# Stochastic birth-death processes

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Here is the problem. Suppose we have a finite population of (for example) radioactive particles, with decay rate $\lambda$. When will the population disappear (go extinct)?

## 1 Poisson process as a birth process

To illustrate the ideas in a simple problem, consider a waiting time problem (Poisson process). How long does it take for $n$ events to occur, if all events are independent, and if the probability of an event in time $dt$ is $\lambda dt$?

The equations

$$\frac{dP_0}{dt} = -\lambda P_0, \tag{1}$$

and

$$\frac{dP_n}{dt} = \lambda P_{n-1} - \lambda P_n, \tag{2}$$

for $n > 1$, with initial data $P_0(0) = 1$, $P_n(0) = 0$ for $n > 1$. The conjecture is that the solution is of the form

$$P_n(t) = \frac{1}{n!}\lambda^n t^n \exp(-\lambda t). \tag{3}$$

This is certainly correct for $P_0(t)$. We check it inductively:

$$\frac{dP_n}{dt} = n\frac{1}{n!}\lambda^n t^{n-1}\exp(-\lambda t) - \lambda\frac{1}{n!}\lambda^n t^n \exp(-\lambda t = \lambda P_{n-1} - \lambda P_n \tag{4}$$

as desired.

It is also easy to find the generating function. Set $g(z,t) = \sum_{k=0}^{\infty} P_k z^k$ so that

$$\begin{aligned}
\frac{\partial g}{\partial t} &= \sum_{k=1}^{\infty} \lambda P_{k-1} z^k - \lambda \sum_{k=0}^{\infty} P_k z^k, && (5)\\
&= z\lambda \sum_{k=0}^{\infty} P_k z^k - \lambda \sum_{k=0}^{\infty} P_k z^k, && (6)\\
&= \lambda(z-1)g, && (7)
\end{aligned}$$

with initial data $g(z,0) = 1$. This is actually an ordinary differential equation, with solution

$$g(z,t) = \exp((z-1)\lambda t), \tag{8}$$

and Taylor series

$$g(z,t) = \exp(-\lambda t) \sum_{k=0}^{\infty} \frac{1}{k!} (\lambda t)^k \tag{9}$$

so that $P_n(t) = \frac{1}{n!} \lambda^n t^n \exp(-\lambda t)$, as stated above.

## 2 stochastic birth process

Start with the stochastic birth problem

$$\frac{dp_n}{dt} = b(n-1)p_{n-1} - bnp_n, \qquad n = 1, 2, \cdots, \tag{10}$$

and $p_a(0) = 1$. Then the solution is the negative binomial distribution

$$p_n(t) = \begin{pmatrix} n-1 \\ a-1 \end{pmatrix} (\exp(-bt))^a (1-\exp(-bt))^{n-a}, n = a, a+1, \cdots. \tag{11}$$

The proof uses induction.

Mean and variance are $\mu = a\exp(bt)$ and $\sigma^2 = a\exp(bt)(\exp(bt) - 1)$.

We can also use a generating function

$$g = \sum_{k=1}^{\infty} p_k z^k \tag{12}$$

and then observe that

$$\begin{aligned}
\frac{\partial g}{\partial t} &= \sum_{k=1}^{\infty} b(k-1)p_{k-1}z^k - \sum_{k=1}^{\infty} bkp_k z^k && (13)\\
&= bz^2 \sum_{k=2}^{\infty} (k-1)p_{k-1}z^{k-2} - bz \sum_{k=1}^{\infty} kp_k z^{k-1} && (14)\\
&= bz^2 \frac{\partial}{\partial z} \sum_{k=2}^{\infty} p_{k-1}z^{k-1} - bz \frac{\partial}{\partial z} \sum_{k=1}^{\infty} p_k z^k && (15)\\
&= b(z^2 - z)\frac{\partial g}{\partial z}, && (16)\\
& && (17)
\end{aligned}$$

with initial data $g(0,z) = z^a$.

The solution can be found using the method of characteristics. Set $\frac{dz}{d\tau} = f$, $\frac{dt}{d\tau} = 1$, and then

$$\frac{dg}{d\tau} = \frac{\partial g}{\partial t}\frac{dt}{d\tau} + \frac{\partial g}{\partial z}\frac{dz}{d\tau} \tag{18}$$

$$= \frac{\partial g}{\partial t} + \frac{\partial g}{\partial x} b(z - z^2) = 0 \tag{19}$$

with $\frac{dz}{d\tau} = b(z - z^2)$. This we solve easily: $g = z_0^a$ along

$$\ln(\frac{z}{z-1}) = \ln(\frac{z_0}{z_0 - 1})bt, \tag{20}$$

or along

$$z_0 = \frac{z \exp(-bt)}{1 - z(1 - \exp(-bt))}. \tag{21}$$

From this we easily find the solution using the negative binomial expansion

$$(1 - z)^{-a} = \sum_{k=0}^{\infty} \left( \begin{array}{c} a + k - 1 \\ a - 1 \end{array} \right) z^k. \tag{22}$$

The problem is that with the usual continuous population model

$$\frac{du}{dt} = -\lambda u, \tag{23}$$

the population never goes extinct, because the solution

$$u(t) = \exp(-\lambda t), \tag{24}$$

cannot become zero. Of course, the problem is that we are using a continuous model when only a discrete model can work. So we write the master equation for $P_n$, the probability that at time $t$ the population has $n$ members

$$\frac{dP_n}{dt} = \lambda(n+1)P_{n+1} - \lambda n P_n, \tag{25}$$

with initial conditions $P_N(0) = 1$ and $P_n(0) = 0$ for $n \neq N$.

It takes some work, but one can show by induction, that the solution to this problem is

$$P_j(t) = \left( \begin{array}{c} N \\ j \end{array} \right) \exp(-\lambda N t)(\exp(\lambda t) - 1)^{N-j}. \tag{26}$$

The calculation is left to the reader. This is exactly the binomial distribution with $p(t) = \exp(-\lambda t)$.

Try a generating function, as well. $g(z,t) = \sum_{k=0}^{\infty} P_k z^k$, and observe that

$$\frac{\partial g}{\partial t} = \sum_{k=0}^{\infty} \lambda(k+1)P_{k+1}z^k - \sum_{k=0}^{\infty} \lambda k P_k z^k,$$

$$= \lambda \sum_{k=0}^{\infty} (k+1)P_{k+1}z^k - \lambda z \sum_{k=0}^{\infty} k P_k z^{k-1},$$

$$= \lambda \frac{\partial}{\partial z} \sum_{k=0}^{\infty} P_{k+1} z^{k+1} - \lambda z \frac{\partial}{\partial z} \sum_{k=0}^{\infty} P_k z^k,$$

$$= \lambda \frac{\partial}{\partial z} \sum_{k=0}^{\infty} P_k z^k - \lambda z \frac{\partial}{\partial z} \sum_{k=0}^{\infty} P_k z^k,$$

$$= \lambda (1 - z) \frac{\partial g}{\partial z}. \tag{27}$$

The initial data for this are

$$g(z, 0) = z^n. \tag{28}$$

and the solution is found using the method of characteristics. The solution is constant along characteristics, satisfying

$$\frac{dz}{dt} = \lambda (z - 1). \tag{29}$$

It follows easily that

$$\ln(z - 1) = \ln(z_0 - 1)\lambda t, \tag{30}$$

or

$$z_0 = 1 + (z - 1)\exp(-\lambda t), \tag{31}$$

Thus, the solution is

$$g(z, t) = (1 - \exp(-\lambda t) + z \exp(-\lambda t))^N, \tag{32}$$

which can easily be expanded using the binomial expansion.

The mean and variance are easily calculated using facts about the binomial distribution, namely

$$\mu(t) = N \exp(-\lambda t), \qquad var(t) = N(\exp(-\lambda t) - \exp(-2\lambda t)), \tag{33}$$

which is the deterministic answer for the population size.

Now the extinction probability is

$$P_0(t) = (1 - \exp(-\lambda t))^N. \tag{34}$$

The expected time of going extinct is given by

$$E(t) = \int_0^{\infty} t P_0'(t) dt, \tag{35}$$

but I can't calculate this explicitly.

More generally, if $\lambda$ is a function of time,

$$\ln(z - 1) = \ln(z_0 - 1) \int_0^t \lambda(s) ds, \tag{36}$$

or

$$z_0 = 1 + (z - 1)\exp(-\int_0^t \lambda(s) ds), \tag{37}$$

Thus, the solution is

$$g(z, t) = (1 + (z - 1)\exp(-\int_0^t \lambda(s) ds))^N, \tag{38}$$

which can easily be expanded using the binomial expansion. More generally,

## 3 The full birth-death problem

Suppose we have a birth-death process

$$\frac{dP_n}{dt} = \alpha(n+1)P_{n+1} - \alpha n P_n + \beta(n-1)P_{n-1} - \beta n P_n, \tag{39}$$

Past experience tells us that there is a generating function $g(z,t) = \sum_{k=0} P_k z^k$, and that

$$\begin{aligned}
\frac{\partial g}{\partial t} &= \alpha \sum_{k=0}^{\infty}(k+1)P_{k+1}z^k - \sum_{k=0}^{\infty}\alpha k P_k z^k + \beta\sum_{k=1}^{\infty}(k-1)P_{k-1}z^k - \beta\sum_{k=0}^{\infty} kP_k z^k, \\
&= \alpha\frac{\partial}{\partial z}\sum_{k=0}^{\infty}P_{k+1}z^{k+1} - \alpha z\frac{\partial}{\partial z}\sum_{k=0}^{\infty}P_k z^k + \beta z^2\frac{\partial}{\partial z}\sum_{k=1}^{\infty}P_{k-1}z^{k-1} - \beta z\frac{\partial}{\partial z}\sum_{k=0}^{\infty}P_k z^k, \\
&= (1-z)(\alpha - \beta z)\frac{\partial g}{\partial z}.
\end{aligned} \tag{40}$$

Of course, the solution is found using the method of characteristics, $g = z_0^n$ (say), where

$$\frac{dz}{dt} = (1-z)(\beta z - \alpha), \tag{41}$$

which we can solve to find

$$\ln(\frac{\beta z - \alpha}{z-1}) = -\ln(\frac{\beta z_0 - \alpha}{z_0 - 1})(\alpha - \beta)t, \tag{42}$$

from which we find that

$$(\frac{\beta z - \alpha}{z-1})\exp((\alpha-\beta)t) = (\frac{\beta z_0 - \alpha}{z_0 - 1}). \tag{43}$$

We solve for $z_0$ to find

$$z_0 = \frac{(\beta z - \alpha)\exp((\alpha-\beta)t) - \alpha(z-1)}{(\beta z - \alpha)\exp((\alpha-\beta)t) - \beta(z-1)}. \tag{44}$$

It is possible to find the Taylor series expansion of $g$, however, the original problem was to find $P_0(t)$, which we can easily do. In fact,

$$P_0(t) = \left(\frac{\alpha\exp((\alpha-\beta)t) - \alpha}{\alpha\exp((\alpha-\beta)t) - \beta}\right)^N. \tag{45}$$

It is interesting to calculate the probability of extinction: If $\alpha > \beta$, then

$$\lim_{t\to\infty} P_0(t) = 1, \tag{46}$$

whereas if $\beta > \alpha$, then

$$\lim_{t\to\infty} P_0(t) = (\frac{\alpha}{\beta})^N. \tag{47}$$

Some questions to answer (maybe):

- What is the expected time of extinction in a birth-death process? (as a function of initial population size, $N$)? (at least I can calculate this numeically, if not analytically)
- What is the variance in population size in a birth death process? (can the moment equations be solved? How about the moment generating function?)

# 4 Ion Channels

A similar model describes the behavior of an ion channel with $k$ independent subunits, all of which must be open in order for the ion channel to conduct ions. Let $p_j$ be the probability that $j$ subunits are open. Then

$$\frac{dp_j}{dt} = \alpha(k-j+1)p_{j-1} + \beta(j+1)p_{j+1} - (\beta j + \alpha(k-j))p_j, \tag{48}$$

with appropriate restriction on the indices.

There are two interesting observations about this model. First, it is relatively easy to show that there is an invariant manifold given by

$$p_j = \left( \begin{array}{c} k \\ j \end{array} \right) n^j (1-n)^{k-j}, \tag{49}$$

with

$$\frac{dn}{dt} = \alpha(1-n) - \beta n. \tag{50}$$

I don't know how to show that this is a stable invariant manifold, but I believe it is. (I can show it in a few easy cases, like $k = 2, 3$.)

Second, we can find the equation for the generating function

$$g(t,z) = \sum_{j=0}^{k} p_j z^j, \tag{51}$$

to be

$$\begin{aligned}
\frac{\partial g}{\partial t} &= \alpha \sum_{j=1}^{k+1} (k-j+1)p_{j-1}z^j + \beta \sum_{j=-1}^{k-1} (j+1)p_{j+1}z^j - \sum_{j=0}^{k} (\beta j + \alpha(k-j))p_j z^j \\
&= \alpha k \sum_{j=1}^{k+1} p_{j-1}z^j - \alpha \sum_{j=1}^{k+1} (j-1)p_{j-1}z^j + \beta \sum_{j=-1}^{k-1} (j+1)p_{j+1}z^j - (\beta-\alpha)\sum_{j=0}^{k} j p_j z^j - \alpha k \sum_{j=0}^{k} p_j z^j \\
&= \alpha k \sum_{j=0}^{k} p_j z^{j+1} - \alpha \sum_{j=0}^{k} j p_j z^{j+1} + \beta \sum_{j=0}^{k} j p_j z^{j-1} - (\beta-\alpha)\sum_{j=0}^{k} j p_j z^j - \alpha k \sum_{j=0}^{k} p_j z^j \\
&= \alpha k(z-1) \sum_{j=0}^{k} p_j z^j + (1-z)(\beta + \alpha z) \sum_{j=0}^{k} j p_j z^{j-1} \\
&= \alpha k(z-1) g + (1-z)(\beta + \alpha z) \frac{\partial g}{\partial z}.
\end{aligned} \tag{52}$$

It is not hard to check that one solution of this pde is

$$g(z,t) = (nz + 1 - n)^k, \tag{53}$$

provided (50) holds. And, of course, (49) follows from the binomial expansion.

Notice also that if $n(0) = 0$, then $g(z, 0) = 1$, which implies all subunits are initially closed.

The general solution in the case that $\alpha$ and $\beta$ are constant can be found using the method of characteristics. We suppose that $g(z, 0) = 1$ (all subunits are initially closed), and then the characteristic equations are

$$\frac{dg}{dt} = \alpha k(z-1)g, \qquad \frac{dz}{dt} = (1-z)(\beta + \alpha z). \tag{54}$$

We find that the characteristic curves are

$$(\frac{\beta + \alpha z}{z-1}) \exp(-(\alpha+\beta)t) = (\frac{\beta + \alpha z_0}{z_0 - 1}). \tag{55}$$

It is also possible to integrate the "phase plane" equation for $g$,

$$\frac{dg}{dz} = -\frac{\alpha k g}{\beta + \alpha z}, \tag{56}$$

to find

$$g = \left(\frac{\beta + \alpha z_0}{\beta + \alpha z}\right)^k. \tag{57}$$

To find $g(z, t)$, we now solve (55) for $z_0$ and substitute into (57).

$$z_0 = \frac{(\beta + \alpha z)\exp(-(\alpha+\beta)t) + \beta(z-1)}{(\beta + \alpha z)\exp(-(\alpha+\beta)t) - \alpha(z-1)}. \tag{58}$$

Something seems wrong here, since the answer is supposed to be a polynomial of degree $k$. Oh well, this is not the interesting case, anyway.