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?
  - **Answer:** Birth
  - **Answer:** Death
  - **Answer:** Immigration and emigration
  - **Answer:** 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!
  - **Answer:** They usually correspond to exponential growth
    - **Answer:** ...or exponential decline

1.2 Examples

Moth example

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

Bacteria

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

Dandelions

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

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?
  - **Answer:** $N_{T+1} = (pN_T + fN_T) = (p+f)N_T$
- 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 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
  - (Δt has units of time)

Model

- Dynamics:
  - $N_{T+1} = \lambda N_T$
  - $t_{T+1} = t_T + \Delta t$
- Solution:
  - $N_T = N_0 \lambda^T$
  - $t_T = T \Delta t$
- Poll: How does N behave in this model?
  - **Answer:** Increases exponentially (geometrically) when $\lambda > 1$
  - **Answer:** Decreases exponentially when $\lambda < 1$

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

- 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

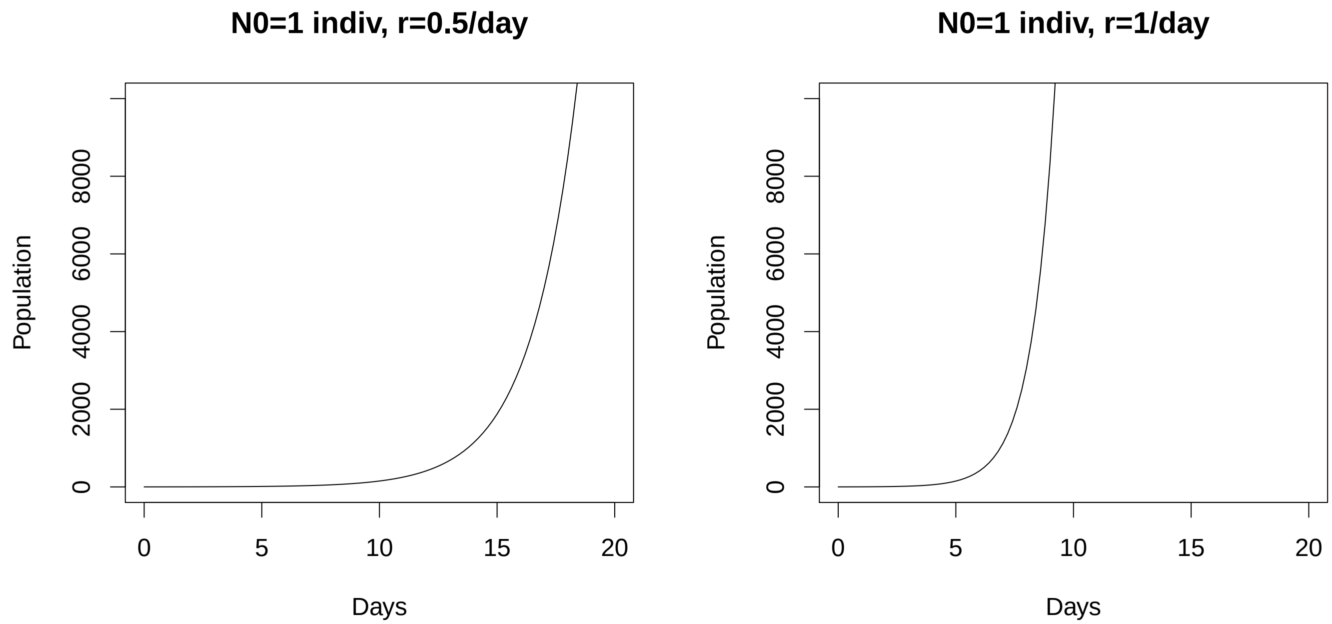
- b is the **birth rate**
- d is the **death rate**
- $r \equiv b - d$ is the **instantaneous rate of increase**.
- These quantities are not associated with a time period, but they have units:
  - **Answer:** 1/[time]
    - **Answer:** $\equiv$ (indiv/[time])/indiv

Model

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

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 $3\,\mathrm{day} \cdot 4\,\mathrm{espressoes/\,day}$?
  - **Answer:** $12\,\mathrm{espressoes}$
- What is $1\,\mathrm{wk} \cdot 0.02/\,\mathrm{day}$?
  - **Answer:** $1\,\mathrm{wk} \cdot 0.02/\,\mathrm{day}$
  - **Answer:** $1\,\mathrm{wk} \cdot 0.02/\,\mathrm{day} \cdot \frac{7\,\mathrm{day}}{\mathrm{wk}}$
  - **Answer:** 0.14

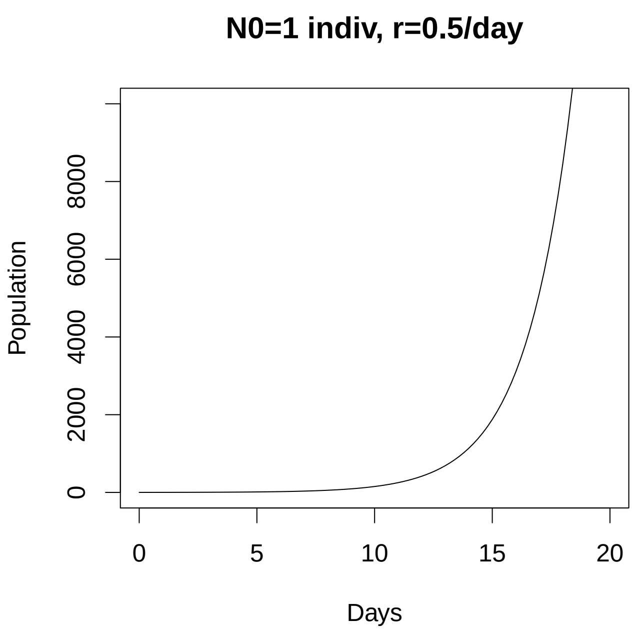
Manipulating units

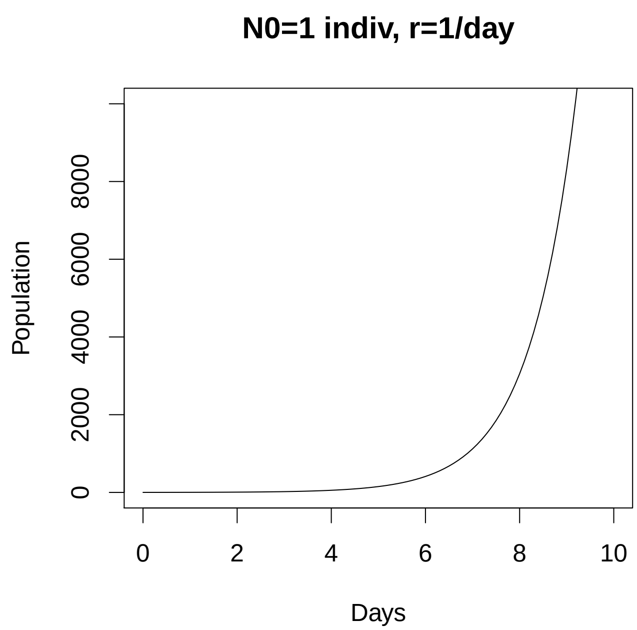
- We can multiply quantities with different units by keeping track of the units
- We *cannot* add quantities with different units (unless they can be converted to the same units)
- Poll: How many seconds are there in a day?
  - **Answer:** $\frac{60\,\mathrm{sec}}{\mathrm{min}} \cdot \frac{60\,\mathrm{min}}{\mathrm{hr}} \cdot \frac{24\,\mathrm{hr}}{\mathrm{day}}$
  - **Answer:** $86400\ \mathrm{sec}/\,\mathrm{day}$
- http://www.alysion.org/dimensional/fun.htm

Scaling

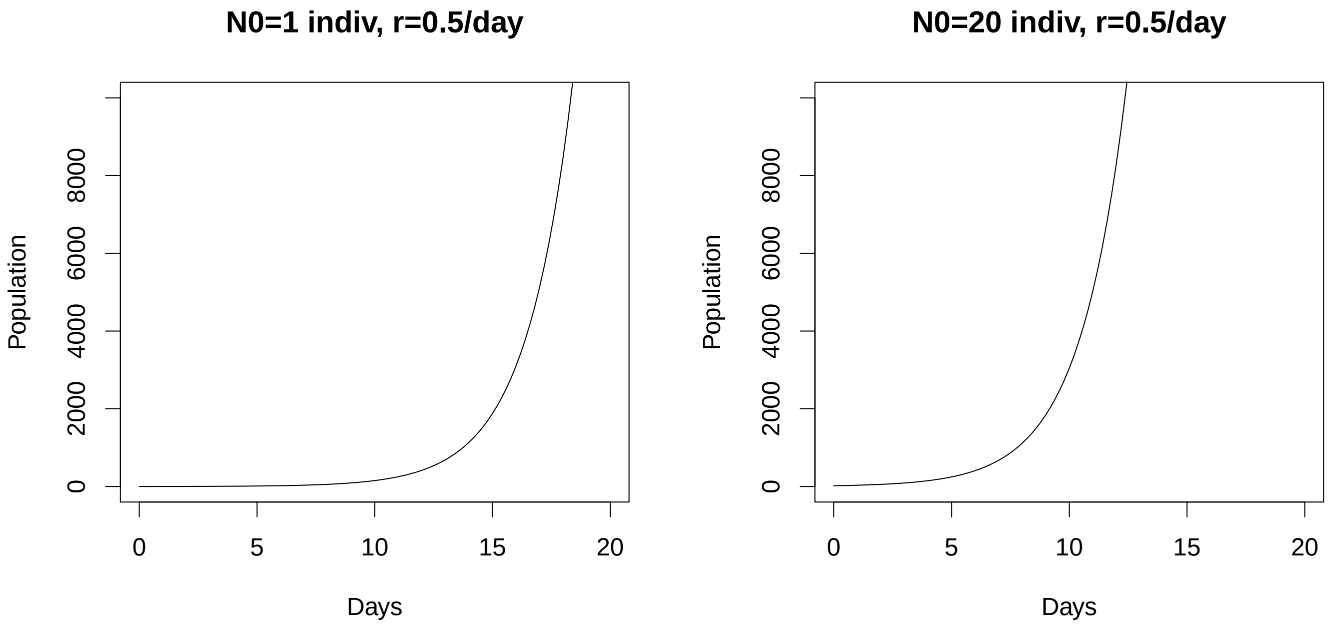
- Quantities with units set scales, which can be changed
  - If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale
  - If a multiply all the quantities with units of dandelions in my model by 10, I should get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

Scaling time in bacteria





Answer slide: *Scaling population*



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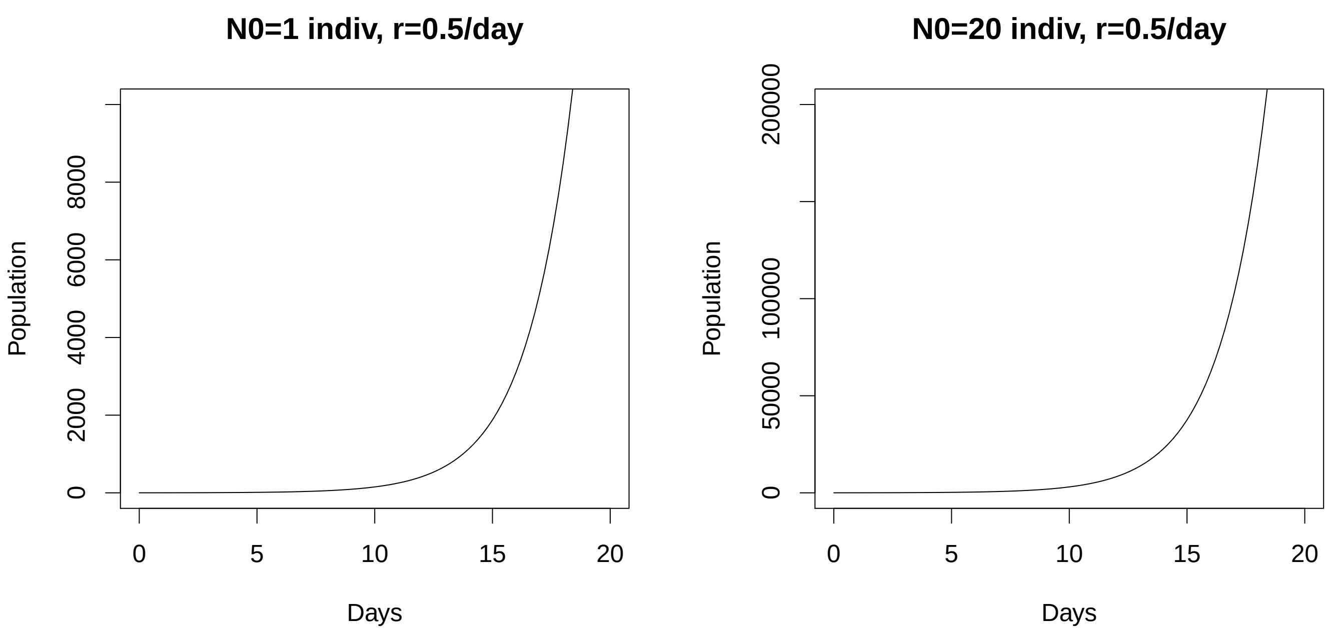

Thinking about units

- Poll: What is $10^{3\,\mathrm{day}}$?
  - **Answer postponed:**
- What is $10^{72\,\mathrm{hr}}$?

- **Answer:** Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.

- What is $3\,\mathrm{day} \cdot 3\,\mathrm{day}$?
  - **Answer:** $9\,\mathrm{day}^2$ – this *could* make sense, but it's very different from 9 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:
    * $0\mathrm{km} = 0\mathrm{cm}$
- Examples include λ and $\mathcal{R}$.

Moths

- $600\,\mathrm{egg}/\,\mathrm{rF}$
- $\cdot 0.1\,\mathrm{larva}/\,\mathrm{egg}$
- $\cdot 0.1\,\mathrm{pupa}/\,\mathrm{larva}$
- $\cdot 0.5\,\mathrm{A}/\,\mathrm{pupa}$
- $\cdot 0.5\,\mathrm{rA}/\,\mathrm{A}$
- Poll: What's the product?
  - **Answer:** $1.5\,\mathrm{rA}/\,\mathrm{rF}$
  - **Answer:** 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
    * **Answer:** Pupae are easy to count
- 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?
  - **Answer:** We multiply by λ over and over
  - **Answer:** 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

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 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
- Poll: The population will increase when $\mathcal{R}\ldots$:
  - **Answer:** $\mathcal{R} > 1$
- Poll: What are the units of $\mathcal{R}$?
  - **Answer:** $\mathcal{R}$ must be unitless

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:
  - **Answer:** $\mu = 1 - p$
- How many time steps do you expect to survive, on average?
  - **Answer:** $1/\mu$
    - **Answer:** Roughly makes sense, and is also right
  - **Answer:** 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?
  - **Answer:** Because f is also measured per time step
  - **Answer:** $\mathcal{R}$ 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?
  - **Answer:** Population is increasing each time step when $\lambda > 1$
- What does $\mathcal{R}$ tell us about whether the population is increasing?
  - **Answer:** 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!
  - **Answer:** Both come down to $f > \mu$.

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 instaneous rate
  - Units of [1/time] – implies what assumption?
    - **Answer:** New individuals are effectively the same as old individuals
    - **Answer:** 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]

Instaneous rate of increase

- Population increases when $r = b - d > 0$
- r is not unitless, units are:
  - **Answer:** [1/time]
- So how can $r = 0$ be a criterion?
  - **Answer:** Because 0 anything is unitless!
  - **Answer:** 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?
  - **Answer:** Population is increasing at any particular time step when $r > 0$
- What does $\mathcal{R}$ tell us about whether the population is increasing?
  - **Answer:** 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!
  - **Answer:** Both come down to $b > d$.

3.3 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:
  - **Answer:** $r = \log_e(\lambda)/\Delta t$

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

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

Long-term growth rate

- What is the long-term average exponential growth rate (using either r or λ) of:
  - A successful population?
    * **Answer:** Very close to $r = 0$ or $\lambda = 1$
    * **Answer:** But a little larger
  - An unsuccessful population?
    * **Answer:** *Probably* very close to $r = 0$ or $\lambda = 1$
    * **Answer:** But a little smaller
    * **Answer:** If much smaller, it would disappear very fast

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?
  - **Answer:** $\mathcal{R}$ is extremely close to 1 for every species
- How is this possible
  - **Answer:** Growth rates change through time

Changing growth rates

- Poll: What sort of factors can make species growth rates change?
  - **Answer:** Seasonality
  - **Answer:** Environmental changes (gradual or dramatic)
  - **Answer:** Competition within species
  - **Answer:** Competition between species
  - **Answer:** Predators and diseases
  - **Answer:** Resources (food and space)

Regulation

- What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - **Answer:** In the long-term, it will grow or shrink according to some average value
  - **Answer:** We don't expect perfect balance, so we don't expect population to stay under control
- What sort of mechanism could keep a population in a reasonable range for a long time?
  - **Answer:** If the growth rate is directly or indirectly affected by the size of the population
  - **Answer:** There should be some mechanism that decreases population growth rate when population is large
- This is even true for modern humans!