Dynamics of a single population in continuous time

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In this lecture, we will look at the simplest kinds of dynamics: dynamics of a single population abstracted away from its interaction with other species, or within its own species. In the spirit of toy models, we will see that this abstraction is nonetheless useful, and it will also help us introduce concepts that we'll see throughout the class in other settings.

The fundamental equation of population dynamics is the following:

$$\left[\begin{array}{c} \text{Change in} \\ \text{population size} \end{array}\right] = \left[\begin{array}{c} \text{An individual's} \\ \text{contribution to} \\ \text{population growth} \end{array}\right] \times \left[\text{Population size}\right] \quad (1)$$

One way of reading this equation is literal: all individuals do contribute to the population at some average rate, independent of their interactions with others. That's fairly unrealistic, but conceptually simple: one can think of a population as simply a collection of individuals, and if one understands what happens to a single individual, one only needs to multiply that with the number of individuals to know what happens to the whole population. In this view, there is no organizational unit between the individual and the population. The second interpretation is that this is simply descriptive: individuals' contributions will vary depending on the population composition, etc, but we are simply taking the gross reproduction rate of the whole population, and dividing it by the population size, to get a per-capita average. This is more realistic, since it admits the possibility of additional levels of organization between the individual and the population (e.g., social groups), but it also admits that equation (1) is a snapshot of what might happen in a particular population composition, and not necessarily a general law of how that population will behave. Nonetheless, as we will see, this formulation allows us to handle a lot of cases, including many cases where the population composition affects the contribution of a single individual.

An important decision that we often have to face in representing dynamics is whether we'll treat time as discrete or continuous. The choice depends, as it usually does, on what we are interested in keeping in the model, and what we want to abstract away from. Continuous time models might seem more realistic, after all, time is continuous (at least for our purposes). Yet sometimes a discrete time model might in fact be better, if we are describing a population that is only censused in discrete time points (e.g., on successive field seasons at a particular time every year). In such cases, we might not have nor need the information that describes the population dynamics within the discrete intervals,

if we have enough data to go from one census point to the next. Frequently, an important consideration in the choice between discrete and continuous models is analytical convenience: some problems are easier to formulate and/or analyze in continuous time, and some in discrete time. The choice is not always innocent, however: as we'll see in the next lecture, the continuous and discrete time versions of the same biological scenario might have very different dynamics. In short, the choice between continuous time and discrete time depends on a lot of factors, and frequently there is no "right" answer. But if one can obtain the same biological results ("robust theorems" sensu Levins (1966)) one has a stronger case, which is why we will learn both ways of modeling, and also the mapping between them.

Exponential growth

Let's start with the simplest possible case. Two things for sure happen to every living organism: it is born, and it dies. So, our population dynamics has to have at least a birth rate and a death rate. In the simplest possible case, all individuals have the same constant birth and death rates no matter what. Suppose that an individual gives birth to b offspring per unit time, and dies with rate d, which gives "how fast" an individual is dying. [1] Let us consider the population size at a time t and at the end of a small time interval Δt after t:

$$n(t + \Delta t) = (1 - d\Delta t)(1 + b\Delta t)n(t) , \qquad (2)$$

where the first parentheses take into account that any individual has probability $d\Delta t$ to die within this short interval, and the second one $b\Delta t$ probability of giving birth to an offspring. We haven't specified the order of these events; the equation is compatible with deaths happening first surviving individuals giving potentially birth then, or births happening first and everyone (including newborns) dying with the same probability. The next steps show why this ordering isn't important. Let's multiply out equation (2), subtract $n(t)$ from both sides, and divide by Δt:

$$\frac{n(t + \Delta t) - n(t)}{\Delta t} = (b - d - bd\Delta t)n(t) . \qquad (3)$$

Taking the limit of this equation as $\Delta t \to 0$, we get:

$$\frac{dN(t)}{dt} = (b - d)N(t) = rN(t) , \qquad (4)$$

where $r = b - d$ is called the per capita growth rate or intrinsic rate of increase. Note that the $bd\Delta t$ term vanished as we took the limit, corresponding to the fact that in an infinitesimal time interval, the probability that both birth and death events for happen is going to be negligible, hence it didn't matter (in this case) which order we specified things happened.

Equation (4) is perhaps the second easiest differential equation to solve.[2]

[1] More precisely, d, when multiplied with a small enough time increment, gives the probability that an individual dies in that time increment. The same interpretation applies to b as well, though somehow it is easy to describe b as the number of births per unit time per individual whereas number of deaths per unit time per individual sounds strange.

[2] The easiest would be where the right-hand side is a constant.

One can solve it by separation of variables. Start with dividing by $N(t)$ and multiplying by dt to get:

$$\frac{dN(t)}{N(t)} = r\,dt\,. \tag{5}$$

Next, we remember $\frac{dN(t)}{N(t)} = d[\ln(N(t))]$, and integrate both sides from $t' = t_0$ to $t' = t$ [3] and go through a few manipulations:

$$\int_{t'=t_0}^{t} d[\ln(N(t'))] = \ln(N(t)) - \ln(N(t_0)) = \int_{t'=t_0}^{t} rt' = rt - rt_0$$

$$\ln\left(\frac{N(t)}{N(t_0)}\right) = r(t - t_0)$$

$$\frac{N(t)}{N(t_0)} = \exp[r(t - t_0)]$$

$$N(t) = N(t_0)\exp[r(t - t_0)] \tag{6}$$

The plot of an exponentially growing population is shown in the figure on the right.

Example

Exponential growth might not seem something you might be interested for application in real life, since it makes patently absurd predictions in the long run. But as someone once said, in the long run we're all dead, and there's plenty of exponential growth in the short run. Consider the graph on the right, depicting the infection counts from the 2014 Ebola outbreak in West Africa. This is currently an exponentially growing epidemic. Strictly speaking, the dynamics of epidemics like these are different than simplistic exponential growth, but as one can see in these graphs, the initial outbreak of an epidemic is well-described by an exponential.[4] According to the data compiled by the CPID, on August 3th, 2014, there were 500 reported cases. On September 14th, this number was 2710. So, in 42 days, the infection count grew by 5.42-fold. What's the r in this case?

$$\exp[r * 42] = 5.42$$

$$r = \ln(5.42)/42 \approx 0.040 \text{ infections/day}$$

If this rate stays unchanged, we could have expect $200,000$ infections by the end of the year. This is an unprecedented number for this virus, and why people are freaking out about this outbreak.

Many other ecologically important scenarios exist where one might expect to find populations undergoing exponential growth: for example invasive species in a new habitat or resident species after severe disturbances (e.g., many microbial populations that are subject to frequent flushing or dislodgment). In these cases, many of the important aspects of population ecology might be driven by the exponential growth phase for significant amounts of time.

[3] The differential of a function $f(x)$, $d[f(x)]$ is simply $f'(x)dx = \frac{df(x)}{dx} * dx$. The derivative of $\ln(x)$ is simply $1/x$, so $d[\ln(x)] = dx/x$.
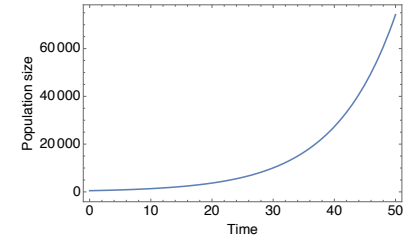
Exponential growth with $r = .1$, and $N(0) = 500$

[4] According to a paper in PLoS Current Outbreaks when the epidemic was still going on, a slight modification of the simple exponential growth, where $N_t = (\lambda/(1+d)^t)^t N_0$ might better describe the dynamics, because it takes into account the gradual diminishing of the basic reproductive rate due to interventions, depletion of the susceptible pool, etc. (Fisman et al., 2014).
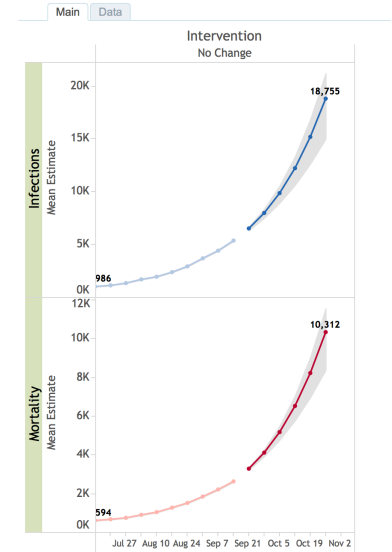
The historical and projected case count and mortality from the 2014 West African Ebola outbreak. Graphs retrieved from Columbia Prediction of Infectious Diseases website `http://cpid.iri.columbia.edu/index.html` on September 23rd, 2014. Graphs shows projections with no intervention for the combined infections and mortality in Guinea, Liberia and Sierra Leone.

Linear and non-linear systems

In general, the dynamics of a single variable x (e.g., the population size) can be written as:

$$\frac{dx}{dt} = f(x) , \qquad (7)$$

where $f(x)$ is some function of the variable x (its value at time t). The exponential growth equation is an example of a linear system: the function $f(x)$ is linear in x. Linear systems are easy to work with, because their components can be solved separately and added together at the end. Not so for non-linear systems, where the function $f(x)$ includes higher powers of x, products of x with other state variable (for more than one-dimensional systems) or any other function of x (e.g., trigonometric functions). But non-linear systems are also where a lot of interesting stuff happens and as a rule, nature is non-linear until you linearize it.

Density dependence

The first example of a non-linear system is density dependent population growth: even though it's not impossible, or even uncommon, exponential growth is something of a special case. More generally, the demographic rates of a population will depend on how many individuals it currently is comprised of (which is usually referred to as density of the population).

Logistic growth

The logistic growth equation was first proposed by the Belgian mathematician Pierre François Verhulst, who upon reading Malthus, thought that a population growth rate that is linear in population size was not quite the right model. He proposed that the population growth rate should be a quadratic function of population size, with the coefficient of the quadratic term negative to represent the fact that as population size increases, resource scarcity should decrease the birth rate or increase the death rate of individuals. In other words, he proposed to formally model density dependence.

It turns out that the logistic equation is the simplest form of density dependence, because it is what one obtains when the *per capita* birth and death rates depend linearly on current population size, the former decreasing and the latter increasing with population size. In other words:

$$\frac{dN(t)}{dt} = ((b - aN(t)) - (d + cN(t)))N(t) . \qquad (8)$$

Immediately one can see that linear density dependence produces non-linear dynamics, since $N(t)$ is squared on the RHS. To put this equation in the more

familiar form, factor our $b - d$ to get:

$$\frac{dN(t)}{dt} = (b - d)\left(1 - \frac{a + c}{b - d}N(t)\right)N(t)$$

$$= r\left(1 - \frac{N(t)}{K}\right)N(t),\qquad(9)$$

where r as before is the intrinsic growth rate equal to $b - d$, the difference of density independent birth and death rates, and $K = \frac{b-d}{a+c}$ is the carrying capacity.

Now, integrating this equation is somewhat harder than the exponential, but it can be done. First, divide it by $N(t)^2$ to read:

$$\frac{1}{N(t)^2}\frac{dN(t)}{dt} = r\left(\frac{1}{N(t)} - \frac{1}{K}\right).$$

Next, define a new variable $z(t) = \frac{1}{N(t)} - \frac{1}{K}$ and observe that $z'(t) = -N'(t)/N(t)^2$ (by the chain rule), so that we have

$$z'(t) = -rz(t),$$

in other words, our old friend the exponential, which we know how to solve. So, we have $z(t) = z(t_0)\exp[-r(t - t_0)]$. Now we can solve for $N(t)$ from our substitution above[5] and find:

$$N(t) = \frac{K}{1 + [(K - N(t_0))/N(t_0)]\exp[-r(t - t_0)]}\qquad(10)$$

You can see the logistic plotted on the right.

One dimensional flows

This is all nice and well, we have seen two models for population dynamics and were able to solve both of them. But it bears to keep in mind that these two are the absolute simplest models one can build, and therefore easy to solve. In general, we are not so lucky to be able to obtain analytical (or "closed form") solutions to non-linear dynamics. But it turns out we can still say a lot about a system, even without solving it, by analyzing "flows" (or "flow patterns")[6]. In particular, flow analysis can tell us about the place and stability of fixed points, as well as the dynamics that happen between those points.

Flow analysis is a graphical way of representing a dynamical system, in particular, showing which way the state variable "flows". In one dimension, this is particularly easy to visualize. One simply plots the function $f(x)$ against x (as we did for the ligistic growth): if $f(x) > 0$, i.e., above the horizontal axis, the state variable increases in time $dx/dt > 0$ and the flow is to the right; if $f(x) < 0$, the state variable decreases, and the flow is to the left. When $f(x)$ crosses the horizontal axis, i.e. $f(x) = 0$, we have a **fixed point** or an **equilibrium** of the dynamics, which means that a system that starts out in that particular state (and is not disturbed exogenously) will always stay there.
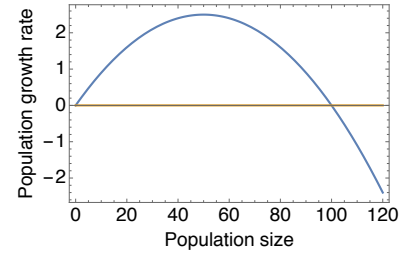
Density-dependent growth rate as a function of population size, with $r = 0.1$ and $K = 100$.
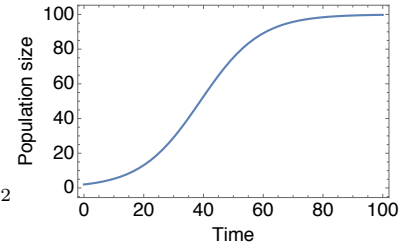
Dynamics of a logistically growing population, with $r = 0.1$ and $K = 100$.
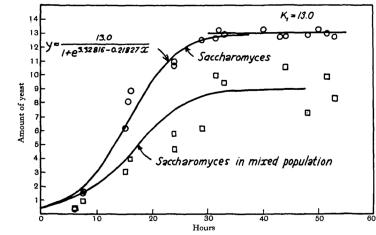
[5] Recommended as exercise.

Logistic growth of *S. cerevisiae* in one of Gause's famous competition experiments (Gause, 1932).

[6] Strogatz (2001) is an excellent reference for non-linear dynamics in general, with a lot of biological examples, and for the material covered in this section.
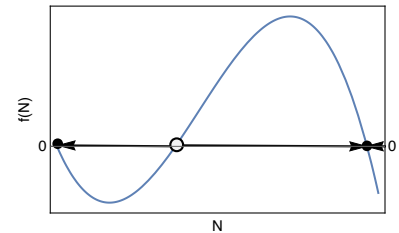
Example: "two-sex" model of population dynamics

Suppose we have a sexual species, so that reproduction requires two individuals of the opposite sex bumping into each other. We are going to assume that the sex ratio of the population is even (and constant) so that we can represent the dynamics with a single number N. The rate at which a male and a female meet each other is then going to be proportional to N^2.[7] We will further assume there is density dependence of reproductive rate, so that when two individuals do bump into each other, the number of offspring they produce is a linearly decreasing function of the population density. We assume, for simplicity, no density dependence in the growth rate, so that the population dynamics are given by:

[7] For even sex ratio, the proportionality constant is going to be 1/4, but we'll simply ignore that constant.

$$\frac{dN}{dt} = N^2(b - aN) - dN = bN^2(1 - aN) - dN \, , \qquad (11)$$

where we suppressed the time-dependence of N for notational simplicity. Let us plot the right-hand side of this equation. For $N = 0$, the right-hand side is going to be 0, which makes sense, and also implies that no population is an equilibrium. What happens for small N? There is a negative linear term, a positive quadratic term, and a negative cubic term. For small N, the linear term dominates, so initially the RHS is going to decrease. Since it starts at zero, that means it will go negative. Then, as N increases further, the RHS is starting to increase and eventually will cross the zero line. This model is an example of an Allee effect, where populations have lower growth rates at low densities. Allee effects are a major issue for many endangered species. In this case, the Allee effect is caused by the inability of finding mates in low population densities (e.g., many non-selfing plants are subject to this effect, as their pollen might not find their way to other plants of the same species). As N increases further, the negative cubic term will start dominating, so eventually the RHS will start decreasing again, and for large enough N, will again cross the zero line. The graph of the RHS will look something like the one on the margin.

The flow of the dynamics described by equation (11). The population growth $f(N)$ (given by the RHS of (11)) is negative for small N, before getting positive again. The arrows on the horizontal axis depict which way N "flows".

Linear stability analysis

Equilibria can be of two types: **stable**, or **unstable**. Stable equilibria "attract" flows: when the state variable is in the neighborhood of a stable equilibrium, it will tend to go to that equilibrium[8]. Conversely, an unstable equilibrium will "repel" flows: when the system is near an unstable equilibrium, it will move away from it[9].

[8] Or equivalently, when the system starts out from an equilibrium but is "nudged" out of it, it will return back to its original state, provided the nudge isn't too big

[9] Or will not return to it when nudged away from that equilibrium

Why are we interested in the stability properties of equilibria? Remember, our model does not capture all that's happening in nature. So there will be factors affecting our system that are outside of the description of the dynamics we

give. If we are lucky, these factors can be represented by small (in some sense) perturbations to our system. Stable equilibria robust to such small perturbations, so we can say with more confidence that they are informative about the long-term behavior; whereas we wouldn't expect to find a system at an unstable equilibrium in the long term.

The flow diagram gives us a way to graphically determine stability: if arrows on both sides of an equilibrium point to that equilibrium, the dynamics will approach it from either side, so it is stable. But we can also determine stability without the graphical analysis, by linearizing the system near the equilibrium.[10] Formally, consider a dynamics given by $\frac{dx}{dt} = f(x)$, with an equilibrium at x^*. Suppose the dynamics starts at $x = x^* + \delta$, where δ is a small deviation from the equilibrium. We want to know if the deviation δ will grow or shrink in time; in the latter case the equilibrium is stable, in the former not. Since $\delta = x - x^*$, we can write its dynamics as:

$$\frac{d\delta}{dt} = \frac{d(x - x^*)}{dt} = \frac{dx}{dt} = f(x) \,, \tag{12}$$

because x^* is a constant. So δ obeys the same dynamics as x. We then write the Taylor expansion of $f(x)$ around x^*:

$$f(x^* + \delta) = f(x^*) + f'(x^*)\delta + \frac{1}{2}f''(x^*)\delta^2 + \cdots . \tag{13}$$

Now, since x^* is an equilibrium, $f(x^*) = 0$ by definition. Further, since we assumed that δ is small, higher order terms (e.g., δ^2 and higher) are going to be much smaller than the linear term, so we can approximate $f(x^* + \delta)$ by $f'(x^*)\delta$:

$$\frac{d\delta}{dt} \approx f'(x^*)\delta \,. \tag{14}$$

Thus, a deviation from the equilibrium will grow, and the equilibrium is unstable, if $f'(x^*) > 0$, and the deviation will shrink, resulting in a stable equilibrium if $f'(x^*) < 0$. In the two-sex model above, one can verify the concordance between the linear stability analysis and the graphical flow method: if $f(x)$ intersects the zero-line from below, its derivative is positive at that point, and the flow is away from the equilibrium, making it unstable. Conversely, if $f(x)$ intersects from above, the flows go towards the equilibrium, making it stable.

[10] In one dimensional flows, the graphical technique is straightforward and effective, but in more dimensions it isn't, whereas the linear stability analysis generalizes to arbitrary dimensions just fine.

References

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