UNIT 2: Linear population models

Outline

Constructing models
- Dynamical models
- Examples
- A simple discrete-time model
- A simple continuous-time model

Units and scaling

Key parameters
- Discrete-time model
- Continuous-time model
- Links

Growth and regulation

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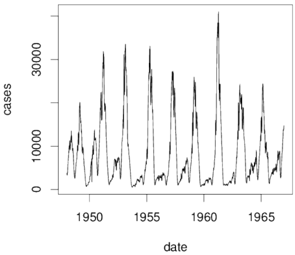
Dynamical models

Tools to link scales

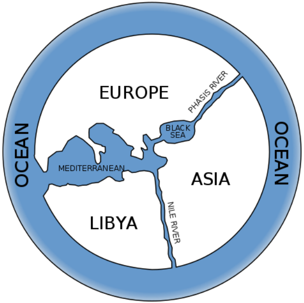
- Models are what we use to link:
  - Individual-level to population-level processes
  - Short time scales to long time scales
- In both directions

Measles reports from England and Wales



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**
- 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

- **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

How do populations change?

- I survey a population in 2009, and again in 2013. I get a different answer the second time.
- What are some reasons why this answer might change?
  - * Birth
  - * Death
  - * Immigration and emigration
  - * Sampling (ie., my counts are not perfectly correct)

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!
  - What behaviour do we expect from a linear model?
    - * They usually correspond to exponential growth
    - * ...or exponential decline

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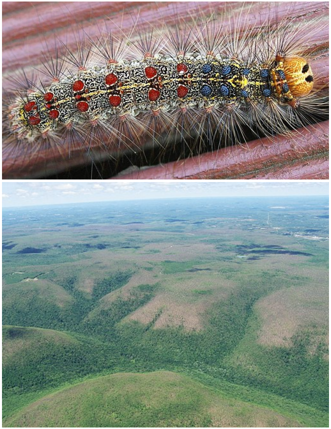
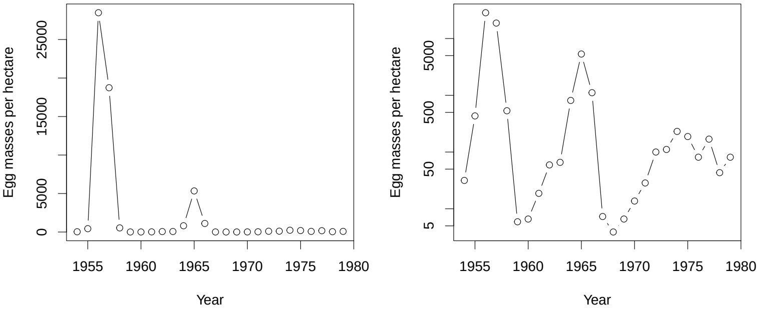
Growth and regulation

Gypsy moths (repeat)

- 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 (repeat)

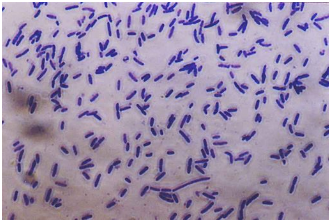


Moth example

- State variable
  - * Number of moths/ha
- Parameters
  - * Number of eggs
  - * sex ratio
  - * larval survival, pupal survival, adult survival
  - * Time step
- Census time
  - * Annually; use the same time (and stage) each year

Bacteria

- State variables
  - * Number of bacteria/ml
- Parameters
  - * Division rate, death rate, washout rate
- Census time
  - * Always!



Dandelions

- State variables
  - * Number of dandelions in a field
  - Are there intermediate variables?
    - * Number of seeds
- Parameters
  - * Seed production, survival to adulthood, adult survival
- Census time
  - * Annually, before reproduction
  - * When new and returning individuals are most similar

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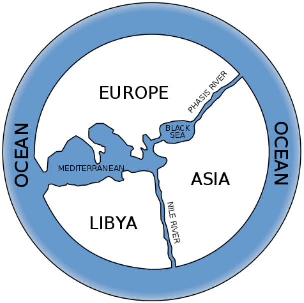
Assumptions

- 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?
  - * $N_{T+1} = (pN_T + fN_T) = (p+f)N_T$
- Diagram

Assumptions

- 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 $\Delta t = 1\,\text{yr}$
- 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
  - (Δt has units of time)

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?
  - * Increases exponentially (geometrically) when $\lambda > 1$
  - * Decreases exponentially when $\lambda < 1$

Example (present)

	A	B	C	D
1	**Date**	**Income**	**Expenses**	**Profit**
2	2005-12-17	235 €	128 €	107 €
3	2005-12-18	311 €	124 €	187 €
4	2005-12-19	457 €	466 €	-9 €
5	2005-12-20	232 €	132 €	100 €
6	2005-12-21	122 €	134 €	-12 €
7	2005-12-22	128 €	223 €	-95 €
8	2005-12-23	432 €	218 €	214 €
9	2005-12-24	256 €	121 €	135 €
10		**2.173 €**	**1.546 €**	**627 €**
11				
12	**Avg. Profit**	=AVERAGE(D2:D9)		

- Spreadsheet (see resource page)

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

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Growth and regulation

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?
  - * $\frac{dN}{dt} = (b - d)N$
  - * That's what calculus is *for* – describing instantaneous rates of change

Assumptions

- 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 have true units:
  - * 1/[time]
    - * $\equiv$ (indiv/[time])/indiv
- *With units, we don't need to mess with "associated with a time period"*

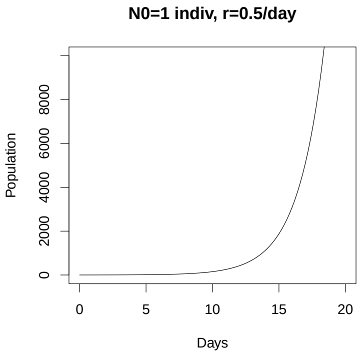
Model

- Dynamics:
  - $\frac{dN}{dt} = rN$
- Solution:
  - $N(t) = N_0 \exp(rt)$
- Behaviour
  - * Increases exponentially when $r > 0$
  - * Decreases exponentially when $r < 0$

Bacteria

- Conceptually, this is just as simple as the dandelions or the moths
  - In fact, simpler
- On the computer, it's a little more complicated to simulate

Bacteria


N0=1 indiv, r=0.5/day
Population
0
2000
4000
6000
8000
0
5
10
15
20
Days
N0=1 indiv, r=1/day
Population
0
2000
4000
6000
8000
0
5
10
15
20
Days

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

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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 $3\,\text{day} \cdot 4\,\text{espressoes/ day}$?
  - * $12\,\text{espressoes}$
- What is $1\,\text{hr} \cdot 0.2\,\text{cm/ day}$?
  - * $1\,\text{hr} \cdot 0.2\,\text{cm/ day}$
  - * $1\,\text{hr} \cdot 0.2\,\text{cm/ day} \cdot \frac{1\,\text{day}}{24\,\text{hr}}$
  - * $0.0083\,\text{cm}$

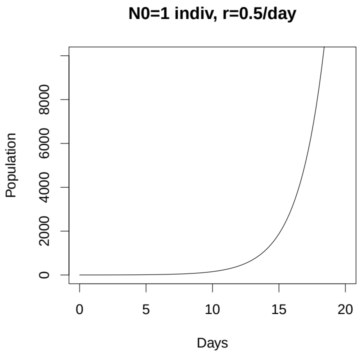
Manipulating units

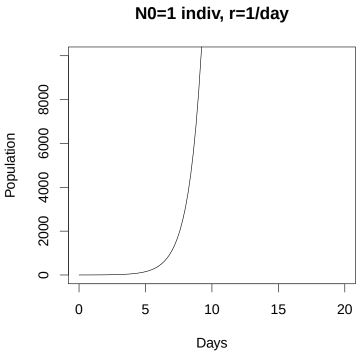
- We can multiply quantities with different units by keeping track of the units
- We *cannot* add quantities with different units (unless they can be converted to the same units)
- How many seconds are there in a day?
  - * $\frac{60\,\text{sec}}{\text{min}} \cdot \frac{60\,\text{min}}{\text{hr}} \cdot \frac{24\,\text{hr}}{\text{day}}$
  - * $86400\ \text{sec}/\text{day}$

Scaling

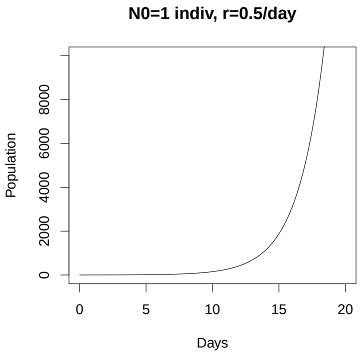
- Quantities with units set scales, which can be changed
  - If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale
  - If a multiply all the quantities with units of dandelions in my model by 10, I should get an answer that looks the same, but with a different number of dandelions

Scaling time in bacteria (present)

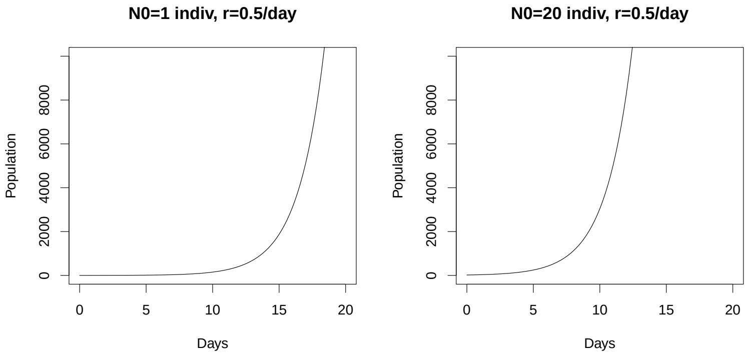




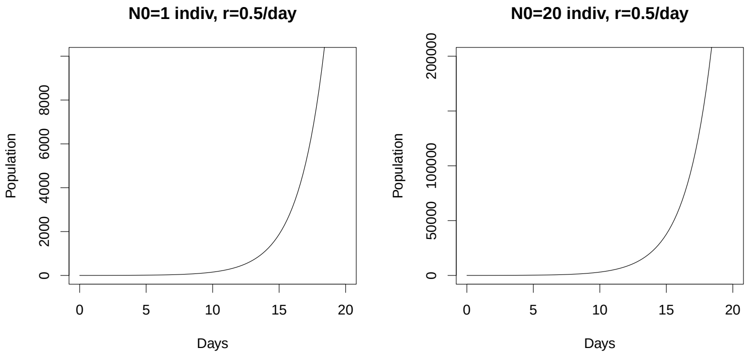
Scaling time in bacteria



Scaling population



Scaling population



Thinking about units

- What is $10^{3\,\mathrm{day}}$?
  - * NOANS
- What is $10^{72\,\mathrm{hr}}$?
  - * Nonsense! $72\,\mathrm{hr}$ means *exactly* the same thing as $3\,\mathrm{day}$ – there is no way to resolve this to make sense.
- What is $3\,\mathrm{day} \cdot 3\,\mathrm{day}$?
  - * $9\,\mathrm{day}^2$ – this *could* make sense, but it's probably wrong
  - * …very different from $9\,\mathrm{day}$.

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:
    - $0\text{km} = 0\text{cm}$
- What unitless quantities have we already talked about?
  - * λ, f and p.
  - * These all depend on a time period

Moth calculation (repeat)

- 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

Moths

- 600 egg/ rF
- ·0.1 larva/ egg
- ·0.1 pupa/ larva
- ·0.5 A/ pupa
- ·0.5 rA/ A
- What's the product?
  - * 1.5 rA/ rF
  - * Not enough information to make a prediction!
  - * Need to multiply by something with units rF/rA to close the loop

Closing the loop

- 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
    - * Pupae are easy to count
    - * Egg masses, too (depending on species)
- If we don't close the loop, we can't correctly move from step to step

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?
    - * We multiply by λ over and over
    - * Therefore λ must be unitless
- Therefore p and f must be unitless
    - example, rA/rA; seed/seed
    - to do it right, we close the loop

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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 (maternity)
  - Probability of offspring surviving to census
- Need to end where we started
- Diagram

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
  - 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 $\mathcal{R}\ldots$:
  - * $\mathcal{R} > 1$
- What are the units of $\mathcal{R}$?
  - * $\mathcal{R}$ must be unitless

Lifespan

- In this model world, how long do individuals live, on average?
- If p is the proportion of individuals that survive, then the proportion that die is:
  - * $\mu = 1 - p$
- How many time steps do you expect to survive, on average?
  - * $1/\mu$
    - * Roughly makes sense, and is also right (but I'm not proving it)
  - * Average lifetime is $1/\mu * \Delta t$

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?
  - * Because f is also measured per time step
  - * $\mathcal{R}$ must be unitless

Comparison

Lifetime reproduction

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

Reproduction over one time step

- $\lambda = f + p = f + (1-\mu)$
- 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?
  - * Population is increasing each time step when $\lambda > 1$
- What does $\mathcal{R}$ tell us about whether the population is increasing?
  - * Population is increasing when $\mathcal{R} > 1$. Each individual is (on average) more than replacing itself over its lifetime
- Therefore, these two criteria must be the same!
  - * Both come down to $f > \mu$.

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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?
    - * New individuals are cancelling with old individuals in the equation
    - * New individuals are being treated the same as old individuals
    - * Not very realistic – a potential problem with our model world

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]
- Is there a concern with these units?
  - * Not really. The individuals dying are exactly the same ones we're counting.

Instaneous rate of increase

- Population increases when $r = b - d > 0$
- r is not unitless, units are:
  - * [1/time]
- So how can $r = 0$ be a criterion?
  - * Because $0\times$anything is unitless!
  - * Does 0km $=$ 0cm?

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

Lifetime reproduction

- $\mathcal{R} = bL = b/d$
- Unitless
- Population behaviour depends on the comparison $\mathcal{R} : 1$
  - Equivalent to $b : d$

Instantaneous change

- $r = b - d$
- 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?
  - * Population is increasing at any particular time step when $r > 0$
- What does $\mathcal{R}$ tell us about whether the population is increasing?
  - * Population is increasing when $\mathcal{R} > 1$. Each individual is (on average) more than replacing itself over its lifetime
- Therefore, these two criteria must be the same!
  - * Both come down to $b > d$.

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Links

- After one time step in a discrete-time model
  - $N_0 \to N_0\lambda$
  - $t \to t + \Delta t$
- In a continuous model
  - $N_0 \to N_0 \exp(r\Delta t)$ in the same time period
- To link them, we set:
  - $\lambda = \exp(r\Delta t)$
- In the other direction:
  - * $r = \log_e(\lambda)/\Delta t$

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
  - $\exp(3) = 20.1$

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Long-term growth rate (preview)

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

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?
  - * $N(t) = N(0)\exp(rt)$
    - * $r = \log_e(N/N(0))/t$
    - * $r = \log_e(7000000000/1000)/50000\,\mathrm{yr} = 0.0003/\,\mathrm{yr}$
  - * $N_T = N_0 \lambda^T$
    - * $T = t/\Delta t = 50000\,\mathrm{yr}/20\,\mathrm{yr} = 2500$
    - * $\lambda = (N_T/N_0)^{1/T}$
    - * $\lambda = (7000000000/1000)^{1/2500} = 1.006$

Long-term growth rate

- What is the long-term average exponential growth rate (using either r or λ) of:
  - A successful population?
    - * Very close to $r = 0$ or $\lambda = 1$
    - * But a little larger
  - An unsuccessful population?
    - * *Probably* very close to $r = 0$ or $\lambda = 1$
    - * But a little smaller
    - * If more than a little, it would probably be gone by now!

Summary

- We can make simple model worlds where populations are composed of individuals that reproduce and die independently
  - Discrete or continuous time
- We can do structured closed-loop calculations and predict how these populations will change
- If individuals are independent, we expect populations to change exponentially through time
  - * The rate at which the population changes is proportional to the size of the population