UNIT 1: Linear population models

1 Example populations

1.1 Dandelions

- Start with one dandelion; it produces 100 seeds, of which only 4% survive to reproduce the next year.
- How many dandelions after 3 years?
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  - See spreadsheet on resource page
- The spreadsheet is an implementation of a dynamical model!

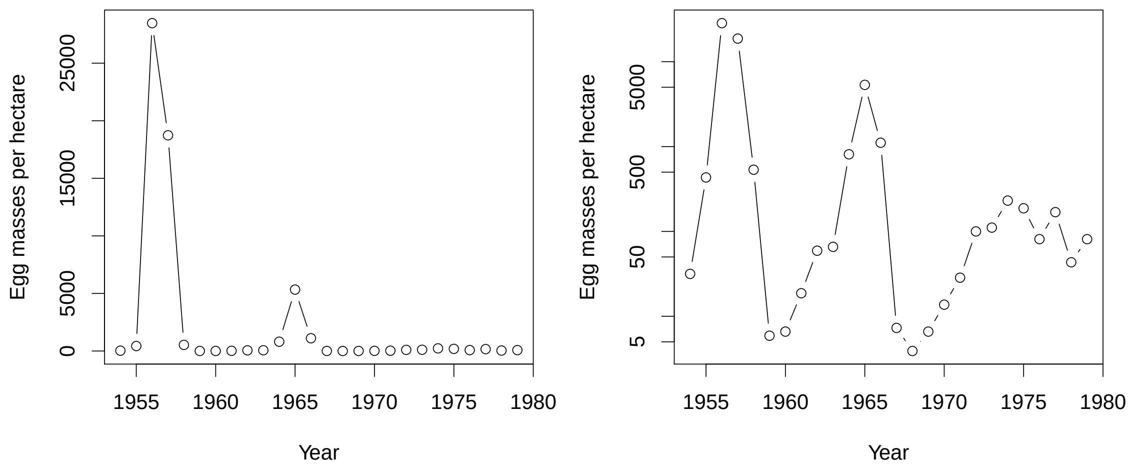
Dynamical models

- Make rules about how things change on a small scale
- Assumptions should be clear enough to allow you to calculate or simulate population-level resuls
- Challenging and clarifying assumptions is a key advantage of models

1.2 Gypsy moths

- A pest species that feeds on deciduous trees
- Introduced to N. America from Europe 150 years ago
- Capable of wide-scale defoliation

Gypsy moth populations



Moth calculation

- Researchers studying a gypsy moth population make the following estimates:
  - The average reproductive female lays 600 eggs
  - 10% of eggs hatch into larvae
  - 10% of larvae mature into pupae
  - 50% of pupae mature into adults
  - 50% of adults survive to reproduce
  - All adults die after reproduction
- What happens if we start with 10 moths?
  -

Stochastic version

- Obviously, we will not get *exactly* 7.5 moths.
- If we consider moths as individuals, we need a **stochastic** model
- What do we mean by stochastic?

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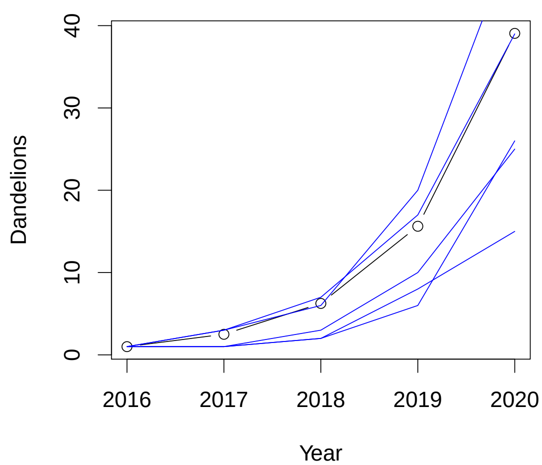
Stochastic model

- A stochastic model has randomness in the model.
- If we run it again with the same parameters and starting conditions, we get a different answer



1.3 Bacteria

- Imagine we have some bacteria growing in a big tank, constantly dividing and dying:
  - They divide (forming two bacteria from one) at a rate of 0.04/ hr
  - They wash out of the tank at a rate of 0.02/ hr
  - They die at a rate of 0.01/ hr
- Rates are **per capita** (i.e., per individual) and **instaneous** (they describe what is happening at each moment of time)
- We start with 10 bacteria/ml
  - How many do we have after 1 hr?

– What about after 1 day?

Bacteria, rescaled

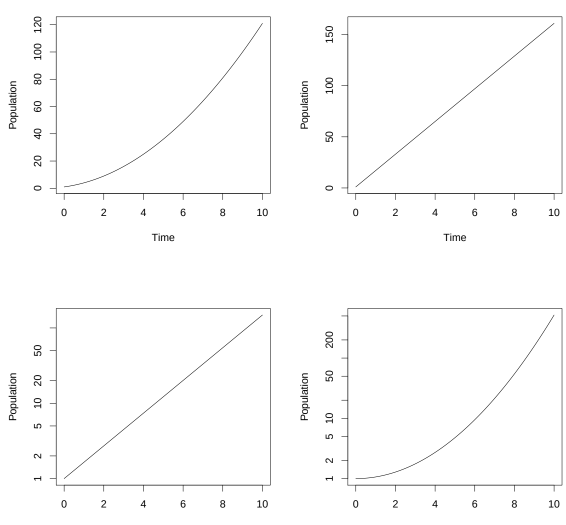
- Imagine we have some bacteria growing in a big tank:
  - They divide (forming two bacteria from one) at a rate of 0.96/day
  - They wash out of the tank at a rate of 0.48/day
  - They die at a rate of 0.24/day
- If we start with 10 bacteria/ml, how many do we have after 1 day?

Units

- When we attach units to a quantity, the meaning is concrete
  - 0.24/day *must* mean exactly the same thing as 0.01/hr
  - The two questions above *must* have the same answer

2 Exponential growth

- What is exponential growth?
- Which of these is an example?



Types of growth

- arithmetic/linear:
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- geometric/exponential:
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- other:
  - Many possibilities, we may discuss some later

Exponential decline?

- What does exponential decline look like?
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Terminology

- Sometimes people distinguish
  - **arithmetic** from **linear** growth, or
  - **geometric** from **exponential** growth
- Based on:
  -
- We won't worry much about this.

2.1 Log and linear scales

Scales of comparison

- 1 is to 10 as 10 is to what?
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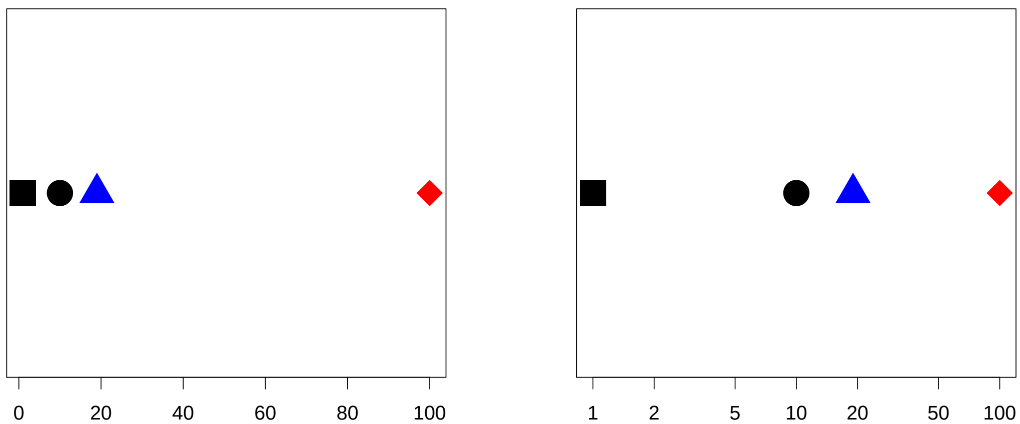
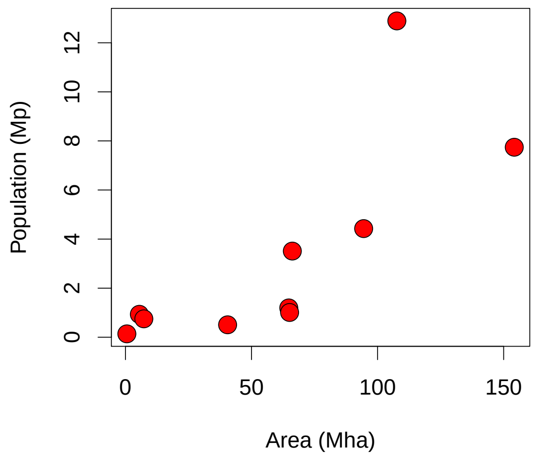
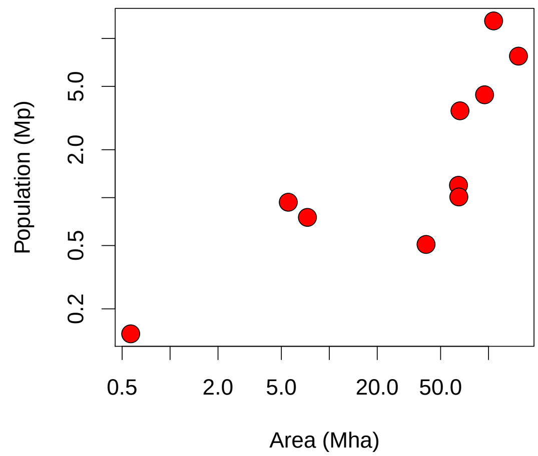
Scales of display



There is only one log scale; it doesn't matter which base you use!

Canadian provinces





Predation comparison

- A 500 lb lion is attacking a 1000 lb buffalo!
- This is analogous to a 15 lb red fox attacking:
  - A 30 lb beaver (twice as heavy)?
  - A 515 lb elk (500 lbs heavier)?

Different scales

- The log scale and linear scale provide different ways of looking at the same data
- Equally valid
- What are some advantages of each?

Advantages of arithmetic view

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Advantages of geometric view

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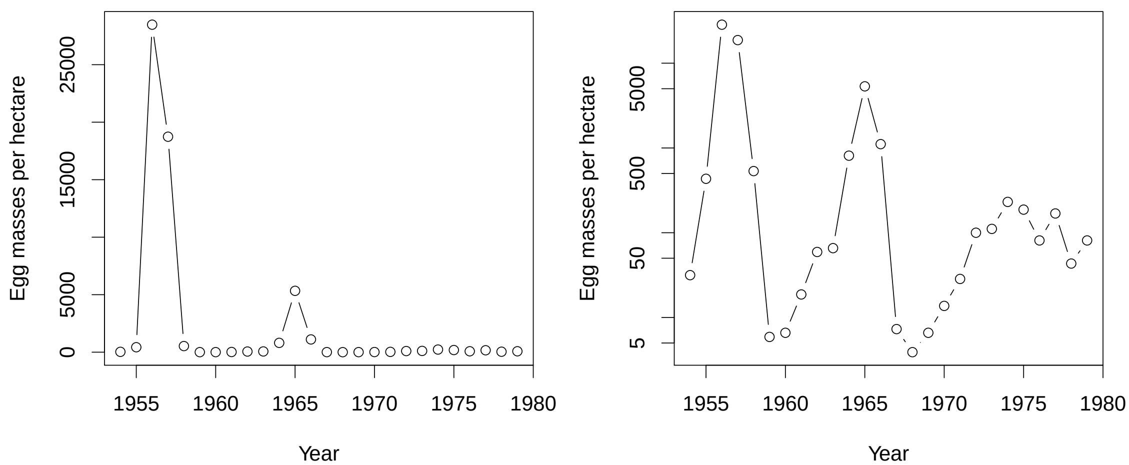
Gypsy-moth example



Scales in population biology

- The linear scale looks at differences at the population scale
- The log scale looks at differences at the individual scale (per capita)

2.2 Time scales

Characteristic times

- If something is declining exponentially, the rate of change (units [widgets/time]) is always proportional to the size of the thing ([widgets]).
- The constant ratio between the rate of change and the thing that is changing is:
  - the **characteristic time** (something/change), or
  - the **rate of exponential decline** (change/something)

Bacteriostasis

- What if we add an agent to the tank that makes the birth and death rates nearly zero?
- Now the bacteria are merely washing out at the rate of 0.02/hr
- If we start with 10 bacteria/ml, how many do we have after:
  - 1 hr?
  - 1 wk?

Bacteriostasis answers

- Bacteria wash out at the rate of 0.02/hr
  -
  -
- Start with 10 bacteria/ml:
  -
  -

Bacteriostasis analysis

- Rate of exponential decline is $r = 0.02/\,\mathrm{hr}$
- Characteristic time is $T_c = 1/r = 50\,\mathrm{hr}$
- If experiment time $t \ll T_c$, then proportional decline $\approx t/T_c$
- The answer makes sense for short times and for long times

Euler's e

- The reason mathematicians like e is that it makes this link between instantaneous change and long-term behaviour
- If I drive for an hour, how much closer do I get to the ideal town of Speed?
  -

- e or $1/e$ is the approximate answer to a lot of questions like this one
  - If I compound 1%/year interest for 100 years, how much does my money grow?
  - If two people go deal out two decks of cards simultaneously, what is the probability they will never match cards?
  - If everyone picks up a backpack at random after a test, what's the probability nobody gets the right backpack?

Exponential growth

- We can think about exponential growth the same way as exponential decline:
  - Things are always changing at a rate that would take a fixed amount of time to get (back) to zero
  - This is the characteristic time
  - Exponential growth follows $N = N_0 \exp(rt) = N_0 \exp(t/T_c)$

Doubling time

- Some people prefer to think about doubling times.
- These make just as much sense as characteristic times, but don't have the direct link to the instantaneous change.
  - It takes T_c time to increase by a factor of e
  - It takes $\log_e(2)T_c \approx 0.69T_c$ to increase by a factor of 2
  - We can write $T_d = \log_e(2)T_c$
- You should be able to do this calculation
  - $\exp(rT_d) = 2$
  - $T_d = \log_e(2)/r$
  - $T_d = \log_e(2)T_c$

Half life

- The half life plays the same role for exponential decline as the doubling time does for exponential growth:
  - $T_h = \log_e(2)T_c$
  - It takes T_c time for a declining population to decrease by a factor of e
  - It takes $\log_e(2)T_c \approx 0.69T_c$ to decrease by a factor of 2
  - We can write $T_h = \log_e(2)T_c$

3 Constructing models

3.1 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

Assumptions

- 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

- **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

States and state variables

- Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- 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

- **Parameters** are the quantities that describe the rules for our system
- Examples:
  - Birth rate, death rate, fecundity, survival probability

How do populations change?

- I survey a population in 2005, and again in 2009. I get a different answer the second time.
- What are some reasons why this answer might change?
  -
  -
  -
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Censusing and intermediate variables

- 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

Linear population models

- 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!
  -

3.2 Examples

Moth example

- State variables
  -
- Parameters
  -
  -
- Census time
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Bacteria

- State variables
  -
- Parameters
  -
- Census time
  -

Dandelions

- State variables
  -
- Parameters
  -
- Census time
  -
  -

3.3 A simple discrete-time model

Assumptions

- If we have N individuals after T time steps, what determines how many individuals we have after $T+1$ time steps?
  - A fixed proportion p of the population (on average) survives to be counted at time step $T+1$
  - Each individual creates (on average) f new individuals that will be counted at time step $T+1$
- How many individuals do we expect in the next time step?
  -

- Individuals are **independent**: what I do does not depend on how many other individuals are around
- The population is censused at regular time intervals Δt
  - Usually $\Delta t = 1\,\mathrm{yr}$
- All individuals are the same at the time of census
- Population changes deterministically

Definitions

- p is the **survival probability**
- f is the **fecundity**
- $\lambda \equiv p + f$ is the **finite rate of increase**
  - ... associated with the time step Δt

Model

- Dynamics:
  - $N_{T+1} = \lambda N_T$
  - $t_{T+1} = t_T + \Delta t$
- Solution:
  - $N_T = N_0 \lambda^T$
  - $t_T = T\Delta t$
- How does N behave in this model?
  -
  -

Interpretation

- Assumptions are simplifications based on reality
- We can understand why populations change exponentially sometimes
- We can look for *reasons* when they don't

Examples

- Moths
  - $p = 0$, so $\lambda = f$.
    - Moths are **semelparous** (reproduce once); they have an **annual** population
- Dandelions
  - If $p > 0$, then the dandelions are **iteroparous**; they are a **perennial** population

3.4 A simple continuous-time model

Assumptions

- If we have N individuals at time t, how does the population change?
  - Individuals are giving birth at per-capita rate b
  - Individuals are dying at per-capita rate d
- 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
  -

Definitions

- b is the **birth rate**
- d is the **death rate**
- $r \equiv b - d$ is the **instantaneous rate of increase**.
- These quantities are not associated with a time period, but they have units:
  -

Model

- Dynamics:
  - $\frac{dN}{dt} = rN$
- Solution:
  - $N(t) = N_0 \exp(rt)$
- Behaviour
  -
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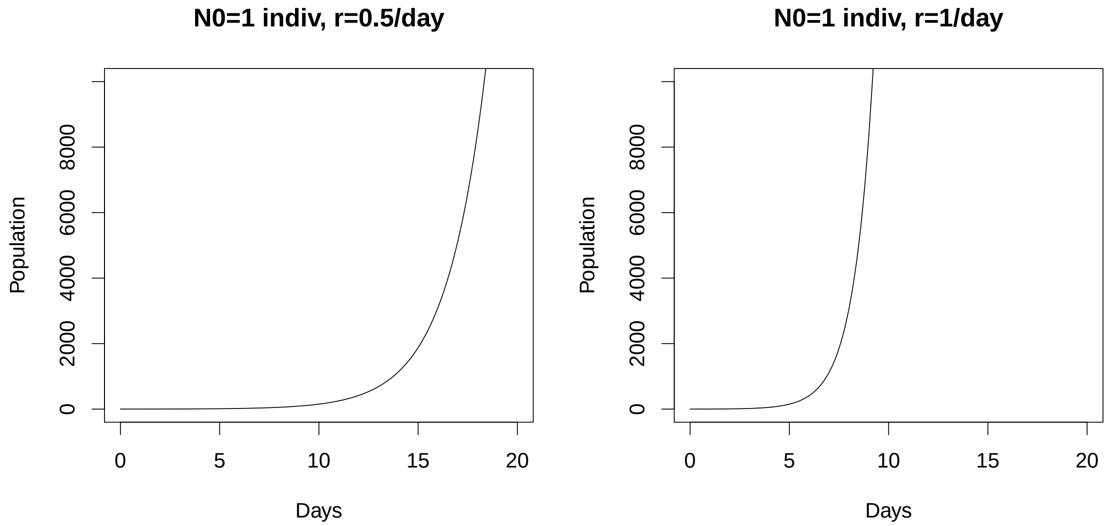
Bacteria

- 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



Summary

- 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

4 Units and scaling

Units are our friends

- 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 $3\,\mathrm{day} \cdot 4\,\mathrm{espressoes}/\,\mathrm{day}$?
  -
- What is $1\,\mathrm{wk} \cdot 0.02/\,\mathrm{day}$?

-
-

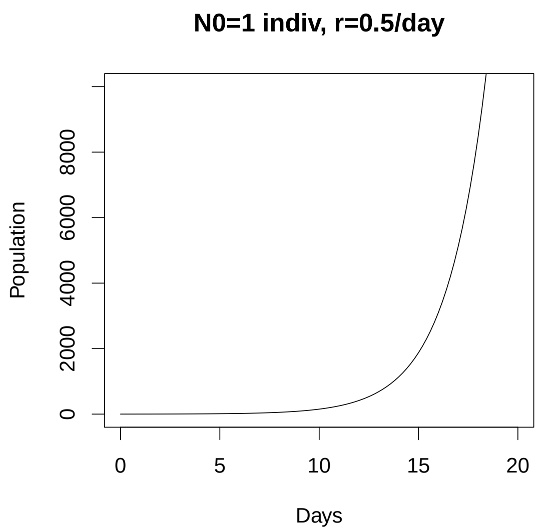
Manipulating units

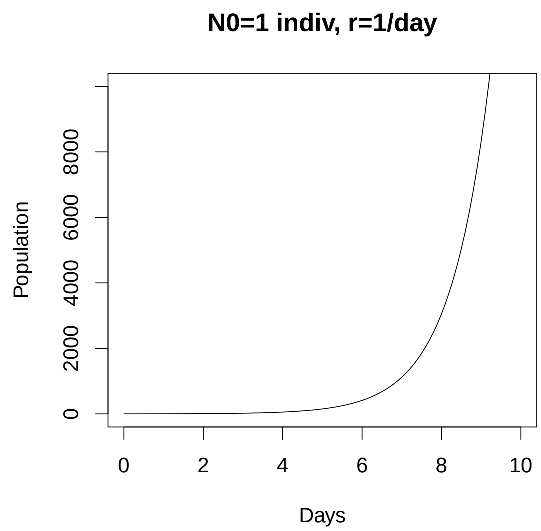
- We can multiply quantities with different units by keeping track of the units
- We *cannot* add quantities with different units (unless they can be converted to the same units)
- How many seconds are there in a day?
  -
  -
- http://www.alysion.org/dimensional/fun.htm

Scaling

- 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

Scaling time in bacteria





Thinking about units

- What is $10^{3\,\text{day}}$?
  -
- What is $10^{72\,\text{hr}}$?
  -
- What is $3\,\text{day} \cdot 3\,\text{day}$?
  -

Unit-ed quantities

- 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

Unitless quantities

- 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
- Examples include λ and $\mathcal{R}$.

Moths

- 600 egg/ rF
- ·0.1 larva/ egg
- ·0.1 pupa/ larva
- ·0.5 A/ pupa
- ·0.5 rA/ A
- What's the product?
  -
  -

Moth spreadsheet

- 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
    -

Calculating λ

- $\lambda \equiv p + f$ is the **finite rate of increase**
- If $N_{T+1} = \lambda N_T$, what are the units of λ?
  -
- Therefore p and f must be unitless
  - example, rA/rA; seed/seed
  - to do it right, we close the loop

5 Key parameters

5.1 Discrete-time model

- $N_{T+1} = \lambda N_T$
- $\lambda \equiv p + f$

Calculating fecundity

- Fecundity f in our model must be unitless
- Multiply:
  - Probability of surviving from census to reproduction
  - Expected number of offspring when reproducing
  - Probability of offspring surviving to census
- Need to end where we started

Calculating survival

- Survival p must be unitless
- Multiply:
  - Probability of surviving from census to reproduction
  - Probability of surviving the reproduction period
  - Probability of surviving until the next census

Finite rate of increase

- Population increases when $\lambda > 1$
- So λ must be unitless
- But it is *associated with* the time step Δt
  - This means it is potentially confusing. It is often better to use $\mathcal{R}$ or r (see below).

Reproductive number

- The reproductive number $\mathcal{R}$ measures the average number of offspring produced by a single individual over the course of its lifetime
- The population will increase when $\mathcal{R}$ ...:
  -
- What are the units of $\mathcal{R}$?
  -

Lifespan

- What is the lifespan of an individual in this model?
- If p is the proportion of individuals that survive, then the proportion that die is:
  -
- How many time steps do you expect to survive, on average?
  -
    *
  -

Calculating $\mathcal{R}$

- $\mathcal{R}$ is fecundity multiplied by lifespan
- $\mathcal{R} = f/\mu = f/(1-p)$
- Why do we multiply by time *steps* instead of lifetime?
  -

Comparison

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

Is the population increasing?

- What does λ tell us about whether the population is increasing?
  -
- What does $\mathcal{R}$ tell us about whether the population is increasing?
  -
- Therefore, these two criteria must be the same!
  -

5.2 Continuous-time model

Calculating birth rate

- The birth rate b in the continuous-time model is new individuals per individual per unit time
    - An instaneous rate
    - Units of [1/time] – implies what assumption?
        -
        -

Calculating death rate

- The death rate d in the continuous-time model is deaths per individual per unit time
    - An instaneous rate
    - Units of [1/time]

Instaneous rate of increase

- Population increases when $r = b - d > 0$
- r is not unitless
    -
- But we still have a unitless criterion: $r = 0$
    -
    -

Calculating $\mathcal{R}$

- The mean lifespan is $L = 1/d$
    - Equivalent to the characteristic time for the death process
- $\mathcal{R}$ is the average number of births expected over that time frame:
    - $\mathcal{R} = bL = b/d$

Comparison

- $\mathcal{R} = bL = b/d$
- Unitless
- Population behaviour depends on the comparison $\mathcal{R} : 1$
  - Equivalent to $b : d$
- $r = b - d = f + (1 - \mu)$
- Units [1/t] (a rate)
- Population behaviour depends on the comparison $r : 0$
  - Equivalent to $b : d$

Is the population increasing?

- What does r tell us about whether the population is increasing?
  -
- What does $\mathcal{R}$ tell us about whether the population is increasing?
  -
- Therefore, these two criteria must be the same!
  -

5.3 Links

- If a population grows at rate r for time period Δt, how much does it change?
  - $N_0 \exp(r\Delta t)$ must correspond to $N_0\lambda$, where 1 is:
- To link a continuous-time model to a discrete-time model, we set:
  - $\lambda = \exp(r\Delta t)$
  -

Characteristic time

- We can now find characteristic times of exponential change:
  - $T_c = 1/r$ for exponential growth when $r > 0$
  - $T_c = -1/r$ for exponential decline when $r < 0$
- Rule of thumb: population changes by a factor of 20 after 3 characteristic times

6 Growth and regulation

Example: Human population growth

- In the last 50,000 years, the population of modern humans has increased from about 1000 to about 7 billion
- What value of r does this correspond to? If we use a time step of 20-year generations, what value of λ does it correspond to?
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    *
    *
  -
    *
    *
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Long-term growth rate

- What is the long-term average exponential growth rate (using either r or λ) of:
  - A successful population?
    *
    *
  - An unsuccessful population?

*
*
*

Time scales

- 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

Balance

- If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
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- How is this possible
  -

Changing growth rates

- What sort of factors can make species growth rates change?
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  -
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  -
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Regulation

- 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!