

## UNIT 2: Linear population models

# 1 Constructing models

## 1.1 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**
- 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

## How do populations change?

- 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?
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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!
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## 1.2 Examples

## Moth example

- Poll: State variable

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- Parameters

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- Census time

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## Bacteria

- State variables

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- Poll: Parameters

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- Census time

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## Dandelions

- State variables

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- Poll: Are there intermediate variables?

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- Parameters

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- Census time

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## 1.3 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?
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- 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  $\Delta t$ 
  - Usually  $\Delta t = 1$  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  $\Delta t$
  - ( $\Delta t$  has units of time)

## Model

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

## 1.4 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?
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- 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:

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## Model

- Dynamics:

$$- \frac{dN}{dt} = rN$$

- Solution:

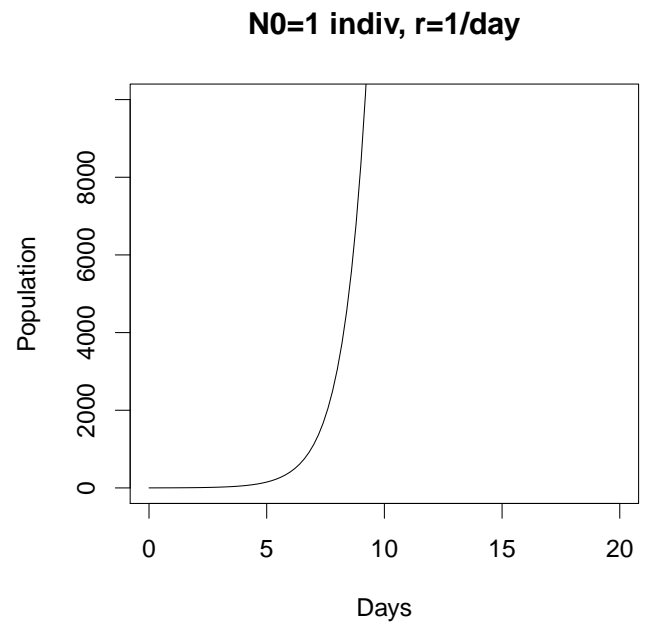
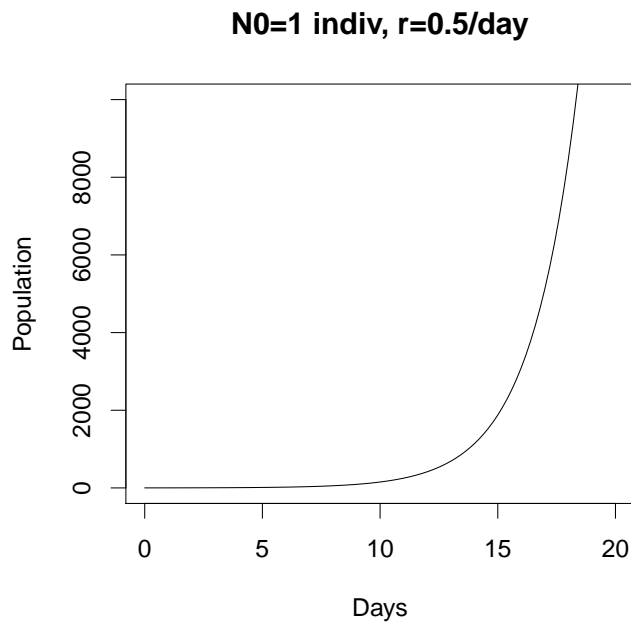
$$- N(t) = N_0 \exp(rt)$$

- 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
  - We need fancier methods



## 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

## 2 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  $3 \text{ day} \cdot 4 \text{ espressoes/day}$ ?
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- What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
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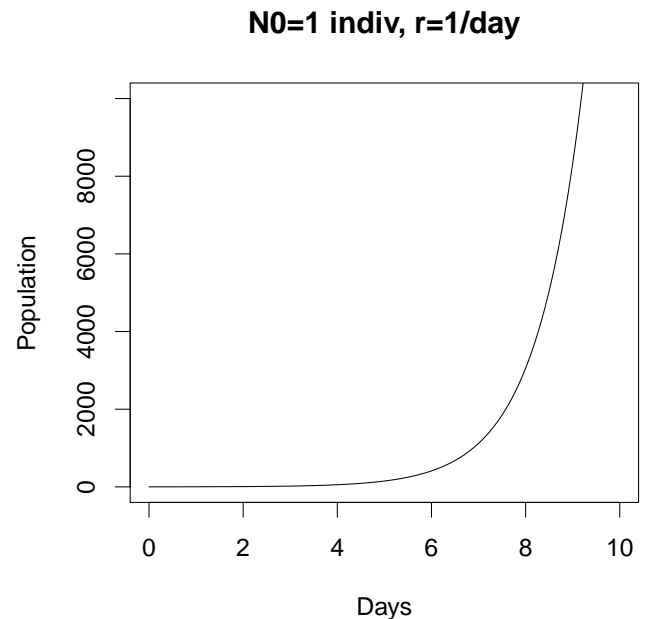
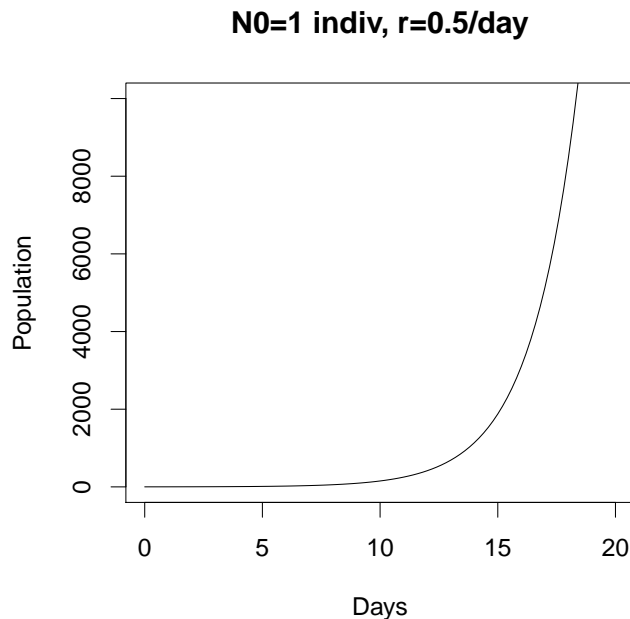
## Manipulating units

- 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)
- Poll: How many seconds are there in a day?
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- <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 I 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

- Poll: What is  $10^3 \text{day}$ ?

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- What is  $10^{72}\text{hr}$ ?

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- What is  $3\text{ day} \cdot 3\text{ day}$ ?

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## 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?

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## Moths

- $600\text{ egg/rF}$
- $\cdot 0.1\text{ larva/egg}$
- $\cdot 0.1\text{ pupa/larva}$
- $\cdot 0.5\text{ A/pupa}$
- $\cdot 0.5\text{ rA/A}$
- Poll: What's the product?

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## 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
- \*
- If we don't close the loop, we can't correctly move from step to step

## Calculating $\lambda$

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

## 3 Key parameters

### 3.1 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 (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  $\lambda$  must be unitless
- But it is *associated with* the time step  $\Delta t$ 
  - 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
- Poll: The population will increase when  $\mathcal{R} \dots$ :
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- Poll: What are the units of  $\mathcal{R}$ ?
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## Lifespan

- In this model world, how long do individuals live, on average in this model?
- If  $p$  is the proportion of individuals that survive, then the proportion that die is:
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- How many time steps do you expect to survive, on average?
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  - \*
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## 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?
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## 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  $\lambda$  tell us about whether the population is increasing?
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- What does  $\mathcal{R}$  tell us about whether the population is increasing?
  -
- Therefore, these two criteria must be the same!
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## 3.2 Continuous-time model

## Calculating birth rate

- The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - An instantaneous rate
  - Units of  $[1/\text{time}]$  – implies what assumption?
    - \*
    - \*
    - \*

## Calculating death rate

- The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - An instantaneous rate
  - Units of  $[1/\text{time}]$
- Is there a concern with these units?

## Instantaneous rate of increase

- Population increases when  $r = b - d > 0$
- $r$  is not unitless, units are:
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- So how can  $r = 0$  be a criterion?
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## 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?
  -
- What does  $\mathcal{R}$  tell us about whether the population is increasing?
  -
- Therefore, these two criteria must be the same!
  -

## 3.3 Links

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

## 4 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  $\lambda$  does it correspond to?

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### Long-term growth rate

- What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) 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
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## Changing growth rates

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

- What do we expect to happen if a population's growth rate is affected only by seasons and climate?
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- What sort of mechanism could keep a population in a reasonable range for a long time?
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- This is even true for modern humans!