

How to build a model, and how to deal with time



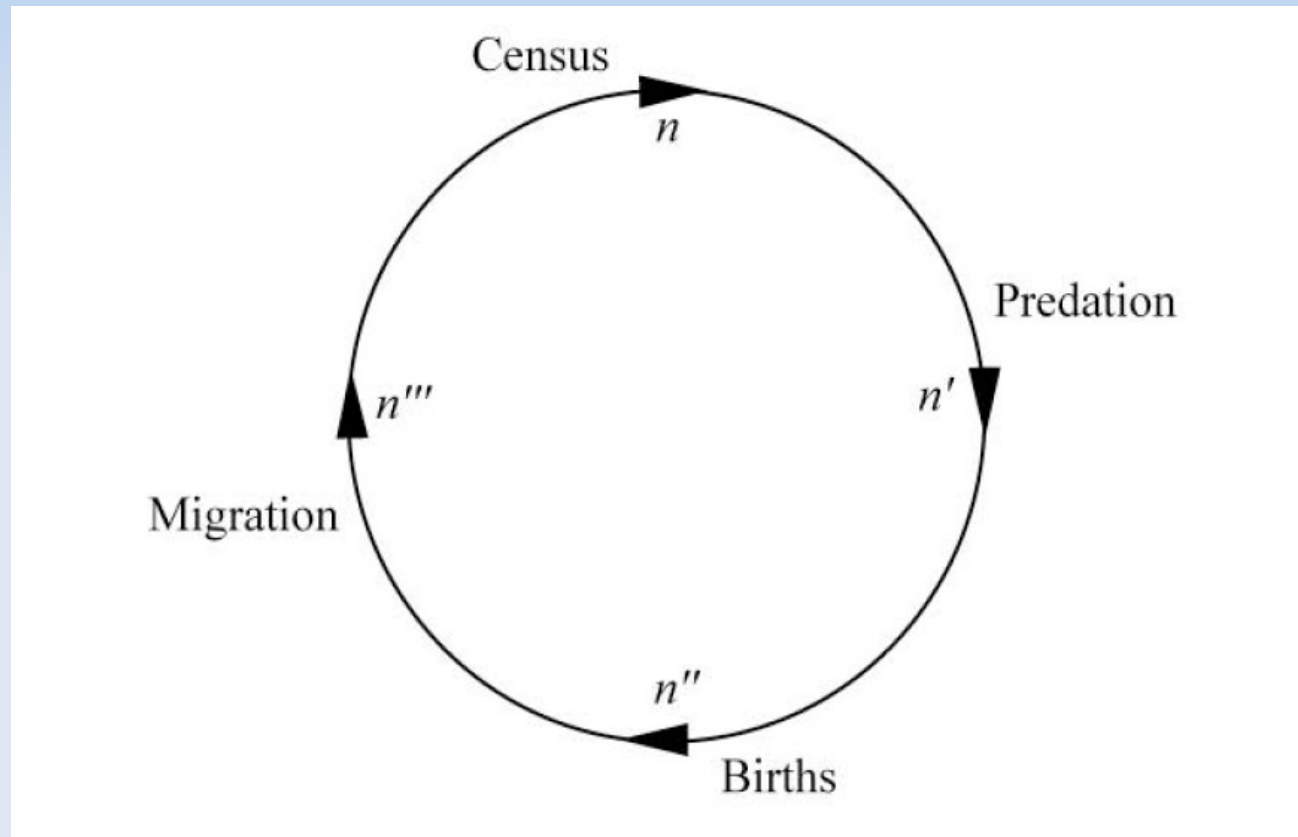
7 steps to build a model

- 1) Formulate the question
- 2) Determine the basic ingredients
(variables and their interactions, parameters, time)
- 3) Qualitatively describe the system
(e.g., life-cycle or flow diagrams)
- 4) Quantitatively describe the system
- 5) Analyze the equations
- 6) Doublecheck the analysis
- 7) Interpret the results

Variables and parameters

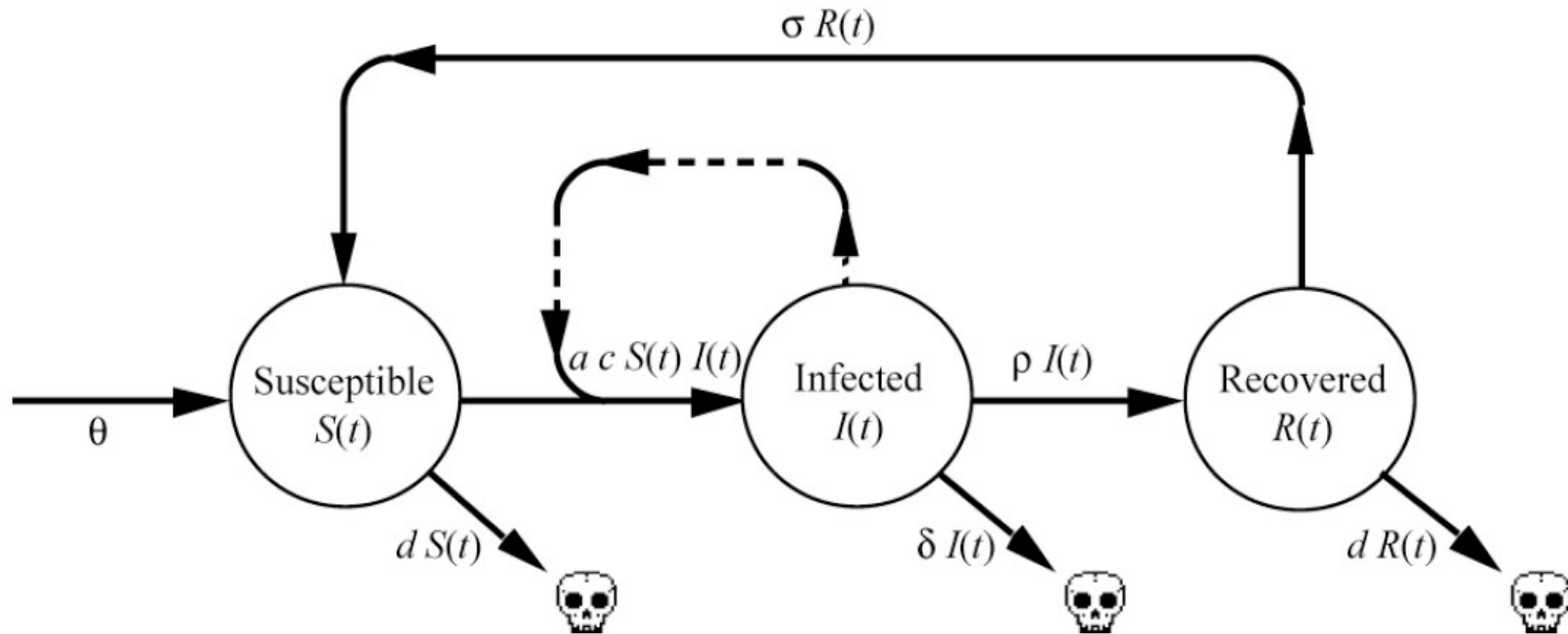
- **Variables** are the entities of interest that change over time, such as population sizes, allele frequencies or mean phenotypes.
- **Parameters** are constants that do not change over time, for example, population growth rate, mutation rate, recombination rate, number of loci, carrying capacity etc.
- For example, in a model of exponential population growth, $N(t + 1) = R N(t)$, N is a variable (population size) and R a parameter (reproductive factor).
- Of course, in evolution, nothing really is constant, so parameters in one model can be variables in another one (e.g., we might be interested in the evolution of the mutation rate).

Life cycle diagrams



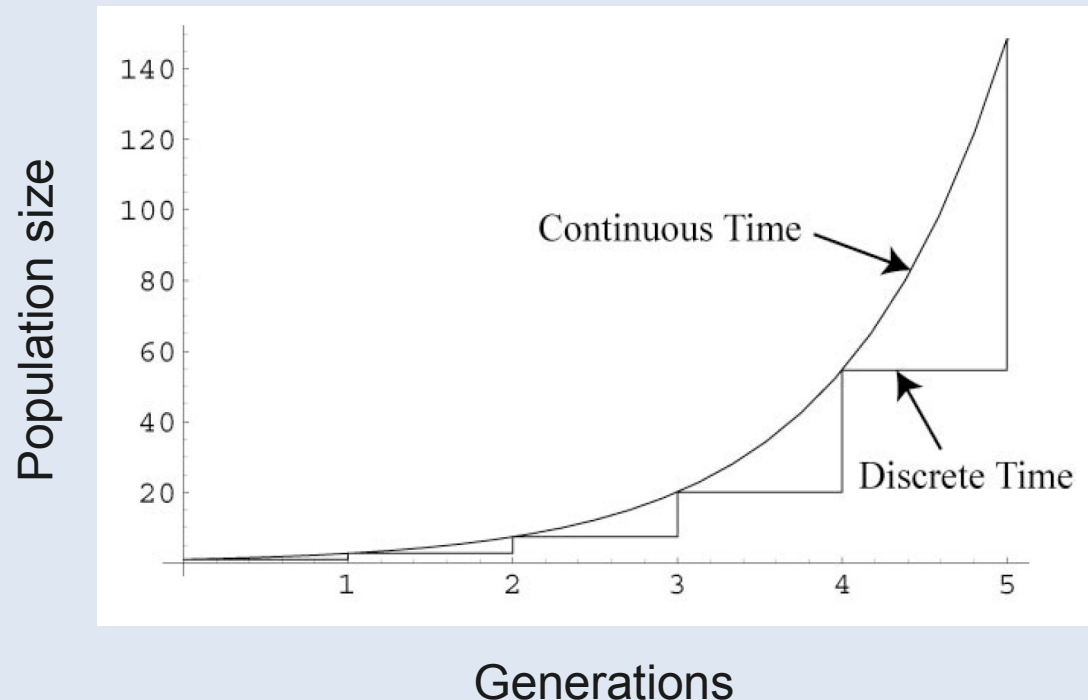
Flow diagrams

Figure 3.9: A flow diagram for the Susceptible-Infected-Recovered (SIR) model.



Discrete versus continuous time

- A **discrete-time model** tracks changes to variables in discrete time steps (years, generations, etc.), leading to sudden jumps.
- A **continuous-time model** allows variables to change at any point in time, in a smooth fashion.



Comparison

- Discrete-time models are often associated with **non-overlapping generations**, and continuous-time models with **overlapping generations**. Note, however, that overlapping generations can also be investigated in a discrete time setting, especially in age-structured models.
- In discrete time, things happen **sequentially**, and the order of events may be important. In continuous time, everything happens quasi **simultaneously**.
- Discrete-time models might appear simpler, but they behave more wildly than continuous-time models (due to **overshooting** effects), and there are fewer methods for analyzing them.

Difference vs. differential equations

Discrete-time models are formulated in terms of **recursion equations**, e.g.

$$N(t+1) = R N(t)$$

or **difference equations**, e.g.

$$\Delta N = (R - 1) N(t) = r_d N(t)$$

Continuous-time models are formulated in terms of **differential equations**, e.g.

$$\frac{dN(t)}{dt} = r_c N(t)$$

Keeping track of the r 's

The various parameters used to describe population growth can be quite confusing. Here, we adopt the following convention:

- $R = N(t+1) / N(t)$ is the **reproductive factor**. The population grows if $R > 1$.
- $r_d = R - 1$ is the **per capita change** in the discrete-time model. The population grows if $r_d > 0$.
- r_c is the per capita change or **growth rate** in the continuous-time model. Again, the population increases in size if $r_c > 0$.
- As we see below, discrete and continuous exponential growth lead to the same results if $1 + r_d = \exp(r_c)$.

From discrete to continuous time: the compound interest effect

In discrete-time models, variables are updated only once per time step. In continuous-time, update is instantaneous, leading to the "compound interest effect":

- Assume you invest an amount X of money, and your bank grants you r percent interests per year. So your account grows by $X(t+1) = (1+r)X(t)$, which leads to $X(t) = (1+r)^t X(0)$.
- You would make even more money if the bank gave you $r/2$ percent interests twice a year: $X(t) = (1+r/2)^{2t} X(0)$
- Or more generally, for k times per year: $X(t) = (1+r/k)^{kt} X(0)$.
- In the limit of instantaneous interests, we get

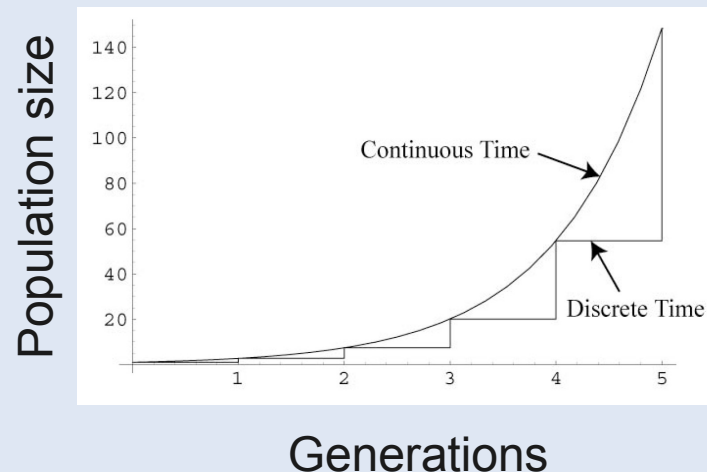
$$X(t) = \lim_{k \rightarrow \infty} (1+r/k)^{kt} X(0) = e^{rt} X(0)$$

Exponential growth

Because of the compound interest effect, population growth is faster in continuous time than in discrete time, if the underlying parameters are the same:

- Discrete: $N(t) = (1 + r_d)^t N(0)$
- Continuous: $N(t) = e^{r_c t} N(0)$

To get the same amount of change, we have to set $1 + r_d = e^{r_c}$



More details

- A similar calculation can be performed to derive a differential equation from a difference equation. To gain some more insight, we now consider birth and death events separately.
- In discrete time, we have $N(t+1) = RN(t) = (1-d)(1+b)N(t)$ where d and b are the fraction of individuals dying and reproducing in one time step.
- In an interval Δt , these fractions are reduced to Δtd and Δtb .
- By letting Δt shrink, we get
$$\begin{aligned} \frac{dN(t)}{dt} &= \lim_{\Delta t \rightarrow 0} \frac{N(t + \Delta t) - N(t)}{\Delta t} \\ &= \lim_{\Delta t \rightarrow 0} \frac{(1 - d\Delta t)(1 + b\Delta t)N(t) - N(t)}{\Delta t} \\ &= \lim_{\Delta t \rightarrow 0} \frac{(b\Delta t - d\Delta t - bd(\Delta t)^2)N(t)}{\Delta t} = (b - d)N(t) \end{aligned}$$
- Thus, the multiplicative interaction of death and birth is transformed into an additive one, because the two events cannot happen together within a very short time frame.

Fractions versus rates

- In discrete-time models, parameters related to change are **fractions** or **probabilities** (e.g. the fraction of individuals that die or reproduce per time step). These parameters are confined to the interval from 0 to 1.
- Continuous-time change is measured in terms of **rates** (amount of change per unit time, "flow"), which can have any value.
- The formal difference is that fractions are dimensionless, whereas rates have unit per time.
- Fractions are often applied **multiplicatively**, whereas rates combine **additively**.

Logistic growth

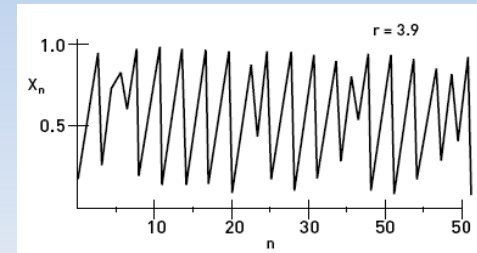
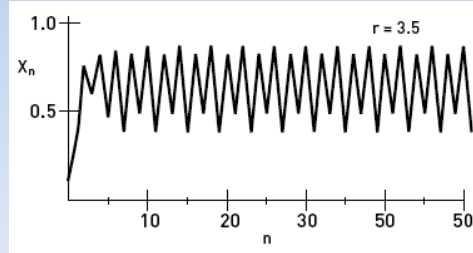
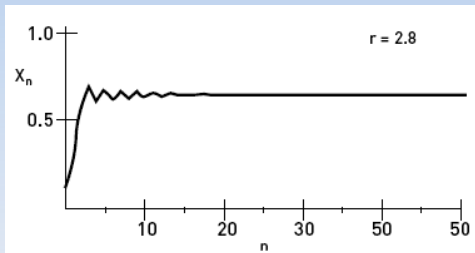
- In the previous models, populations could grow to infinite sizes, which is clearly unrealistic. As the number of individuals increases, competition for resources is expected to become more and more severe, which leads to **density-dependent population regulation**.
- The simplest models of density-dependent population growth assume that the population growth rate r decreases linearly with population size (or density) N .
- This leads to the **logistic equation**, whose discrete and continuous versions look very much alike:

$$\Delta N = r_d N (1 - N/K)$$

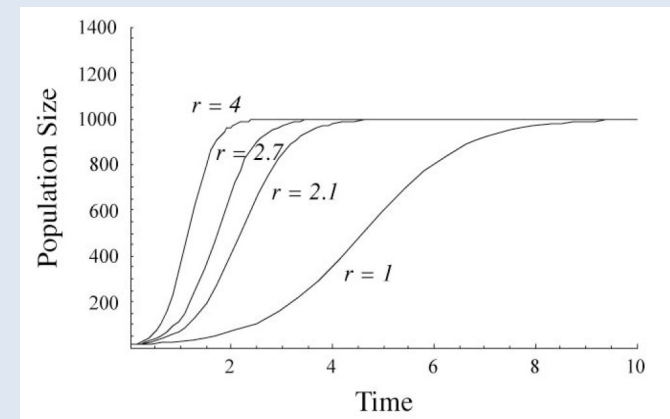
$$\frac{dN}{dt} = r_c N (1 - N/K)$$

Dynamics of the logistic equations

- As we already know, the discrete version of the logistic equation can produce complex dynamics like cycles and chaos.



- In contrast, the continuous version always smoothly approaches the **carrying capacity** K .
- The reason is that the net growth rate is constantly re-adjusted to the present population size.
- Thus, simple difference equations can behave very differently from the corresponding differential equations.



The Beverton-Holt model

- It is generally not possible to find a differential equation that extrapolates a given difference equation. (For example, a single differential equation can never produce chaos.)
- However, the reverse is possible, that is finding a difference equation that behaves like a given differential equation.
- The the continuous logistic equation, this discrete-time counterpart is the Beverton-Holt model:

$$N(t+1) = \frac{(1-r)N(t)}{1 + N(t)r/K}$$

Slow dynamics

- In general, discrete- and continuous-time models can behave very differently.
- However, they are approximately equivalent if all dynamics are slow (low growth rates, weak selection, etc.).
- In this case, one can choose what ever model is more convenient for a specific purpose.
- We don't even need to adjust the parameters. For example, in the exponential growth models, we don't need to bother setting $1 + r_d = \exp(r_c)$, because for small r , $\exp(r) \approx 1 + r$ anyway.