

Chapter 2 – Single-species Population Dynamics

2.1 Exponential Growth

The simplest thing to assume about a population is that all of the individuals are identical and non-interacting. In this case the rate of change of the population size N will be proportional to the population size:

$$\frac{dN}{dt} = rN \quad (2.1)$$

We will often refer to the parameter r as the (per capita) growth rate of the population, but it is important to remember that the parameter r is in principle composed of both birth and death rates:

$$r = b - d \quad (2.2)$$

For now we will be considering deterministic dynamics, in which case only the value of r will matter; however, when stochastic dynamics are considered this will no longer be the case. The solution of this differential equation is then

$$N(t) = N_0 e^{rt} \quad (2.3)$$

Although we will often refer to this as exponential growth, it is important to remember that the parameter r can be either positive or negative. In particular, if the death rate d is larger than the birth rate b then $r < 0$ and the population will decay exponentially to zero.

Simplest example of evolutionary change

Now suppose that we have two populations, each of which are growing exponentially with their own per capita growth rate:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \\ \frac{dN_2}{dt} &= r_2 N_2 \end{aligned}$$

In this situation each population will grow exponentially. However, the fraction of the individuals that are type 1 will vary over time:

$$f \equiv \frac{N_1}{N_1 + N_2} = \frac{N_{1,i} e^{r_1 t}}{N_{1,i} e^{r_1 t} + N_{2,i} e^{r_2 t}}$$

A simpler time dependence can be obtained by looking at the ratio of the two types over time:

$$\rho(t) \equiv \frac{N_1}{N_2} = \rho_0 e^{(r_1 - r_2)t} \quad (2.4)$$

Up to now I have spoken as if these two populations were different species. However, it is also possible that they could have been different genotypes within a species. In this case, our example of two exponentially growing populations can be thought of as an example of an evolutionary change within a single population.

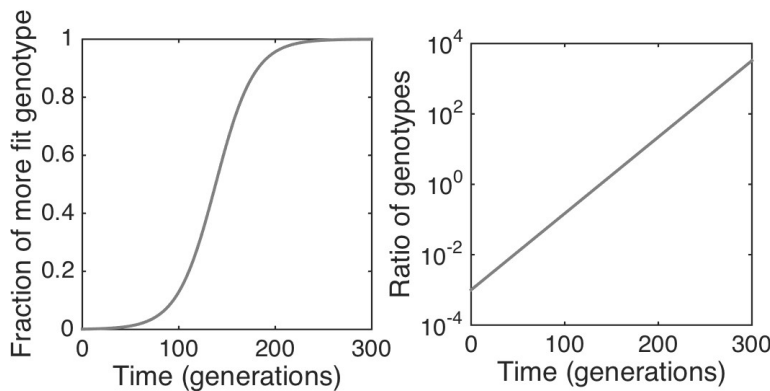


Figure 2.1: A more fit genotype will spread throughout the population exponentially.

There are many situations in the laboratory in which one is interested in the fitness of a mutant relative to the fitness of the “wildtype” strain that lacks this mutation. The most obvious way to determine this is to measure the growth rate of the mutant (r_1) and compare it to the measured growth rate of the wildtype strain (r_2). However, even for microbial experiments in the lab the error on a measured growth rate will typically be a few percent even with a dozen replicates. A much more accurate measurement of the relative fitness of the mutant $\Delta r \equiv r_1 - r_2$ can be obtained by competing the two strains together and then measuring the change in the fraction of the mutant as a function of time. In particular, a plot of the ratio of the two genotype’s fractions vs time on a log-linear plot will yield a straight line (Figure 2.1), with the slope being the difference in fitness of the mutant as compared to the wildtype.

2.2 Logistic Growth

Real populations will always eventually run out of resources or be limited by other factors. This limitation was not included in the simple model of exponential growth assumed in Equation (2.1). Perhaps the simplest way to incorporate this is to assume that the per capita growth rate decreases linearly to some carrying capacity K :

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (2.5)$$

This is a phenomenological description that does not have to be correct for any given population. However, it is a useful approximation for many real populations. An

Problem 2.1: Use separation of variables to derive the solution to the logistic growth equation:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right)$$

especially informative view of growth is to plot the per capita growth rate as a function of population size:

$$\gamma(N) \equiv \frac{1}{N} \frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) \quad (2.6)$$

For small population sizes a logistically growing population will grow exponentially with rate r , but over time the growth rate decreases until the population size reaches equilibrium at the carrying capacity K (Fig 2.2).

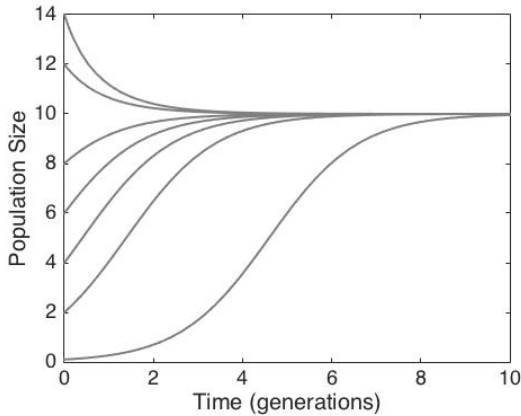


Figure 2.2: Populations that grow logistically saturate at a carrying capacity ($K = 10$ in this figure).

2.3 Real populations will often reach equilibrium in a non-logistic manner

We found in the previous section that real populations cannot grow indefinitely, and instead are eventually limited by either biotic or abiotic factors. Given the complexity of factors that may be limiting the growth of the population, in general there is no reason to believe that the growth rate of the population will have the simple functional form described by Equation (2.5). Indeed, many populations have growth behavior that deviates from simple logistic growth, even when the qualitative behavior is similar (ie growth of the population until saturation).

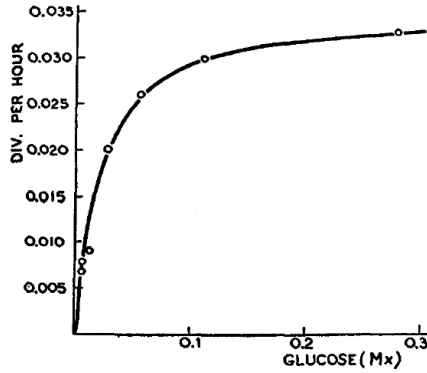


Figure 2.3: Growth rate of *M. tuberculosis* as a function of the glucose available in the medium. Solid line is a fit of the Monod equation with $\gamma_M = 0.037\text{hr}^{-1}$ and $K_S = M/45$. Figure from Monod, J. A. C. Q. U. E. S. "The growth of bacterial cultures." *Selected Papers in Molecular Biology by Jacques Monod* (2012): 139.

As an example of how the population dynamics can differ from the logistic model, we will consider a simple model of how micro-organisms grow on a single limiting resource R . In the Monod model, it is assumed that the per capita growth rate of the population obeys a Michaelis-Menten-like form (Fig 2.3):

$$\frac{1}{N} \frac{dN}{dt} = r_{\max} \frac{R}{R + K_R} \quad (2.7)$$

The half-velocity constant K_R describes the concentration of the resource that allows half-maximal growth rate. As the population grows this limiting nutrient will be consumed. In many (but not all) situations there is a fixed amount of this resource that is required to make each additional cell, in which case the resource concentration changes with time according to:

$$\frac{dR}{dt} = -\beta \frac{dN}{dt} = -\beta N r_{\max} \frac{R}{R + K_R} \quad (2.8)$$

As the population grows the rate that the resource is being used increases until the resource depletes sufficiently to slow down the growth rate of the population.

Simulations of population growth in the Monod model show that not all such populations grow logistically. Instead, logistic growth is observed only when the starting resource concentration R_0 is significantly smaller than the half-velocity constant K_R . For starting resource concentrations larger than K_R the per capita growth rate falls in a very non-linear way: the division rate of the cells does not decrease very much until very close to the final saturating cell density.

Question 2.2: Show that the Monod model reduces to logistic growth for a small population growing on a limiting resource such that $R_0 \ll K_R$.

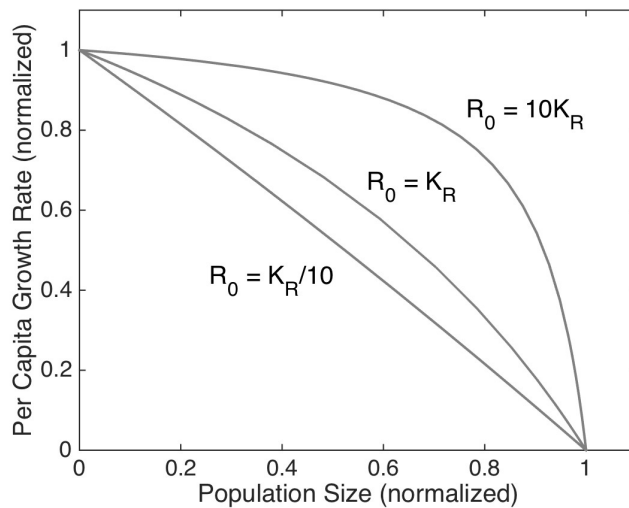


Figure 2.4: Per-capita growth rates as a function of population size for a microbial population growing according to the Monod Equation. Such populations will display approximately logistic growth so long as the initial limiting resource concentration R_0 is much less than the concentration of the resource required to provide half-maximal growth (K_R). If $R_0 > K_R$ then the per capita growth will be a concave down function of the population size.

Indeed, various experimental populations of bacteria are observed to grow with dynamics that are distinctly non-logistic.

Question 2.3: Assume that the bacterium *E. coli* obeys the Monod model with $r_{max} = 1 \text{ hr}^{-1}$ and $K_R = 0.01\%$. If *E. coli* were placed in media with initial glucose concentration of 0.005% , do you think that the logistic model would be a good fit to the resulting growth curve? reduces to logistic growth for a small population growing on a limiting resource such that $R_0 \ll K_R$.

2.4 Cooperatively growing populations can exhibit bistability

In the previous sections we assumed that populations were nearly non-interacting, in that they only competed with each other for resources. However, in many contexts populations benefit each other in some way. In the case of animals, this can arise due to cooperative defense (eg schooling of fish or herding of zebras), cooperative hunting (eg a pack of wolves taking down a bison), or the need to find mates. In these situations populations can display what is known as the Allee effect, in which the per capita growth rate initially increases with the population size N . Of course, resources must eventually become limiting, meaning that the per capita growth rate must eventually decrease for sufficiently large population sizes.

Just as we often use the phenomenological logistic growth model to think about populations that interact via limited resources, in the case of the Allee effect the simplest phenomenological description is perhaps

$$\frac{dN}{dt} = rN(N - N_c)(K - N) \quad (2.9)$$

The per capita growth rate is then a quadratic, with the per capita growth rate equal to zero when the population size is equal to either N_c or K . This equation has qualitatively different behavior depending upon whether N_c is greater than or less than zero. If $N_c < 0$ then the population displays what is known as a weak Allee effect: At low population sizes the population indeed benefits from other members of the population, but this cooperative interaction is not strictly necessary for survival as even a small population can grow up to the carrying capacity K . However, if $N_c > 0$ then the situation is very different, as populations that start below this critical size N_c will go extinct, whereas populations that start above this critical size will survive and grow to reach the carrying capacity K . This case in which the population displays bistability is known as the strong Allee effect. Indeed, deteriorating environments that for example increase death rates can make such populations experience a catastrophic population collapse due to a fold bifurcation (see Fig 2.5).

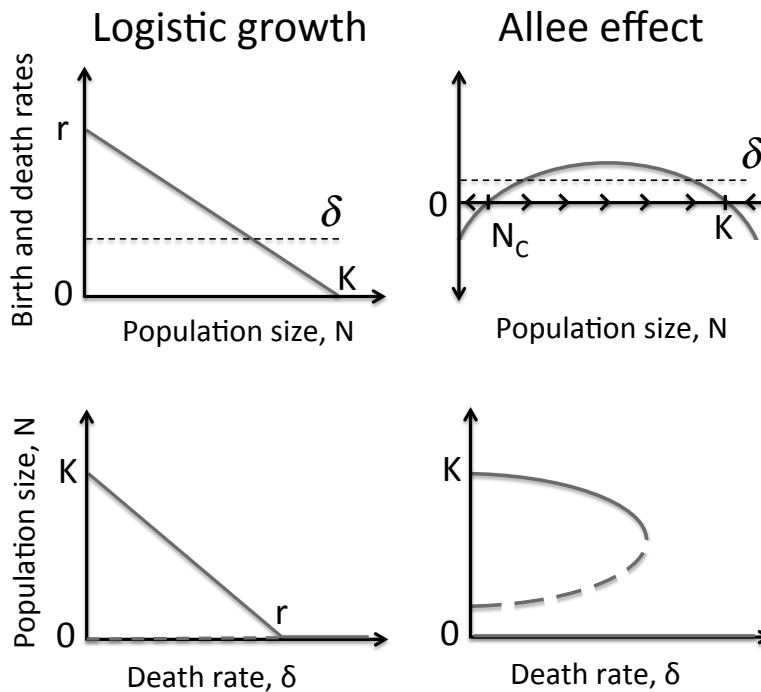


Figure 2.5: Populations experiencing an Allee effect can have a minimal viable population size, whereas populations that grow logistically do not. Moreover, these two types of populations respond very different to an imposed death rate δ (dashed line in the upper two plots). An increase in the death rate on a logistically growing population leads to a graduate decrease in the size of the population (bottom left; solid line indicates a stable fixed point, whereas a dashed line indicates an unstable fixed point). A population experiencing an Allee effect responds very differently to an imposed death rate, as there is a fold (saddle-node) bifurcation that leads to catastrophic collapse of the population in response to a slowly increasing death rate.

In the case of cell populations, a common cause of such cooperative growth is the collective break down of a complex sugar S into a resource R that can be consumed by the cells:

$$\begin{aligned}\frac{dN}{dt} &= rN \frac{R}{R+K_R} \\ \frac{dR}{dt} &= \alpha N \frac{S}{S+K_S} - \beta rN \frac{R}{R+K_R} \\ \frac{dS}{dt} &= -\alpha N \frac{S}{S+K_S}\end{aligned}\tag{2.10}$$

In writing these equations we have assumed that the population follows the Monod growth law on the resource R , that the complex sugar S is converted to resource R according to Michaelis-Menten kinetics, that the resource R is exhausted at a rate proportional to cell division, and that the concentrations of R and S are defined such that one unit of S can be converted into one unit of R .

The growth of such a population can often be divided into three phases. In the initial, low-cell density phase the complex sugar S has not yet been broken down to any significant degree and the population must grow on the small amount of the resource that is initially available. After some time we enter the second phase, as the resource concentration grows to the point that the per-capita concentration increases significantly, perhaps even close to the maximal possible growth rate of the population. Finally, we enter the third phase, in which the complex sugar S and the resource R are both exhausted, and the population reaches saturation.

We can make a back of the envelope estimate of how long it will take for the population to reach the second phase of growth. The per capita growth rate will be approximately given by

$$\gamma_1 = \frac{1}{N} \frac{dN}{dt} = r_{max} \frac{R(0)}{R(0)+K_R}\tag{2.11}$$

where $R(0)$ is the resource initially available. In other cases this low-density growth rate could be due to growth on a different resource or could be due to a low rate of direct utilization of the complex sugar S (see discussion in Ch. 4 on yeast growth in sugar). Regardless of what determines this low-density growth rate, it will take some time T_2 before enough of the complex sugar is broken down for the resource concentration to approximately double, at which point the growth rate of the population increases significantly and the second, cooperative phase of growth begins. We will assume that the rate of complex sugar breakdown is much larger than the rate of resource utilization ($\alpha \gg \beta$) and that the concentration of S is sufficiently large that it operates at saturation ($S(0) \gg K_S$). With these approximations, the dynamics of the system reduce to:

$$\begin{aligned}
\frac{dN}{dt} &= \gamma_1 N \\
\frac{dR}{dt} &\approx \alpha N \\
\frac{dS}{dt} &\approx -\alpha N
\end{aligned}
\tag{2.12}$$

The resource created after time t is then given by:

$$R_{created}(t) = \int_0^t \alpha N(t) dt \tag{2.13}$$

Setting the created resource equal to the starting resource level then gives the condition for the time at which the population begins to grow cooperatively:

$$\begin{aligned}
R_0 &= \int_0^{T_2} \alpha e^{\gamma_1 t} dt \\
&= \alpha N_0 (e^{\gamma_1 T_2} - 1) \\
&\approx \alpha N_0 e^{\gamma_1 T_2}
\end{aligned}
\tag{2.14}$$

Alternatively, we can solve for the time T_2 explicitly:

$$T_2 = \frac{1}{\gamma_1} \ln \left[\frac{R_0}{\alpha N_0} \right] \tag{2.15}$$

We see that the time to switch from the slow-growth to fast-growth phase depends only weakly on the rate that the sugar is broken down or the starting cell density. Another way to think about this is that the fast-growth phase will start at a critical cell density, and in particular when the population size reaches:

$$N_c \approx N_0 e^{\gamma_1 T_2} = R_0 / \alpha \tag{2.16}$$

The population therefore grows slowly until it reaches a critical population density, at which point it has broken down enough sugar to allow for more rapid growth. If the population breaks down the sugar faster (eg due to higher expression of the enzyme responsible for this breakdown), then it will reach this faster-growing phase faster.

Although the mechanistic model illustrated in Eq 2.9 is much more complex than the phenomenological model of Eq 2.8, the two models can both be used to illustrate the same qualitative behavior. In particular, either model can be used to generate a strong Allee effect, in which there is a minimal viable population size, so long as we assume that the individuals die at rate δ .

2.5 Populations in discrete time: The Logistic Map

There are many situations in nature in which the dynamics of populations are best described as taking place in discrete rather than continuous time. The standard example of this situation is when the population is exposed to strong temporal forcing, as occurs during annual cycles of plant or animal species.

The most famous example of a difference equation in all of math is the logistic map:

$$x_{n+1} = x_n(1 - x_n) \quad (2.17)$$

where x_n is the normalized population size during the n th time step. This is the natural discrete time analogue of Equation 2.5 which describes population growth with saturation. If we normalize the population size by the carrying capacity K then the differential equation describing logistic growth is:

$$\frac{dx}{dt} = x(1 - x) \quad (2.18)$$

Although these two equations look very similar, the dynamics are totally different. First, the differential equation describing logistic growth leads to a final population size that is always equal to the carrying capacity. Since in the equation above we have normalized the population size to the carrying capacity, this means that the normalized population size always ends at one (assuming that we start with non-zero population size).

In the case of the discrete logistic map, the equation quickly becomes meaningless if we try to start with a population size larger than one. Indeed, even if we start with a population size less than one the population will not reach one at equilibrium. Therefore, the normalizations mean very different things for the discrete and continuous versions of logistic growth. The solution of the logistic differential equation has the carrying capacity as the single stable fixed point (equilibrium), whereas the normalization in the logistic difference equation corresponds to the maximum population size that can ever be reached (and we will find that it is never going to be a stable equilibrium).

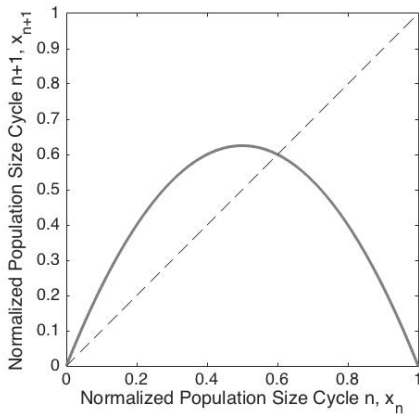


Figure 2.6: The logistic map describes a simple way in which the population size during one discrete “cycle” might relate to the population size during the next cycle.

The logistic equation yields qualitatively different behavior depending upon the value of the fecundity parameter r . Depending upon the value of r the logistic map can display an amazing range of behaviors, including extinction, stable survival, oscillations with different periods, and chaos. Examples of each of these behaviors is included in Figure 2.7.

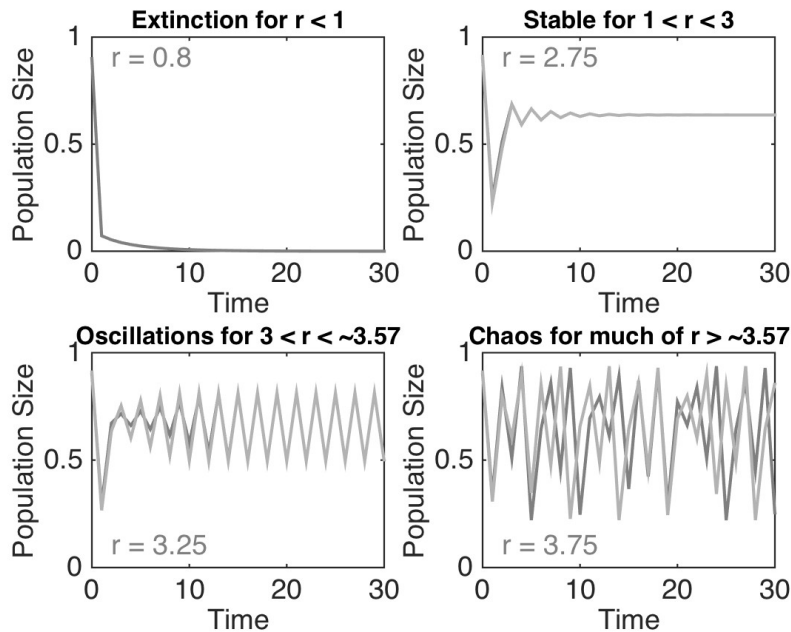


Figure 2.7: The logistic equation has qualitatively different dynamical behavior depending upon the fecundity parameter r . In each plot two trajectories were initiated at initial population size $x = 0.9$ (dark grey) or 0.901 (light grey). The trajectories converge, with the exception of the chaotic regime at $r = 3.75$.

One way to visualize the dynamics of a discrete map like the logistic map is using a bifurcation diagram, in which the population sizes at steady-state are plotted as “points” on a plot as the fecundity parameter r is varied (Figure 2.8). As can be seen, for $r < 1$ the populations go extinct, as $x = 0$ is the unique stable fixed point. For $1 < r < 3$ the population reaches a stable population size (possibly with decaying oscillations during approach to the equilibrium), but for larger values of $r > 3$ the behavior becomes increasingly complex. Initially there are oscillations with period two, but as r gets larger the dynamics experience what is known as a “period-doubling bifurcation”, in which the period of the oscillations doubles repeatedly until eventually there is a transition into chaotic dynamics, in which there is extreme sensitivity to the starting conditions.

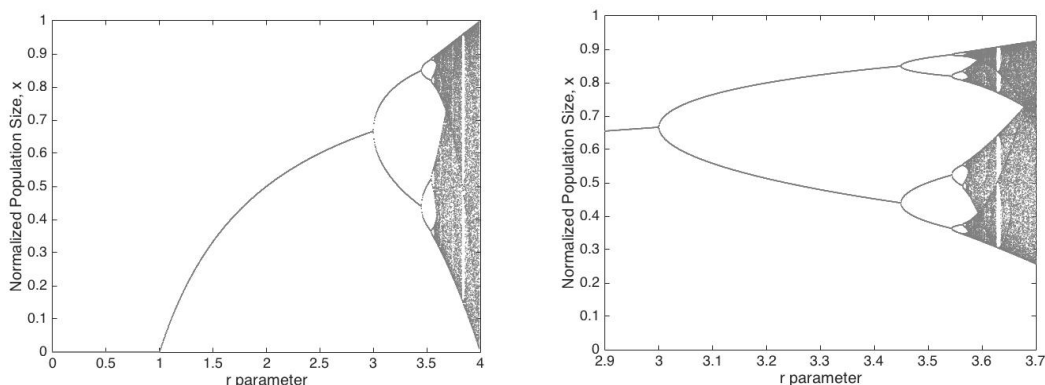


Figure 2.8: Bifurcation diagram of the logistic map.

Summary

- Exponential growth of a population quickly leads to conditions that cause the population growth to slow.
- A simple phenomenological model of population growth is the logistic model, which leads to saturation of the population at a carrying capacity.
- The Monod model of microbial growth does not lead to logistic growth unless the starting resource concentration is small.
- Cooperative growth can lead to bistability, in which there is a minimal population size required for survival, as well as a catastrophic collapse in deteriorating conditions.
- Discrete maps such as the logistic map can have exceedingly complex dynamical behavior, including periodic oscillations and chaos.