

Last class we discussed a simple random walk P.1
model for population growth, where the
of individuals $N(t)$ was governed by:

$$\begin{cases} \Pr[N(t+1) = n+1 | N(t) = n-1] = \beta \\ \Pr[N(t+1) = n-1 | N(t) = n] = 1 - \beta = \delta \end{cases} \quad \text{If } n \neq 0$$
$$\Pr[N(t+1) = 0 | N(t) = 0] = 1$$

Is this a good model? The answer depends on what you mean by "good". It is certainly not a realistic model of biological populations (although it probably is a very realistic model of some gambling games). However, realism is not the only goal of a model. In fact, realism (in the sense of providing accurate quantitative predictions of the real world) is not even a goal of most models.

Here's a related question: why do we study the model

$$N_{t+1} = (b-d) \cdot N_t + N_t$$

Is it because we can carefully measure b , d (P.2) and N_0 and then know how many rabbits we will have? Probably not. Some processes really do almost follow this model, but we would study it regardless.

The key reason to study this model is that it gives important qualitative predictions, and the model is simple enough that we can clearly understand the mechanism for these predictions.

In particular, it shows that there are equilibrium values - populations that do not change - and they can behave in two very different ways (stable vs unstable) depending on whether growth exceeds loss or vice versa. This idea is important in every other model we study. We could have started with a more realistic growth model and found the same features, but then we'd have to decide what was due to birth rate vs. death rate, what was due to the carrying capacity, etc.

(P.3)

Models like this are called "Toy models," but that doesn't mean they're bad. Toy models distill mathematical problems into something just simple enough to capture an idea.

What qualitative ideas have we found from our simple random walk models?

- Probably the most important is that there are two distinct types of "equilibrium" behavior. In our first random walk, where N could be negative, if we let $\beta = \delta = 1/2$, then $\langle N(t) \rangle = 0$ for all t . This is the stochastic version of a fixed point - N stays at zero on average, but can fluctuate, and we need to track the fluctuations.

In our latest random walks we saw a very different type of "equilibrium".

In this case, if $N(t)$ ever hit zero, then it was always zero.

In this case, $N(t) = 0$ is called an "absorbing state". Once probability goes to an absorbing state, it never comes back.

• In the long run, the population either dies out or gets infinitely large, even if β and δ are perfectly balanced. This one might look like an artifact of our model - a result of over simplifying - but it is actually a law of most stochastic processes. In the long term, for any reasonable stochastic problem, you always end up at either an absorbing state or infinity. This should be disheartening news from a biological standpoint: Either a population becomes infinitely large (which is probably impossible) or it eventually goes extinct.

• The effects of stochasticity matter more for small populations. (The randomness in these models is usually called

a "finite size effect".) If births exceed deaths, a deterministic population never goes extinct, but a population of size N_0 goes extinct $(\frac{d}{b})^{N_0}$ percent of the time. As $N_0 \rightarrow \infty$, we recapture the deterministic results.

- "Perfectly balanced" growth rates don't matter.
- In the deterministic model, if $b=d$, the population was exactly balanced. We also encountered this in other ODE/Map models where $f'(x^*)=0$ or $|f'(x^*)|=1$ and we couldn't easily model the behavior. In a stochastic world, these don't matter. N doesn't stop changing just because $B=D$.

These results hold for a wide variety of models, and they'll be important for all the other stochastic models we study.

We will now try to add complexity into our model. One of the big issues with the simple random walk model is that it assumes that, at each time step there are only two possibilities: one birth or one death. It seems obvious that we should include other possibilities:

- 1) Nothing happens in a time step
- 2) More than one thing happens in a time step.

1) This one is easy to incorporate (although it makes our model much harder to solve).

We will loosen the restriction that $B + D = 1$. Instead, we will require $B + D \leq 1$.

This means that B is the probability of one birth, D is the probability of one death and $1 - (B + D)$ is the probability of neither.

2) The second factor is a little more delicate. We will argue in two steps. First, the chance of multiple births/deaths goes down drastically if we only look at one individual. It might be reasonable to say,

$$P_r [N(t+1)=2 | N(t)=1] = \beta$$

$$P_r [N(t+1)=0 | N(t)=1] = \delta$$

$$P_r [N(t+1)=1 | N(t)=1] = 1 - (\beta + \delta).$$

This is better, but still not great. What if the individual has two offspring in a year? We can also look at smaller intervals of time. While a rabbit could definitely have more than one baby per year, they almost certainly won't in a second. But now we have a different issue. Having a 10% chance of death per year (or of birth) is very different from having a 10% chance of death per second. These probabilities have to scale with Δt .

Ultimately, we are interested in finding Pg

$$Pr[N(t) = n | N(0) = N_0] \equiv P_n(t).$$

We can get an equation for P_n by noting that

$$\begin{aligned} Pr[N(t+\Delta t) = n] &= Pr[1 \text{ birth} | N(t) = n-1] \\ &+ Pr[1 \text{ death} | N(t) = n+1] \\ &+ Pr[\text{No change} | N(t) = n]. \end{aligned}$$

$$\begin{aligned} \Rightarrow P_n(t+\Delta t) &= [(n-1)\beta\Delta t + o(\Delta t)] \cdot P_{n-1}(t) \\ &+ [(n+1)\delta\Delta t + o(\Delta t)] \cdot P_{n+1}(t) \\ &+ [1 - (\beta + \delta)\Delta t + o(\Delta t)] \cdot P_n(t) \end{aligned}$$

This is impossible to solve for a couple reasons. First, it has several unknown $o(\Delta t)$ functions. Second, it is an infinite system of coupled difference equations.

The first problem has an obvious solution. $o(\Delta t)$ means that $\lim_{\Delta t \rightarrow 0} \frac{o(\Delta t)}{\Delta t} = 0$. (P.10)

We can rearrange our equation to obtain

$$P_n(t+\Delta t) - P_n(t) = (\lambda - \mu) \Delta t P_{n-1}(t) + o(\Delta t) P_{n-1}(t) \\ + (\lambda + \mu) \Delta t P_{n+1}(t) + o(\Delta t) P_{n+1}(t) \\ - (\beta + \delta) \Delta t P_n(t) + o(\Delta t) P_n(t)$$

$$\Rightarrow \frac{P_n(t+\Delta t) - P_n(t)}{\Delta t} = (\lambda - \mu) P_{n-1}(t) + (\lambda + \mu) P_{n+1}(t) \\ - (\beta + \delta) P_n(t) \\ + \frac{o(\Delta t)}{\Delta t} P_{n-1}(t) + \frac{o(\Delta t)}{\Delta t} P_{n+1}(t) \\ + \frac{o(\Delta t)}{\Delta t} P_n(t)$$

If we take the limit as $\Delta t \rightarrow 0$, the $o(\Delta t)$ terms drop out, so we have

$$\boxed{\frac{dP_n}{dt} = (\lambda - \mu) P_{n-1} + (\lambda + \mu) P_{n+1} - (\beta + \delta) P_n}$$

w/ $P_{N_0}(0) = 1$ and $P_n(0) = 0$ for $n \neq N_0$

Of course, this is still an infinite system of coupled equations, but now they are odes instead of difference equations. It turns out that this makes a big difference, but we'll need some new techniques to solve it.