1-\lambda\mu t(e^{\theta}-1)\right\}^{-\frac{1}{\mu}}$$

Hence:

$$P(z,t) = \left\{(1+\lambda\mu t)-\lambda\mu t z\right\}^{-\frac{1}{\mu}} \qquad \text{prob. gener. funct.}$$

(negative binomial distribution).

$$P_n(t) \equiv P\{X(t)=n \mid X(0)=0\} = \frac{(\lambda t)^n}{n!}(1+\lambda\mu t)^{-n-\frac{1}{\mu}}\prod_{j=1}^{n-1}(1+j\mu)$$

$(n=1,2,\dots)$

From $K(\theta,t)$ we obtain:

$$\langle X(t)\rangle = \lambda t$$

$$\mathrm{Var}\{X(t)\} = \lambda t(1+\lambda\mu t) \quad \sim \text{Poisson for small } t$$

In case $X(0)=a$, one easily gets

$$\psi(u) = (1-u)^{-1-a}$$

Non homogeneous birth and death process.

In place of $\lambda_n = \lambda\cdot n$ and $\mu_n = \mu\cdot n$ we take

$$\lambda_n = \lambda(t)\cdot n \quad \text{and} \quad \mu_n = \mu(t)\cdot n.$$

Basic equations stay unchanged. Hence, we get

$$\begin{cases} \dfrac{\partial F(s,t)}{\partial t} = (s-1)\left\{\lambda(t)s-\mu(t)\right\}\dfrac{\partial F(s,t)}{\partial s} \\ F(s,0) = s^{a} \end{cases}$$

General solution can be shown to be:

$$F(s,t) = \psi\left[\frac{e^{\rho}}{s-1} - \int_0^t \lambda(\tau) e^{\rho(\tau)}d\tau\right] \qquad \psi \text{ arbitrary}$$

with

$$\rho(t) = \int_0^t [\mu(\tau)-\lambda(\tau)]d\tau. \qquad (\rho(0)=0)$$

Using initial condition:

$$s^{a} = \psi\left(\frac{1}{s-1}\right)$$

or:

$$\psi(u) = \left(1+\frac{1}{u}\right)^{a} \qquad u = \frac{1}{s-1}$$

Hence:

$$F(s,t) = \left\{1+\frac{1}{\dfrac{e^{\rho(t)}}{s-1} - \int_0^t \lambda(\tau)e^{\rho(\tau)}d\tau}\right\}^{a}$$

Expanding this as a power series one finds:

$$p_n(t) = \sum_{j=0}^{\min(a,n)} \binom{a}{j}\binom{a+n-j-1}{a-1}\alpha^{a-j}\beta^{n-j}(1-\alpha-\beta)^j$$

$$p_0(t) = \alpha^a$$

where:

$$\alpha = 1 - \frac{1}{e^{\rho(t)}+A(t)}\,, \quad \beta = 1 - \frac{e^{\rho(t)}}{e^{\rho(t)}+A(t)}$$

$$A(t) = \int_0^t \lambda(\tau)e^{\rho(\tau)}d\tau, \qquad \rho(t) = \int_0^t [\mu(\tau)-\lambda(\tau)]d\tau$$

<u>Chance of extinction</u>

$$p_0(t) = \left\{1 - \frac{1}{e^{\rho(t)}+A(t)}\right\}^a$$

Since:

$$e^{\rho(t)}+A(t) = e^{\rho(t)} + \int_0^t \lambda(\tau)e^{\rho(\tau)}d\tau$$

$$= e^{\rho(t)} + \int_0^t \mu(\tau)e^{\rho(\tau)}d\tau - \int_0^t [\mu(\tau)-\lambda(\tau)]e^{\rho(\tau)}d\tau$$

$$= e^{\rho(t)} + \int_0^t \mu(\tau)e^{\rho(\tau)}d\tau - \left[e^{\rho(\tau)}\right]_0^t$$

$$= 1 + \int_0^t \mu(\tau)e^{\rho(\tau)}d\tau$$

In conclusion:

$$p_0(t) = \left\{ \frac{\int_0^t \mu(\tau)e^{\rho(\tau)}d\tau}{1+\int_0^t \mu(\tau)e^{\rho(\tau)}d\tau} \right\}^a$$

The chance of extinction tends to unity as $t\to\infty$ if and only if

$$\lim_{t\to\infty}\int_0^t \mu(\tau)e^{\rho(\tau)}d\tau = \infty.$$

Using the cumulant generating function one then obtains:

$$\kappa_1 \equiv \langle X(t)\rangle = a\,e^{-\rho(t)}$$

$$\kappa_2 \equiv \mathrm{Var}\{X(t)\} = a\,e^{-2\rho(t)}\int_0^t [\lambda(\tau)+\mu(\tau)]e^{\rho(\tau)}d\tau$$

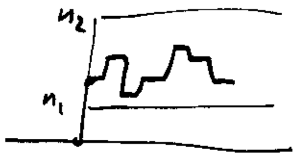
$$\rho(t) = \int_0^t [\mu(\tau)-\lambda(\tau)]d\tau$$

The logistic process

$$\begin{cases} b_n = \frac{\alpha}{n}(n_2 - n) & 0 < n_1 \le n \le n_2 \quad , n_1 < n_2 \in \mathbb{R} \\ b_n = 0 \ , & \text{otherways} \end{cases}$$

$$\begin{cases} d_n = \frac{\beta}{n}(n - n_1) & 0 < n_1 \le n \le n_2 \quad , n_1 < n_2 \in \mathbb{R} \\ d_n = 0 & \text{otherways} \qquad \alpha, \beta > 0 \end{cases}$$

$$\begin{cases} \lambda_n = n\, b_n \\ \mu_n = n\, d_n \end{cases}$$



$$p_{jn}(t) = P\{X(t) = n \mid X(0) = j\}$$

$$\frac{dp_{j n_1}(t)}{dt} = -[n_1 b_{n_1} + n_1 d_{n_1}]\, p_{j n_1}(t) + (n_1+1) d_{n_1+1}\, p_{j, n_1+1}(t)$$

$$\frac{dp_{jn}}{dt} = -[n b_n + n d_n]\, p_{jn}(t) + \overbrace{(n+1)}^{d_{n+1}} p_{j,n+1}(t) + (n-1)\, b_{n-1}\, p_{j,n-1}(t)$$

$$(n = n_1+1, n_1+2, \dots, n_2 - 1)$$

$$\frac{dp_{j,n_2}}{dt} = -[n_2 b_{n_2} + n_2 d_{n_2}]\, p_{j,n_2}(t) + (n_2 - 1)\, b_{n_2-1}\, p_{j,n_2-1}(t)$$

$$p_{j,n}(0) = \delta_{n-j}$$

$$G(z,t) = \sum_{n=0}^{\infty} z^n p_{j,n}(t)$$

$\therefore$

$$\frac{\partial G}{\partial t} = (1-z)(\alpha z + \beta)\frac{\partial G}{\partial z} + (z-1)\left[\alpha n_2 + \frac{\beta n_1}{z}\right] G$$

$$G(z,0) = z^j \qquad n_1 \le j \le n_2$$

$$\frac{dt}{1} = \frac{dz}{(z-1)(\alpha z + \beta)} = \frac{dG}{(z-1)\left[\alpha n_2 + \frac{\beta n_1}{z}\right]}$$

$\therefore$

$$\Phi\left[e^{-(\alpha+\beta)t}\frac{z-1}{\alpha z + \beta}\right] = \frac{z^j}{(\alpha z + \beta)^{n_1 - n_2}} \cdot \frac{1}{G}$$

Φ arbitrary.

Using initial condition:

$$\Phi(u) = \frac{(1+\beta u)^{n_1 - j}(1 - \alpha u)^{j - n_2}}{(\alpha+\beta)^{n_1 - n_2}}$$

$\therefore$

$$G(z,t) = \frac{1}{(\alpha+\beta)^{n_2 - n_1}} z^{n_1}\left[(\alpha + \beta e^{-(\alpha+\beta)t})z + \beta(1 - e^{-(\alpha+\beta)t})\right]^{j - n_1}\left[\alpha(1 - e^{-(\alpha+\beta)t})z + (\alpha e^{-(\alpha+\beta)t} + \beta)\right]^{n_2 - j}$$

$$\langle X(t) \mid X(0)=j \rangle = \frac{1}{\alpha+\beta}\left[(\alpha n_2+\beta n_1) - \left\{ (\alpha n_2+\beta n_1) - j(\alpha+\beta) \right\} e^{-(\alpha+\beta)t} \right]$$

$$\lim_{t\to\infty} G(z,t) = \frac{1}{(\alpha+\beta)^{n_2-n_1}} z^{n_1} (\alpha z+\beta)^{n_2-n_1}$$

$$= \frac{1}{(\alpha+\beta)^{n_2-n_1}} \sum_{k=0}^{n_2-n_1} \binom{n_2-n_1}{k} \alpha^k \beta^{(n_2-n_1)-k} z^{n_1+k}$$

$\therefore$

$$p_{j,n_1+k}(\infty) = \frac{1}{(\alpha+\beta)^{n_2-n_1}} \binom{n_2-n_1}{k} \alpha^k \beta^{(n_2-n_1)-k}$$

$$(0 \le k \le n_2-n_1)$$

$$\lim_{t\to\infty} \langle X(t) \mid X(0)=j \rangle = \frac{\alpha n_2+\beta n_1}{\alpha+\beta}$$

$$\lim_{t\to\infty} \operatorname{Var}\{ X(t) \mid X(0)=j \} = \frac{\alpha\beta(n_2-n_1)}{(\alpha+\beta)^2}$$

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(a)

<u>Kolmogorov Equations</u>

$\{X(t),\ 0 \le t < \infty\}$ Markov process with at most a countable # of states $i = 0,1,2,\dots$

$$p_{ij}(\tau,t) = P\{X(t)=j \mid X(\tau)=i\}, \quad 0<\tau<t$$

We have:

$$p_{ij}(\tau,t) \ge 0$$

$$p_{ij}(\tau,t) = \sum_k p_{ik}(\tau,s)\, p_{kj}(s,t) \quad \text{Chapman-Kolmogorov eqn.}$$

<u>Assume</u>

$$\lim_{\Delta t\to 0} \frac{1-p_{ii}(t,t+\Delta t)}{\Delta t} = q_i(t) \quad (i=0,1,\dots)$$

$$\lim_{\Delta t\to 0} \frac{p_{ij}(t,t+\Delta t)}{\Delta t} = q_{ij}(t) \quad (i,j=0,1,2\dots)$$

the convergence being uniform in t.
For small Δt we then have the following asymptotic equalities:

$$p_{ii}(t,t+\Delta t) \simeq 1 - q_i(t)\Delta t + o(\Delta t)$$

$$p_{ij}(t,t+\Delta t) \simeq q_{ij}(t)\Delta t + o(\Delta t)$$

$q_i(t)$ and $q_{ij}(t)$ are the <u>intensity functions</u>

Theorem Let $p_{ij}(\tau,t)$ be the probability transition function of a Markov process with at most a countable number of states $i=0,1,2,\dots$ Suppose that the intensity functions $q_i(t)$ and $q_{ij}(t)$ exist and are continuous. Then:

A) The functions $p_{ij}(\tau,t)$ satisfy the system of differential equations

$$\frac{\partial p_{ij}(\tau,t)}{\partial\tau} = q_i(\tau)\,p_{ij}(\tau,t) - \sum_{k\neq i} q_{ik}(\tau)\,p_{kj}(\tau,t)$$

with $p_{ij}(t,t)\begin{cases} =1, & j=i \\ =0, & j\neq i\end{cases}$

B) If, moreover, the convergence in

$$q_{ij}(t) = \lim_{\Delta t\to 0}\frac{p_{ij}(t,t+\Delta t)}{\Delta t}$$

is uniform in i for fixed j, then the functions $p_{ij}(\tau,t)$ satisfy the system of differential equations

$$\frac{\partial p_{ij}(\tau,t)}{\partial t} = -p_{ij}(\tau,t)\,q_j(t) + \sum_{k\neq j} p_{ik}(\tau,t)\,q_{kj}(t)$$

with $p_{ij}(\tau,\tau)=\begin{cases} 1, & i=j \\ 0, & i\neq j\end{cases}$

Proof of B

Start from

$$p_{ij}(\tau,t) = \sum_k p_{ik}(\tau,s)\,p_{kj}(s,t)$$

and take $s\to t$, $t\to t+\Delta t$:

$$p_{ij}(\tau,t+\Delta t) = \sum_k p_{ik}(\tau,t)\,p_{kj}(t,t+\Delta t)$$

Hence:

$$\frac{p_{ij}(\tau,t+\Delta t)-p_{ij}(t)}{\Delta t} = \frac{1}{\Delta t}\left[\sum_k p_{ik}(\tau,t)\,p_{kj}(t,t+\Delta t) - p_{ij}(\tau,t)\right]$$

$$= \sum_{k\neq j} p_{ik}(\tau,t)\frac{p_{kj}(t,t+\Delta t)}{\Delta t} - p_{ij}(\tau,t)\frac{1-p_{jj}(t,t+\Delta t)}{\Delta t}$$

$\therefore$

$$\frac{\partial p_{ij}(\tau,t)}{\partial t} = \sum_{k\neq j} p_{ik}(\tau,t)\overbrace{\lim_{\Delta t\to 0}\frac{p_{kj}(t,t+\Delta t)}{\Delta t}}^{q_{kj}(t)} - p_{ij}(\tau,t)\overbrace{\lim_{\Delta t\to 0}\frac{1-p_{jj}(t,t+\Delta t)}{\Delta t}}^{q_j(t)}$$

where use has been made of the absolute convergence of $\sum_k p_{ik}$.

Similarly part A) can be proved.

A. N. Kolmogorov. Über die analytischen Methoden der Wahrschienlichkeitsrechnung, Math. Annalen 104, 415 (1931)

M. Fisz Probability Theory and Mathematical Statistics John Wiley (1963).

It can be shown that forward and backward equations have identical solutions $p_{ij}(\tau,t)$ such that

$$p_{ij}(\tau,t) \geq 0$$

$$p_{ij}(\tau,t) = \sum_k p_{ik}(\tau,s)\, p_{kj}(s,t)$$

and satisfying the initial conditions, and that the corresponding intensity functions exist and are continuous. The proof is in

Kolmogorov (loc. cit.) for the homogeneous case. The non-homogeneous case is considered in

W. Feller. Zur Theorie der stochastischen Prozesse.
Math. Annalen 113, 113 (1936).

Homogeneous processes

$$q_i(t) \to q_i$$

$$q_{ij}(t) \to q_{ij}$$

$$\begin{cases} -\dfrac{dp_{ij}(t)}{dt} = q_i\, p_{ij}(t) - \sum\limits_{k \neq j} q_{ik}\, p_{kj}(t) \\[2ex] \dfrac{dp_{ij}(t)}{dt} = -p_{ij}(t)\, q_j + \sum\limits_{k \neq j} p_{ik}(t)\, q_{kj} \end{cases}$$

$$p_{ij}(0) = \begin{cases} 1, & j = i \\ 0, & j \neq i \end{cases}$$

Existence and finiteness of intensity functions $q_i(t)$ and $q_{ij}(t)$ has been assumed. However, for homogeneous processes their existence follows from the assumption

(*) $\lim\limits_{t \to 0} p_{ii}(t) = 1 \qquad i = 0, 1, \ldots \qquad$ (continuity at zero)

If convergence is uniform in i, then q_i, q_{ij} are finite.
If number of states is finite, assumption (*) suffice to prove the finiteness of q_i, q_{ij}.

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Classification of birth and death process (general)

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$$p_n'(t) = -\left[n b_n + n d_n\right] p_n(t) + (n+1) d_{n+1} p_{n+1}(t) + (n-1) b_{n-1} p_{n-1}(t)$$

$$\begin{cases} b_n = \dfrac{\alpha}{n}(n_2 - n) \\ d_n = \dfrac{\beta}{n}(n - n_1) \end{cases} \qquad \begin{aligned} b_{n-1} &= \frac{\alpha}{n-1}\left[n_2 - (n-1)\right] \\ d_{n+1} &= \frac{\beta}{n+1}\left[n+1-n_1\right] \end{aligned}$$

$\therefore$

$$p_n'(t) = -\left\{\alpha(n_2-n) + \beta(n-n_1)\right\} p_n(t) + \beta(n+1-n_1) p_{n+1} + \alpha\left[n_2 - (n-1)\right] p_{n-1}(t)$$

$$G(z,t) = \sum_{n=0}^{\infty} z^n p_n(t)$$

$$\frac{\partial G}{\partial t} = -\left[\alpha n_2 - \beta n_1\right] \underbrace{\sum_{n=0}^{\infty} z^n p_n(t)} + (\alpha-\beta) \sum_{n=0}^{\infty} n \underbrace{z^n p_n}$$

$$+ \underbrace{\beta \sum_{n=0}^{\infty} (n+1) p_{n+1} z^n} - \underbrace{n_1 \beta \sum_{n=0}^{\infty} z^n p_{n+1}} + \underbrace{\alpha n_2 \sum_{n=1}^{\infty} z^n p_{n-1}}_{\sum_{r=0}^{\infty} z^r z p_r} \qquad n-1=r$$

$$- \alpha \sum_{n=0}^{\infty} z^n (n-1) p_{n-1}$$

$$\frac{\partial G}{\partial t} = -(\alpha n_2 - \beta n_1) G + \alpha n_2 z G - \frac{n_1 \beta}{z} G +$$

$$+ (\alpha-\beta) z \frac{\partial G}{\partial z} + \beta \frac{\partial G}{\partial z} - \alpha z^2 \frac{\partial G}{\partial z}$$

$$\frac{\partial G}{\partial t} = \left(-\alpha n_2 + \beta n_1 + \alpha n_2 z - \frac{n_1 \beta}{z}\right) G + \underbrace{\left[(\alpha-\beta) z + \beta - \alpha z^2\right]}_{\alpha z - \beta z + \beta - \alpha z^2} \frac{\partial G}{\partial z}$$