# Constructing models

## Dynamical models

Tools to link scales

* Models are what we use to link:
  + Individual-level to population-level processes
  + Short time scales to long time scales
* In both directions
* Models are always simplifications of reality
  + “The map is not the territory”
  + “All models are wrong, but some are useful”
* Models are useful for:
  + linking assumptions to outcomes
  + identifying where assumptions are broken
* **Dynamical models** describe rules for how a system changes at each point in time
* We will see what these assumptions about how the system *changes* lead to conclusions about what the system *does* over longer time periods
* Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
* These are the things that follow our rules and change
* Examples:
  + Dandelions: state is population size, described by one state variable (the number of individuals)
  + Bacteria: state is population density, described by one state variable (the number of individuals per ml)
  + Pine trees: state is amount of wood, described by one state variable (tons per hectare)
* Limiting the number of state variables is key to simple models
* **Parameters** are the quantities that describe how the rules for our system work
* Examples:
  + Birth rate, death rate, fecundity, survival probability
* Typically *remain constant* while we are simulating a particular scenario
* *Vary* when we compare different scenarios
* I survey a population in 2009, and again in 2013. I get a different answer the second time.
* Poll: What are some reasons why this answer might change?
* Often, our population models will imagine that the population is **censused** (counted) at particular periods of time
* Calculations of what happens between census times may be part of how we make our population model, without showing up in the main model itself
  + For example, our moth and dandelion examples
* We will focus mostly on births and deaths
* Births and deaths are done by individuals
  + We model the rate of each individual (per capita rates)
  + Total rate is the per capita rate multiplied by population size
* If per capita rates are constant, we say that our population *models* are **linear**
  + Linear models do not usually correspond to linear growth!

## Examples

* Poll: State variable
* Parameters
* Census time
* State variables
* Poll: Parameters
* Census time
* State variables
  + Poll: Are there intermediate variables?
* Parameters
* Census time

## A simple discrete-time model

* If we have individuals after time steps, what determines how many individuals we have after time steps?
  + A fixed proportion of the population (on average) survives to be counted at time step
  + Each individual creates (on average) new individuals that will be counted at time step
* How many individuals do we expect in the next time step?
* Diagram
* Individuals are **independent**: what I do does not depend on how many other individuals are around
* The population is censused at regular time intervals
  + Usually = 1
* All individuals are the same at the time of census
* Population changes deterministically
* is the **survival probability**
* is the **fecundity**
* is the **finite rate of increase**
  + ... associated with the time step
  + ( has units of time)
* Dynamics:
* Solution:
* Poll: How does behave in this model?
* Assumptions are simplifications based on reality
* We can understand why populations change exponentially sometimes
* We can look for *reasons* when they don’t
* Moths
  + , so .
    - Moths are **semelparous** (reproduce once); they have an **annual** population
* Dandelions
  + If , then the dandelions are **iteroparous**; they are a **perennial** population

## A simple continuous-time model

* If we have individuals at time , how does the population change?
  + Individuals are giving birth at per-capita rate
  + Individuals are dying at per-capita rate
* How we describe the population dynamics?
* Individuals are **independent**: what I do does not depend on how many other individuals are around
* The population can be censused at any time
* Population size changes continuously
* All individuals are the same all the time
* is the **birth rate**
* is the **death rate**
* is the **instantaneous rate of increase**.
* These quantities are not associated with a time period, but they have units:
* Dynamics:
* Solution:
* Behaviour
* Conceptually, this is just as simple as the dandelions or the moths
  + In fact, simpler
* But we can’t do an infinite number of simulation steps on the computer
  + We need fancier methods

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* We can construct simple, conceptual models and make them into dynamic models
* If we assume that *individuals* behave independently, then
  + we expect *populations* to grow (or decline) exponentially

# Units and scaling

* Keep track of units at all times
* Use units to confirm that your answers make sense
  + Or to find quick ways of getting the answer
* What is $3\dd \cdot 4 \esp/\dd$?
* What is $1\hr \cdot 0.2\cm/\dd$?
* We can multiply quantities with different units by keeping track of the units
* We *cannot* add quantities with different units (unless they can be converted to the same units)
* Poll: How many seconds are there in a day?
* http://www.alysion.org/dimensional/fun.htm
* Quantities with units set scales, which can be changed
  + If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale
  + If a multiply all the quantities with units of dandelions in my model by 10, I should get an answer that looks the same, but with a different number of dandelions

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* Poll: What is ?
* What is $10^{72\hr}$?
* What is ?
* Quantities with units *scale*
  + If you change everything with the same units by the same factor, you should not change the behaviour of your system
* We typically make sense of quantities with units by comparing them to other quantities with the same units, e.g.:
  + birth rate vs. death rate
  + characteristic time of exponential growth vs. observation time
* Quantities in exponents must be unitless
* Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
* Quantities that determine *how* a system behaves must have a unitless form
  + Otherwise, they could be scaled
  + Zero works as a unitless quantity:
    - 0km = 0cm
* What unitless quantities have we already talked about?
* $600 \uname{egg}/\uname{rF}$
* $\cdot 0.1 \uname{larva}/\uname{egg}$
* $\cdot 0.1 \uname{pupa}/\uname{larva}$
* $\cdot 0.5 \uname{A}/\uname{pupa}$
* $\cdot 0.5 \uname{rA}/\uname{A}$
* Poll: What’s the product?
* Once we close the loop, it doesn’t matter where we start:
  + Reproductive adults to reproductive adults
  + Larvae to larvae
  + Pupae to pupae is common in real studies
* If we don’t close the loop, we can’t correctly move from step to step
* is the **finite rate of increase**
* If , what are the units of ?
* Therefore and must be unitless
  + example, rA/rA; seed/seed
  + to do it right, we close the loop

# Key parameters

## Discrete-time model

* Fecundity in our model must be unitless
* Multiply:
  + Probability of surviving from census to reproduction
  + Expected number of offspring when reproducing (maternity)
  + Probability of offspring surviving to census
* Need to end where we started
* Diagram
* Survival must be unitless
* Multiply:
  + Probability of surviving from census to reproduction
  + Probability of surviving the reproduction period
  + Probability of surviving until the next census
* Population increases when
* So must be unitless
* But it is *associated with* the time step
  + This means it is potentially confusing. It is often better to use $\R$ or (see below).
* The reproductive number  measures the average number of offspring produced by a single individual over the course of its lifetime
* Poll: The population will increase when …:
* Poll: What are the units of ?
* In this model world, how long do individuals live, on average in this model?
* If is the proportion of individuals that survive, then the proportion that die is:
* How many time steps do you expect to survive, on average?
* is fecundity multiplied by lifespan
* $\R = f/\mu = f/(1-p)$
* Why do we multiply by time *steps* instead of lifetime?

*Lifetime reproduction*

* $\R = f/\mu = f/(1-p)$
* Unitless
* Population behaviour depends on the **comparison** $\R:1$
  + Equivalent to

*Reproduction over one time step*

* Unitless
* Population behaviour depends on the comparison
  + Equivalent to
* What does tell us about whether the population is increasing?
* What does $\R$ tell us about whether the population is increasing?
* Therefore, these two criteria must be the same!

## Continuous-time model

* The birth rate in the continuous-time model is new individuals per individual per unit time
  + An instaneous rate
  + Units of [1/time] – implies what assumption?
* The death rate in the continuous-time model is deaths per individual per unit time
  + An instaneous rate
  + Units of [1/time]
* Is there a concern with these units?
* Population increases when
* is not unitless, units are:
* So how can be a criterion?
* The mean lifespan is
  + Equivalent to the characteristic time for the death process
* is the average number of births expected over that time frame:
  + $\R = bL = b/d$

*Lifetime reproduction*

* $\R = bL = b/d$
* Unitless
* Population behaviour depends on the comparison $\R:1$
  + Equivalent to

*Instantaneous change*

* Units [1/t] (a rate)
* Population behaviour depends on the comparison
  + Equivalent to
* What does tell us about whether the population is increasing?
* What does $\R$ tell us about whether the population is increasing?
* Therefore, these two criteria must be the same!

## Links

* After one time step in a discrete-time model
* In a continuous model
  + in the same time period
* To link them, we set:
* In the other direction:
* We can now find characteristic times of exponential change:
  + for exponential growth when
  + for exponential decline when
* Rule of thumb: population changes by a factor of 20 after 3 characteristic times

# Growth and regulation

* In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
* What value of does this correspond to? If we use a time step of 20-year generations, what value of does it correspond to?
* What is the long-term average exponential growth rate (using either or ) of:
  + A successful population?
  + An unsuccessful population?
* Estimated characteristic time scales for exponential growth or decay are usually a few (or a few tens) of generations
  + years to a few kiloyears
* Species typically persist for far longer
  + many kiloyears to megayears
* If populations grow and shrink proportionally to their size, why don’t they go exponentially to zero or infinity?
* How is this possible?
* Poll: What sort of factors can make species growth rates change?
* What do we expect to happen if a population’s growth rate is affected only by seasons and climate?
* What sort of mechanism could keep a population in a reasonable range for a long time?
* This is even true for modern humans!

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