Population Models with Stochastic Stochastic Birth Processes *

CURM Background Material, Fall 2014
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In our previous population models, we consdiered birth and death to be deterministic. Here, we will formulate a simple model of a stochastic process. To simplify the analysis, we will assume that deaths have a negligible effect compared to births, and can be neglected. This is a reasonable approximation for bacteria and other species that grow by mitosis. In other circumstances, this model will need to be replaced by other stochastic models (which will be more difficult to analyze).

Suppose that we cannot say with certainty that there will be a population increase of exactly $R\triangle t$ percent in time $\triangle t$. Instead, we assume that the birth process is random and that a birth associated with an individual may occur randomly at any time with equal probability. We will assume, for simplicity, that the probability of one birth is proportional to $\triangle t$, say $\lambda\triangle t$. The probability of two or more births in a time interval $\triangle t$ is considered to be negligible if $\triangle t$ is small enough. Note that we are assuming that there are no multiple birghts. Therefore, the probability of an individual not giving birth in time $\triangle t$ is $1 - \lambda\triangle t$, since there are only two options: either a birth occurs, or it does not, and the sum of the probabilities must equal one.

In $\triangle t$ time, if the probability of one birth from one individual is $\lambda\triangle t$, then we may "expect" that if there were a large number of individuals, say N_0, then there would be $N_0\lambda\triangle t$ births. Based on this, we may conclude that the birth rate is

$$\frac{\triangle N}{N_0\triangle t} = \lambda,$$

since there are no deaths in this model and so the birth rate equals the growth rate. Therefore, not only is λ the probability of a birth per unit time, it is also the birth rate (if growth occurs deterministically). It turns out that λ is the *expected* growth rate for this stochastic birth process. If λ is unknown, we may estimate $\lambda\triangle t$ by dividing the total number of births in time $\triangle t$ by the total population (if the time $\triangle t$ is sufficiently small taht the number of births is a small percentage of the population).

Example: In a population of 600 hens, if 20 hatchings occur in one hour, then the birth rate is estimated at $\frac{1}{30}$ per hour and also the probability of a birth is estimated as $\frac{1}{30}$ per hour; i.e., $\lambda = \frac{1}{30}$.

We cannot calculate the exact population size at a given time. We may only discuss probabilities. Let $P_N(t)$ be the probability that at time t the population is N. At time $t + \triangle t$, we

*The material in this handout is taken directly from *Mathematical Models* by Richard Haberman wish to know the probability of the population being N. First, we must consider how the population might be N at time $t + \triangle t$. This can occur in two ways: (1) the population was $N - 1$ at the previous time and a birth occurs in time interval $\triangle t$, or (2) the population was N at time t and no births occured during $\triangle t$. Here, we are ignoring the possibility that two or more births occur from different individuals during $\triangle t$, but this is a good approximation if $\triangle t$ is small enough. Thus,

$$P_N(t + \triangle t) = \sigma_{N-1} P_{N-1}(t) + \nu_N P_N(t), \tag{1}$$

where σ_{N-1} is the probability that exactly one birth occurs among the $N - 1$ individuals and ν_N is the probability that no births occur among the N individuals.

Next, we will calculate these probabilities. If the probability of one individual not giving birth is $1 - \lambda\triangle t$, then the probability of no births among the N independent individuals is $(1 - \lambda\triangle t)^N$, i.e.,

$$\nu_N = (1 - \lambda\triangle t)^N.$$

The probability of exactly one birth among m individuals is calculated as follows. Exactly one birth can occur in m different, equally likely, ways. One way is for an individual, say individual 1, to have a birth and the other $m - 1$ individuals not to. The probability of this is

$$\lambda\triangle t(1 - \lambda\triangle t)^{m-1}.$$

Thus, the probability of exactly one birth among m individuals is

$$\sigma_m = m\lambda\triangle t(1 - \lambda\triangle t)^{m-1},$$

and

$$\sigma_{N-1} = (N - 1)\lambda\triangle t(1 - \lambda\triangle t)^{N-2}.$$

However, if $\triangle t$ is extremely small, then, since the probability of at least one birth occuring among N individuals is

$$1 - \nu_N = 1 - (1 - \lambda\triangle t)^N,$$

and the probability of two or more births is negligible,

$$\sigma_{N-1} \approx 1 - (1 - \lambda\triangle t)^{N-1}.$$

Note that the above expression is only valid for $\triangle t$ extremely small. But, if $\triangle t$ is sufficiently small, then

$$\nu_N \approx 1 - \lambda N\triangle t,$$

and

$$\sigma_{N-1} \approx \lambda(N - 1)\triangle t.$$

Then, from Equation (1), we have

$$P_N(t + \triangle t) \approx \lambda(N - 1)\triangle t P_{N-1}(t) + (1 - \lambda N\triangle t)P_N(t).$$

As $\triangle t$ becomes smaller, this equation becomse more accurate. Using a Taylor expansion of the left-hand side gives

$$P_N(t) + \triangle t\frac{dP_N(t)}{dt} + \cdots = P_N(t) + \triangle t[\lambda(N - 1)P_{N-1}(t) - \lambda N P_N(t)].$$

Simplifying, dividing both sides by $\triangle t$, and taking the limit as $\triangle t \to 0$ gives the following system of ordinary differential equations:

$$\frac{dP_N}{dt} = \lambda(N-1)P_{N-1} - \lambda N P_N. \tag{2}$$

To solve this system, initial conditions are needed. The initial conditions are the initial probabilities. The problem we will solve is one in which the initial population (at $t = 0$) is known with certainty to be some value N_0. In this case, then, the initial probabilities are

$$P_N(0) = \begin{cases} 0, & \text{if } N \neq N_0, \\ 1, & \text{if } N = N_0. \end{cases}$$

With these initial conditions, the system of differential equations can be successively solved.

Re-writing the above equation in the form

$$\frac{dP_N}{dt} + \lambda N P_N = \lambda(N-1)P_{N-1} \tag{3}$$

helps us see that we first find P_{N-1} and then use it to determine P_N. For example, the probability of having N_0 individuals is given by

$$\frac{dP_{N_0}}{dt} + \lambda N_0 P_{N_0} = \lambda(N_0 - 1)P_{N_0-1},$$

and since the population must be greater than or equal to N_0, $P_{N_0-1} = 0$, and we obtain

$$P_{N_0}(t) = P_{N_0}(0)e^{-\lambda N_0 t},$$

and the initial condition tells us that $P_{N_0}(0) = 1$, so

$$P_{N_0}(t) = e^{-\lambda N_0 t}. \tag{4}$$

The probability of the population being N_0 decreases in time. As time goes on, the likelihood of the population remaining the same decreases, since there are births but not deaths. Since $P_{N_0}(t)$ is a probability function, its value is alway nonnegative and less than or equal to 1.

The probability of the population being $N_0 + 1$ is determined from Equation (**??**), where $N = N_0 + 1$ and where $P_{N_0}(t)$ is given by Equation (4). We are thus solving

$$\frac{dP_{N_0+1}}{dt} + \lambda(N_0 + 1)P_{N_0+1} = \lambda N_0 e^{-\lambda N_0 t}.$$

This is a nonhomogeneous linear first order differential equation with initial condition $P_{N_0+1}(0) = 0$, which we may solve directly or using Maple, to obtain

$$P_{N_0+1}(t) = N_0 e^{-\lambda N_0 t}(1 - e^{-\lambda t}).$$

The probability of $N_0 + 1$ individuals initially increases from zero, but eventually diminishes to zero.

Question: When is it most likely that there are $N_0 + 1$ individuals?

Answer: When the probability P_{N_0+1} is maximized, i.e., when

$$0 = \frac{dP_{N_0+1}}{dt} = N_0 e^{-\lambda N_0 t}[-\lambda N_0(1 - e^{-\lambda t}) + \lambda e^{-\lambda t}].$$

Solving, we have

$$e^{-\lambda t} = \frac{\lambda N_0}{\lambda(N_0+1)} = \frac{N_0}{N_0+1}, \text{ or } t = \frac{1}{\lambda}\ln\left(\frac{N_0+1}{N_0}\right).$$

Next, we will determine P_{N_0+2}. The differential equation for P_{N_0+2} is

$$\frac{dP_{N_0+2}}{dt} + \lambda(N_0+2)P_{N_0+2} = \lambda(N_0+1)P_{N_0+1}$$
$$\frac{dP_{N_0+2}}{dt} + \lambda(N_0+2)P_{N_0+2} = \lambda(N_0+1)N_0 e^{-\lambda N_0 t}(1-e^{-\lambda t}).$$

The initial condition is $P_{N_0+2}(0) = 0$, so we obtain

$$P_{N_0+2} = \frac{N_0(N_0+1)}{2}e^{-\lambda N_0 t}(1-e^{-\lambda t})^2.$$

If we were to continue the calculations, we would find that, for any $j \geq 1$,

$$P_{N_0+j}(t) = \frac{N_0(N_0+1)\cdots(N_0+j-1)}{j!}e^{-\lambda N_0 t}(1-e^{-\lambda t})^j. \tag{5}$$

We must now verify that this is, in fact, the solution for all integers $j \geq 1$. We will do this by induction, which means we must do the following.

1. Explicitly prove the statement is true for the first value of j, usually $j = 0$ or $j = 1$.
2. Assume that it holds for all j less than or equal to some value j_0. (This is the induction assumption.)
3. Using the assumption, prove that the statement holds for the next value, $j_0 + 1$.

We have done the first step already. Now, let us assume that Equation (5) is valid for all $j \leq j_0$. We next need to determine $P_{N_0+j_0+1}$ using the differential equation Equation (3) with $N = N_0 + j_0 + 1$. Using the formula for $P_{N_0+j_0}$, which is valid by the induction assumption, we obtain

$$\frac{dP_{N_0+j_0+1}}{dt} + \lambda(N_0+j_0+1)P_{N_0+j_0+1} = \frac{N_0(N_0+1)\cdots(N_0+j_0)}{j_0!}e^{-\lambda N_0 t}(1-e^{-\lambda t})^{j_0},$$

with initial condition $P_{N_0+j_0+1}(0) = 0$, whose solution is

$$P_{N_0+j_0+1} = \frac{N_0(N_0+1)\cdots(N_0+j_0)}{(j_0+1)!}e^{-\lambda N_0 t}(1-e^{-\lambda t})^{j_0+1}.$$

Another way to introduce uncertainty into a mathematical model of populations is to assume that the growth rate, R, is a random variable, fluctuating in time over different values, perhaps due to uncontrollable cahnges in the environment.