UNIT 1: Linear population models

Outline

Subsection 1

Dandelions

Dandelions

- Start with one dandelion; it produces 100 seeds, of which only 4% survive to reproduce the next year.
- Poll: How many dandelions after 3 years?
  - * 64?
  - * 125?
  - See spreadsheet

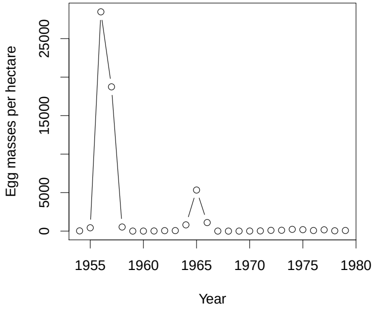
Subsection 2

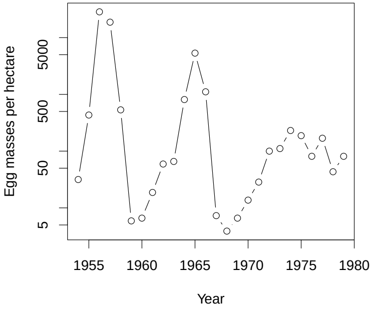
Gypsy moths

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
- Poll: What happens if we start with 10 moths?
  - * We end up with 15 moths
  - ML : intervals are also legit answers
  - JD: What does this mean?

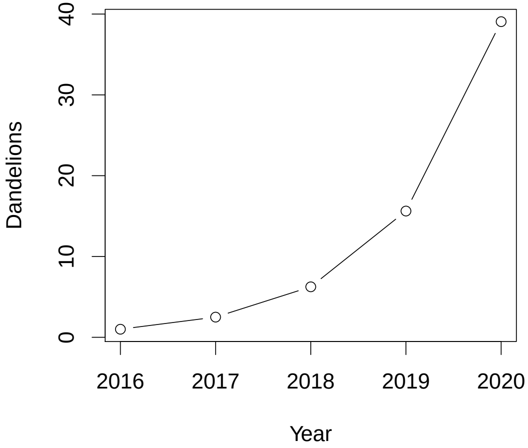
Moth calculation

- Researchers studying a gypsy moth population make the following estimates:
  - The average reproductive female lays 600 eggs
    - * Assume half are female
  - 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?
  - * If 5 are female, we end up with an average of 7.5 moths

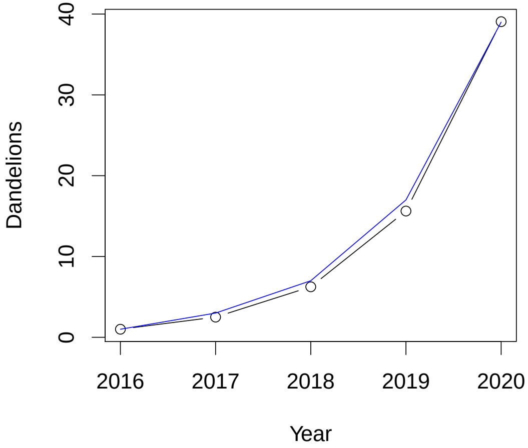
Stochastic version

- 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?
  - * The model has randomness, to reflect details that we can't measure in advance, or can't predict

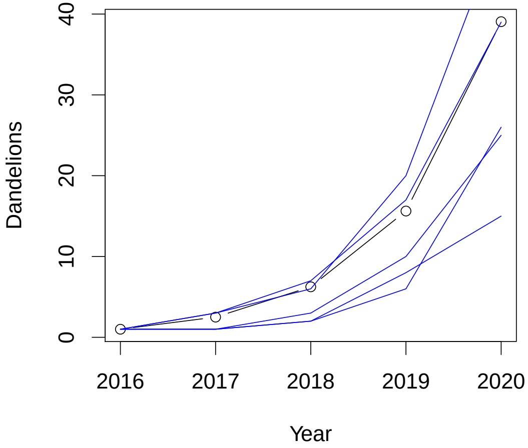
Stochastic model



Stochastic model

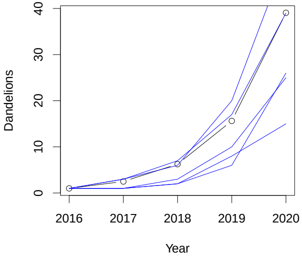


Stochastic model



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



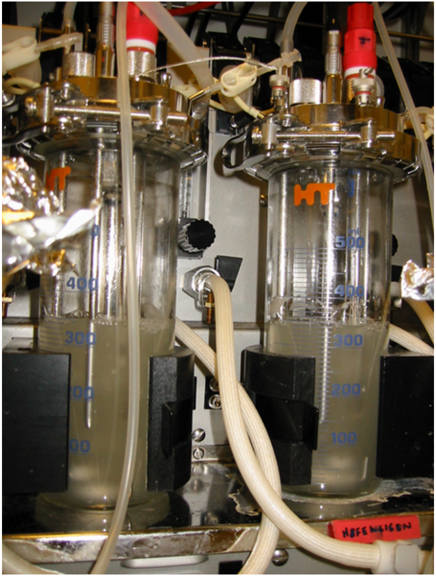
Subsection 3

Bacteria

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 $0.04/\,\mathrm{hr}$
  - They wash out of the tank at a rate of $0.02/\,\mathrm{hr}$
  - They die at a rate of $0.01/\,\mathrm{hr}$
- 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 in a tank



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

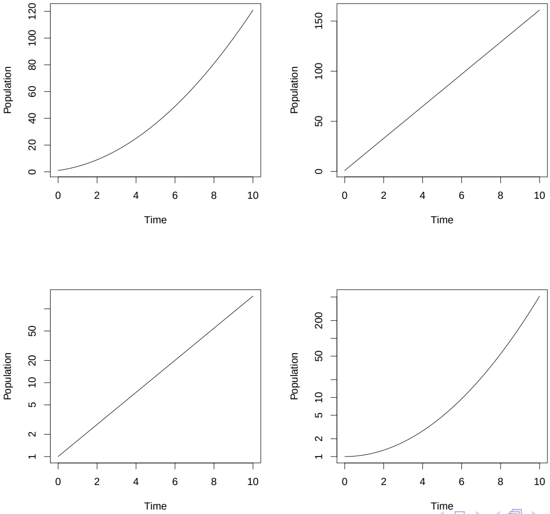
Bacteriostasis

- 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:
  - Poll: 1 hr?
  - Poll: 1 wk?

Outline

Exponential growth

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



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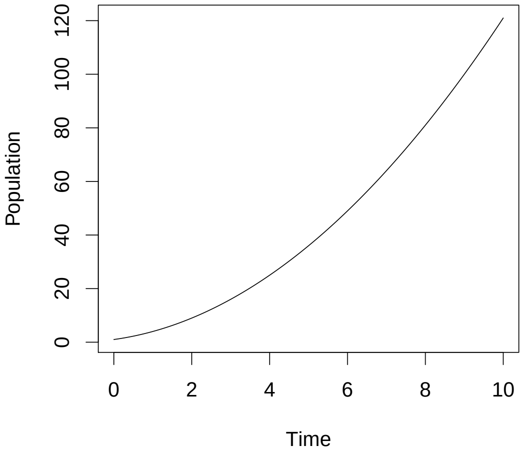

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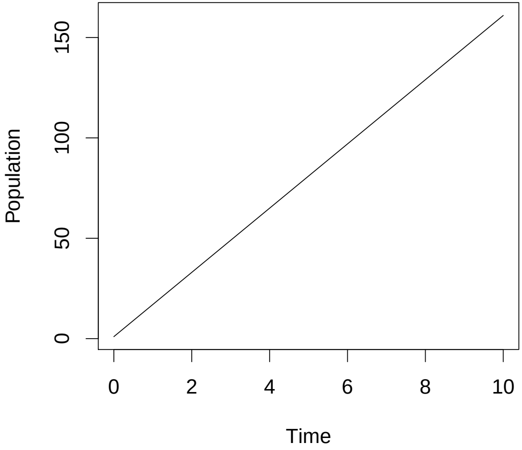

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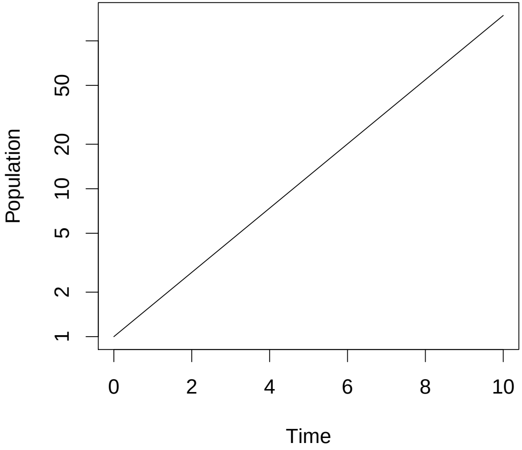

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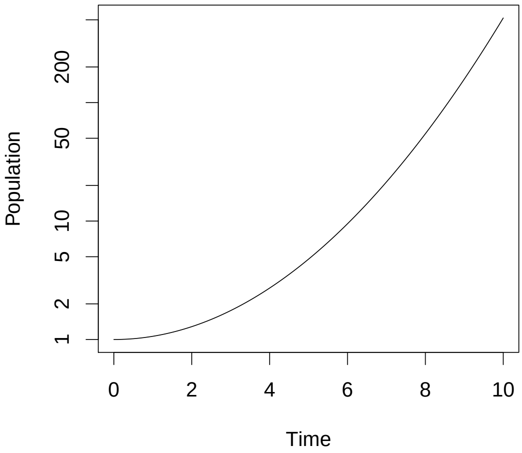
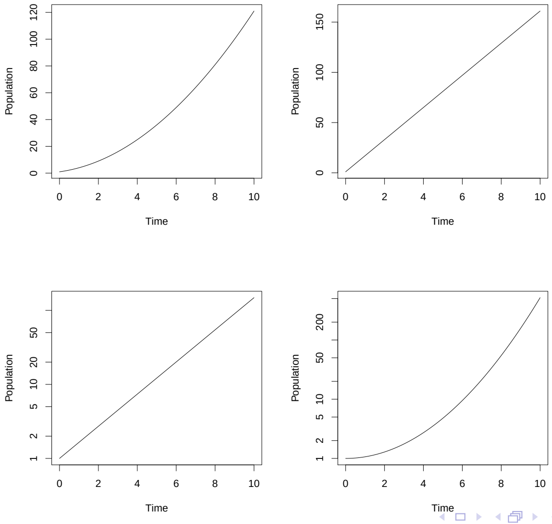
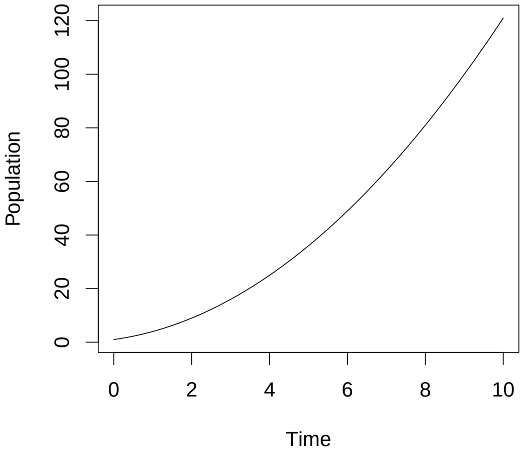


Exponential growth

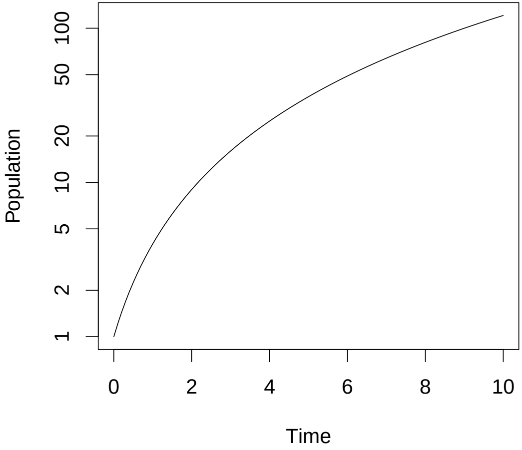
- Poll: What is exponential growth?
- Poll: Which of these is an example?



A on both scales



A on both scales



Types of growth

- arithmetic/linear:
  - * *Add* a fixed amount in a given time interval
  - * Total growth rate is constant
- geometric/exponential:
  - * *Multiply* by a fixed amount in a given time interval
  - * Per-capita growth is constant
- other:
  - Many possibilities, we may discuss some later

Terminology

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

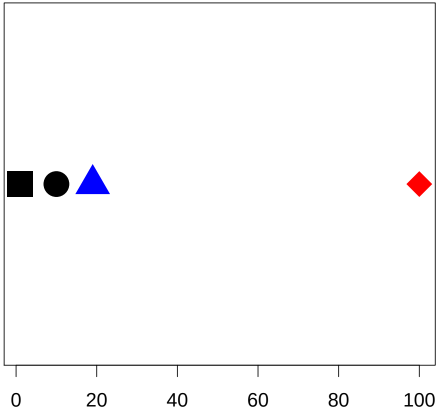
Subsection 1

Log and linear scales

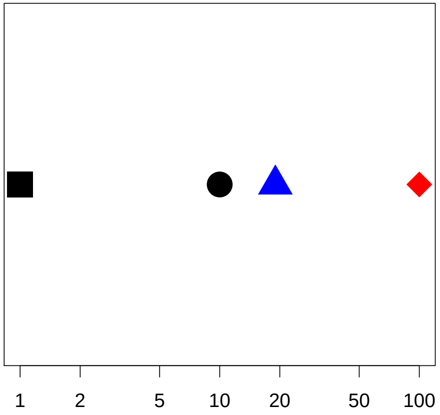
Scales of comparison

- ML : note natural log vs log10?
- JD: What does this mean?
- Poll: 1 is to 10 as 10 is to what?
  - * If you said 100, you are thinking multiplicatively
  - * If you said 19, you are thinking additively

Scales of display

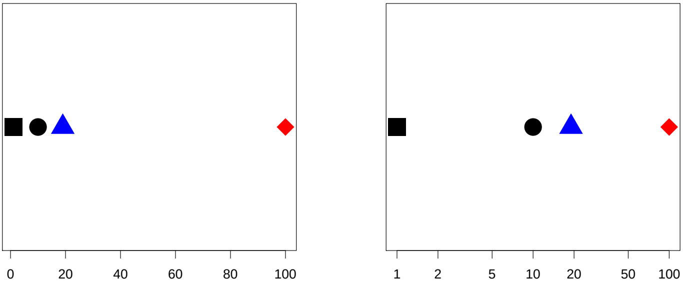


Scales of display

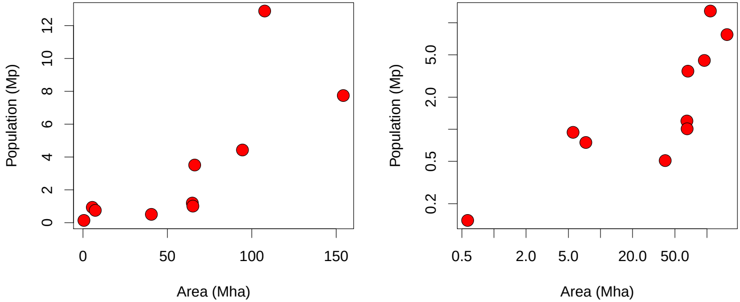


Pre-slides for both of these

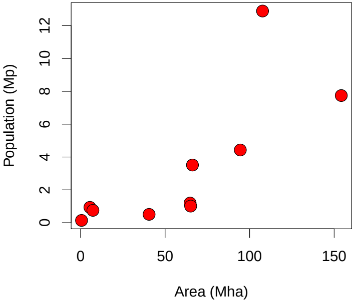
Scales of display

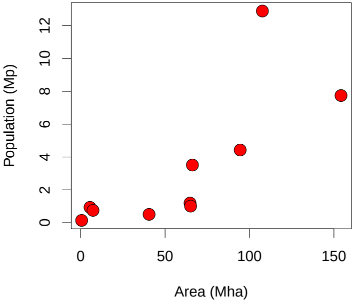


Canadian provinces

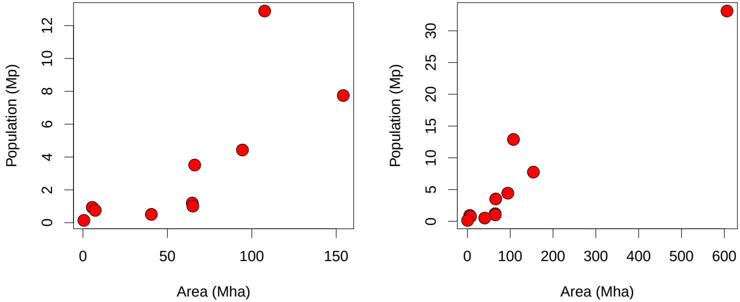


Canadian provinces plus Canada?

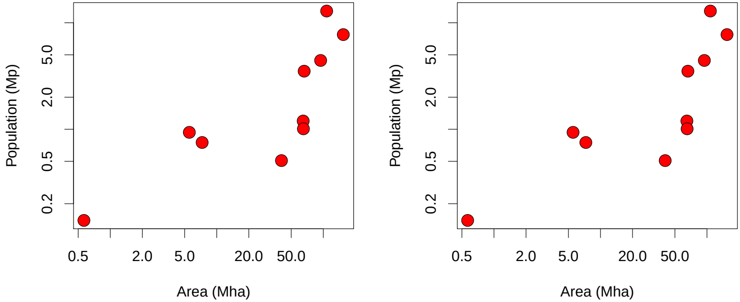




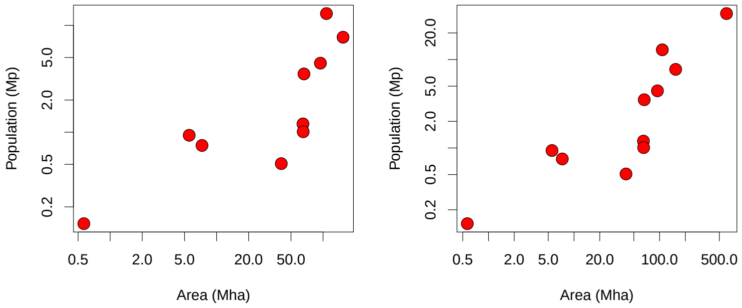
Canadian provinces plus Canada



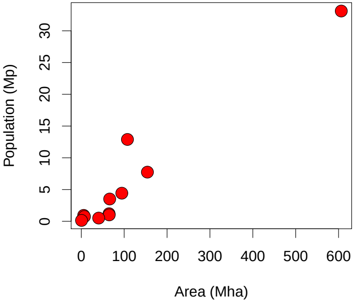
Canadian provinces plus Canada?

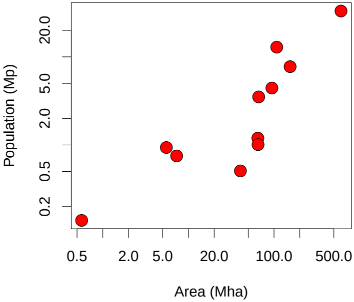


Canadian provinces plus Canada

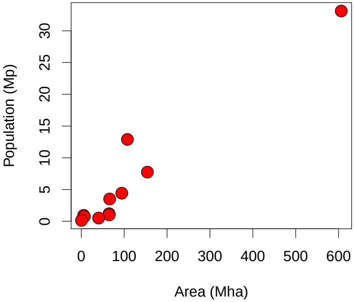


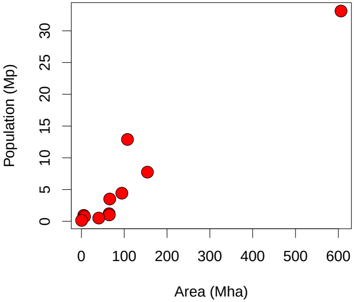
Canadian provinces plus Canada



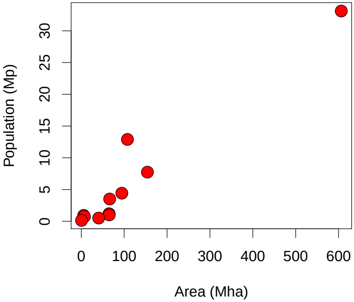


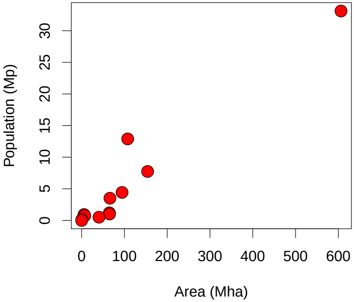
Canada plus room 1105?





Canada plus room 1105





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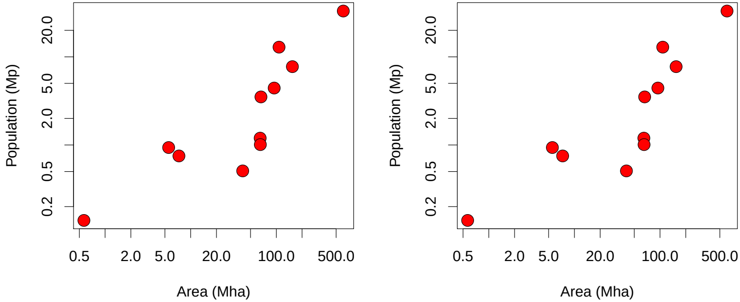

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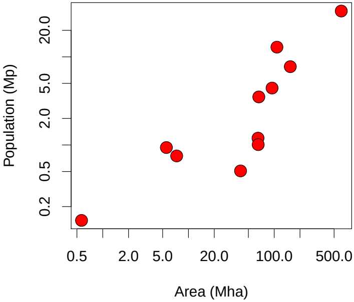

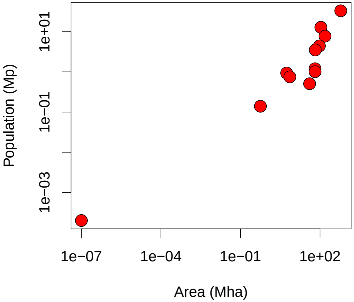

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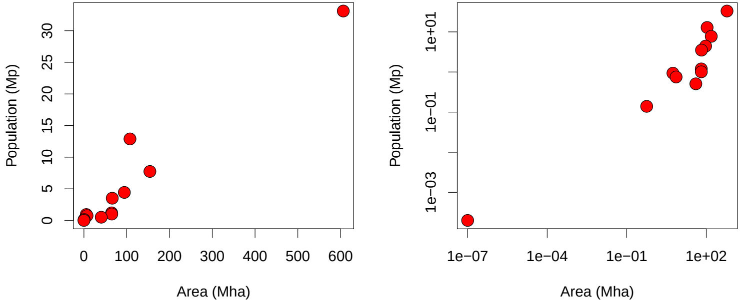
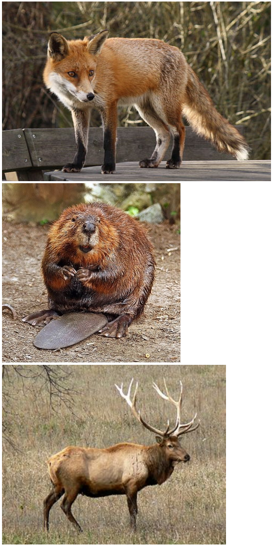


Predation comparison

Predation comparison

- A 500 lb lion is attacking a 1000 lb buffalo!
- Poll: 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?

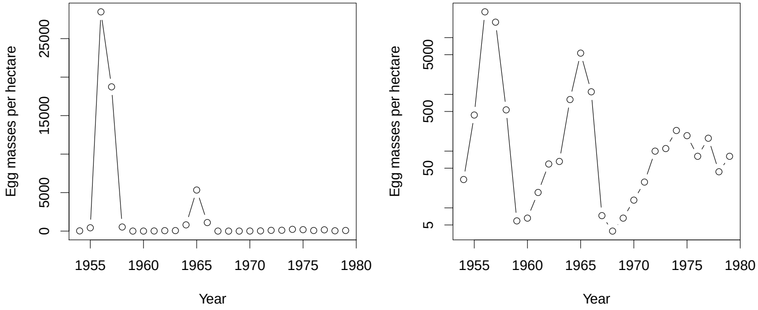
Advantages of arithmetic view

- * When there is no natural zero (or the natural zero is irrelevant)
    - * Often the case for time or geography
- * When zeroes (or negative numbers) can occur
- * When we are interested in adding things up

Advantages of geometric view

- * When comparing physical quantities, or quantities with natural units
- * When comparing proportionally

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)

Subsection 2

Time scales

Speeding in Taiwan

- A life experience
- Some clarifications
  - I was reading the sign wrong
  - I didn't actually know how to say speed
  - The whole thing never happened

Speeding in Taiwan

- Moral:
  - Units (km is *not* a speed)
  - Exponential decay
- Imagine now that I follow the signs exactly and unrealistically.
- Poll: Do I ever arrive in the (ideal) town of Speed?
  - * No
  - * But I do get extremely close (after several hours)
- Does anyone remember Zeno's paradox?
  - * Don't worry about it, then

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)
- *I'm always 1 hour away from the town of Speed*

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:
  - Poll: 1 hr?
  - Poll: 1 wk?

Bacteriostasis answers

- Bacteria wash out at the rate of 0.02/hr
  - * This can only make sense with concrete units if we think of it as an instantaneous rate – more soon
  - * $N = N_0 exp(-rt)$
- Start with 10 bacteria/ml:
  - * After one hour, 9.802 bacteria/ml
  - * After one week, 0.347 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
- *We will come back to this*

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 times closer
- 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

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 $T_h = \log_e(2)T_c$

Outline

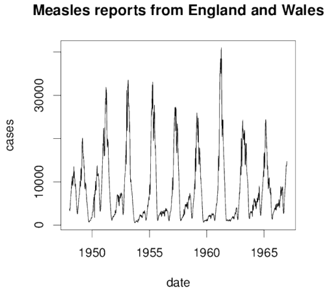
Subsection 1

Dynamical models

Dynamical models

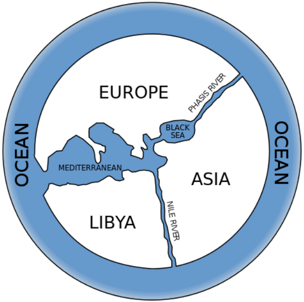
Tools to link scales

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



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
- ML: note. dandelion example

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.
- Poll: What are some reasons why the size of the population 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

CC: you want to restructure this slide

- We will focus mostly on births and deaths
  - These are done by individuals in our population, thus it makes sense to think of them as having per capita rates
- If per capita rates are constant, we say that our population *models* are **linear**
  - Linear models do not usually correspond to linear growth!
  - * They usually correspond to exponential growth – or decline

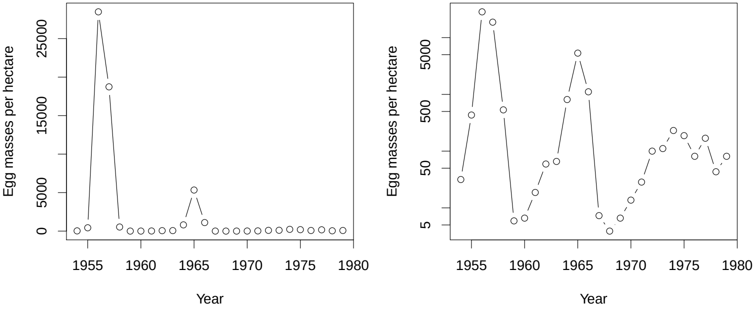
Subsection 2

Examples

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 example

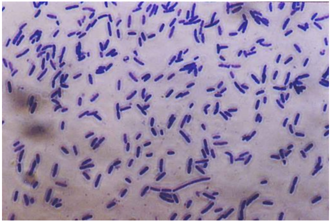
MK: Maybe bring back gypsy moth population time series

- State variables
  - * 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

MK: Work on simplifying spreadsheet
MK: Draw a moth cycle on the slide?

Bacteria

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



Dandelions

MK: Again, think a drawn cycle on the slide would be helpful.

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

MK: Clarify that the census time becomes a choice because you have conceded to only track one state variable.

Subsection 3

A simple discrete-time model

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 $\Delta t = 1$ yr
- All individuals are the same at the time of census
- Population changes deterministically

Interpretation

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

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:
  - $N_T = N_0 \lambda^T$
  - $t_T = T \Delta t$
    - MK: Spend plenty of time here attempting to extract the answer from students.
- Behaviour of N
  - * Increases exponentially (geometrically) when $\lambda > 1$
  - * 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

Subsection 4

A simple continuous-time model

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
  - * Advantageous if reproduction is continuous
- All individuals are the same all the time
  - * Usually disadvantageous

Interpretation

MK: Maybe put this example first

JD: Before what?

- 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 if *for* – describing instantaneous rates of change

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:
  - * 1/[time]

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
- But we can't do an infinite number of simulation steps on the computer
- Bacteria page on web site

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

Outline

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 $3\,\text{day} \cdot 4\,\text{espressoes}/\,\text{day}$?
  - * $12\,\text{espressoes}$
- What is $1\,\text{wk} \cdot 0.02/\,\text{day}$?
  - * $1\,\text{wk}{\cdot}0.02\,\text{day}$
- * $1\,\text{wk}{\cdot}0.02\,\text{day} \cdot \frac{168\,\text{day}}{\text{wk}}$

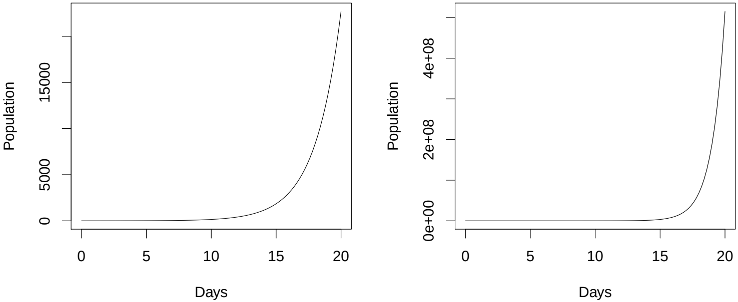
Manipulating units

- 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?
  - * $\frac{60\,\text{sec}}{\text{min}} \cdot \frac{60\,\text{min}}{\text{hr}} \cdot \frac{24\,\text{hr}}{\text{day}}$
  - * $86400\ \ \text{sec/day}$

Scaling

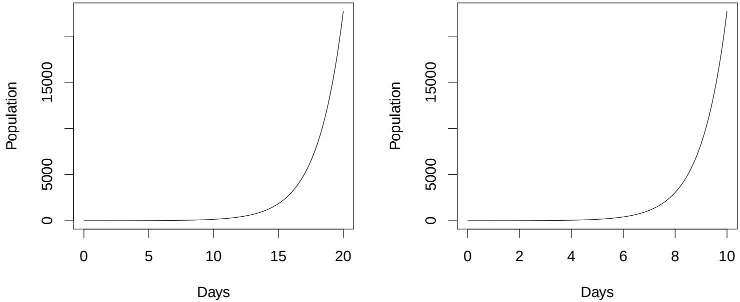
- Quantities with units set scales, which can be changed
  - If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale
  - If a multiply all the quantities with units of dandelions in my model by 10, I should get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

Bacteria example



ML: show the equation? and the little r?

Bacteria example



ML: give some text to follow along, you talk too fast.

Thinking about units

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

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
- ML: Remind people little r is a common example you are going to use
- ML: or put it up once a while.
  - Otherwise, they could be scaled
  - Zero works as a unitless quantity:
    - Is 0km the same as 0in?

Moths

- 600 egg/ rF
- ·0.1 larva/ egg
- ·0.1 pupa/ larva
- ·0.5 A/ pupa
- ·0.5 rA/ A
- Poll: What's the product?
  - * 1.5 rA/ rF
  - * Need to multiply by something with units rF/rA to close the loop

Moth spreadsheet

ML: is there a cleaner way to do the spreadsheet?
ML: need better names for spreadsheet. Too confusing
ML: Be more clear when you say, Adults model gives the right answer
ML: People look confuse, they don't know what to expect.
ML: wasting people's time is a good example. If you waste 1 min/student, and there are 120 students in the class, how much time did you waste?

- 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

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

Outline

Subsection 1

Discrete-time model

Discrete-time model

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

Calculating fecundity

Blackboard

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

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:
  - * $\mu = 1 - p$
- How many time steps do you expect to survive, on average?
  - * $1/\mu$ (not obvious, but true)
  - * Average lifetime is $1/\mu * \Delta t$

Calculating $\mathcal{R}$

- ML: CAn you put R and r side by side?
- JD: Can you explain what you mean?
- $\mathcal{R}$ 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

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 $f > \mu$.

Subsection 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?
    - * We assume all individuals are effectively the same
    - * If we know how many individuals we have, we know how many births there will be

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
  - * [1/time]
- But we still have a unitless criterion: $r = 0$
  - * 0 times anything is really just zero
  - * 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:
  - $\mathcal{R} = bL = b/d$

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 $b > d$.

Subsection 3

Links

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

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

Outline

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?

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

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 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?
  - * $\mathcal{R}$ is extremely close to 1
    - * For all the species?
    - MK: Maybe do not need to restate this again? Just jump to limiting factors?
  - * Growth rates change through time

Changing growth rates

- Poll: What sort of factors can make species growth rates change?
  - * Seasonality
  - * Environmental changes
  - * Competition within species
  - * Competition between species
  - * Predators and diseases
  - * Resources (food and space)
  - MK: Add natural disasters

Regulation

- What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - * In the long-term, it will grow or shrink according to some average value
  - * 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?
  - * If the growth rate is directly or indirectly affected by the size of the population
  - * There should be some mechanism that decreases population growth rate when population is large
- This is even true for modern humans!