UNIT Extra notes

1 Introduction

- In **linear** population models, per capita rates are independent of population size
- In **non-linear** models, not so much
- Why might per capita birth and death rates change with population size?
- What does this imply about population **dynamics**

The first law of population dynamics

- If individuals are behaving independently:
  - the population-level rate of growth (or decline) is proportional to the population size
  - the population grows (or declines) exponentially

The second law of population dynamics

- Exponential growth (or decline) cannot continue forever
- Something is changing the average rate at which populations we observe grow

The third law of population dynamics

- Exponential growth (or decline) cannot continue forever – *even on average*
- Environmental variation cannot be the only thing that changes growth rates
- Populations are, directly or indirectly, limiting their own growth rates
- This is called **density dependence**

Long-term growth rates

- Populations maintain long-term growth rates very close to $r = 0$
- This is almost certainly because factors affecting their growth rate change with the size of population.

Changing growth rates

- Poll: What is an example of a density-dependent mechanism that affects growth rate?
  - **Answer:** Predators
    - **Answer:** But! Unless the amount of predators increases as well, they might do *worse* at controlling the population
  - **Answer:** Diseases
    - **Answer:** Also but. But diseases are very likely to increase in large populations.
  - **Answer:** Insufficient resources
    - **Answer:** Limitation: e.g., oak trees use all the available light
    - **Answer:** Destruction: gypsy moths kill all the oak trees

Population regulation

- All the populations we see are *regulated*
  - On average, population growth is higher when the population is lower
  - Maybe with a time delay
- Why is this interesting?
  - Lots of populations don't *look like* they are regulated

Sometimes regulation is apparent

- Some species seem to fill a niche (mangroves)
- or deplete their own food resources (gypsy moths)

Sometimes regulation is not apparent

- Other species seem like they could easily be more common (pine trees)
  - May be controlled by cryptic (hard to see) natural enemies (like disease or parasites)
  - May be controlled by limitations that occur only at certain times (e.g., during regular droughts)

Regulation works over the long term

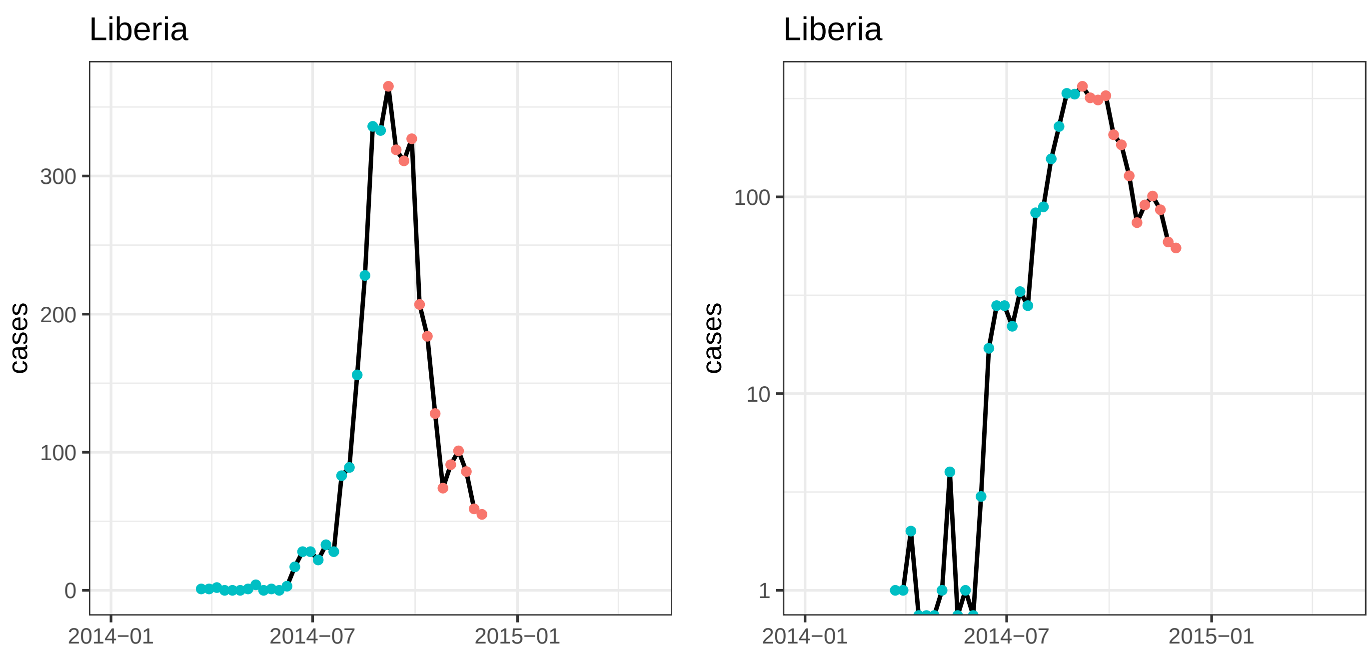
- Not every species is experiencing population regulation at every time
- A species that we see now may be expanding into a niche (e.g., because of climate change)
- Some species are controlled by big outbreaks of disease
- Some species have big outbreaks into marginal habitat, and spend most of their time contracting back to their "core" habitat

How do we know it's regulation?

- Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
  - **Answer:** Because the long-term average value of r has to be *very* close to 0
  - **Answer:** This is true for *every* population
  - **Answer:** This is unlikely to occur by chance
  - **Answer:** Thus, it must be through direct or indirect responses to the population size

1.1 Population Examples

Comment slide: *Ebola*



Gypsy moths

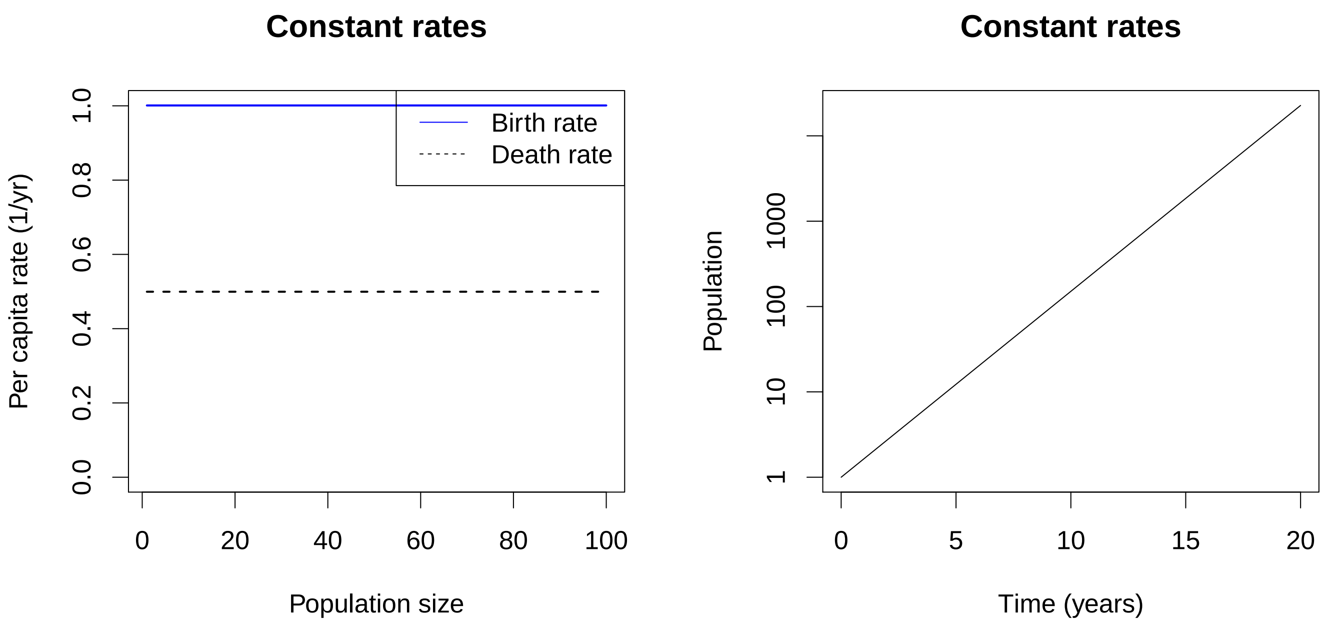
- Poll: What are some factors that limit gypsy-moth populations?
- Which are likely to be affected by the moths?
  - Directly or indirectly, in the short or long term?

2 Continuous-time regulation

Build on the linear model

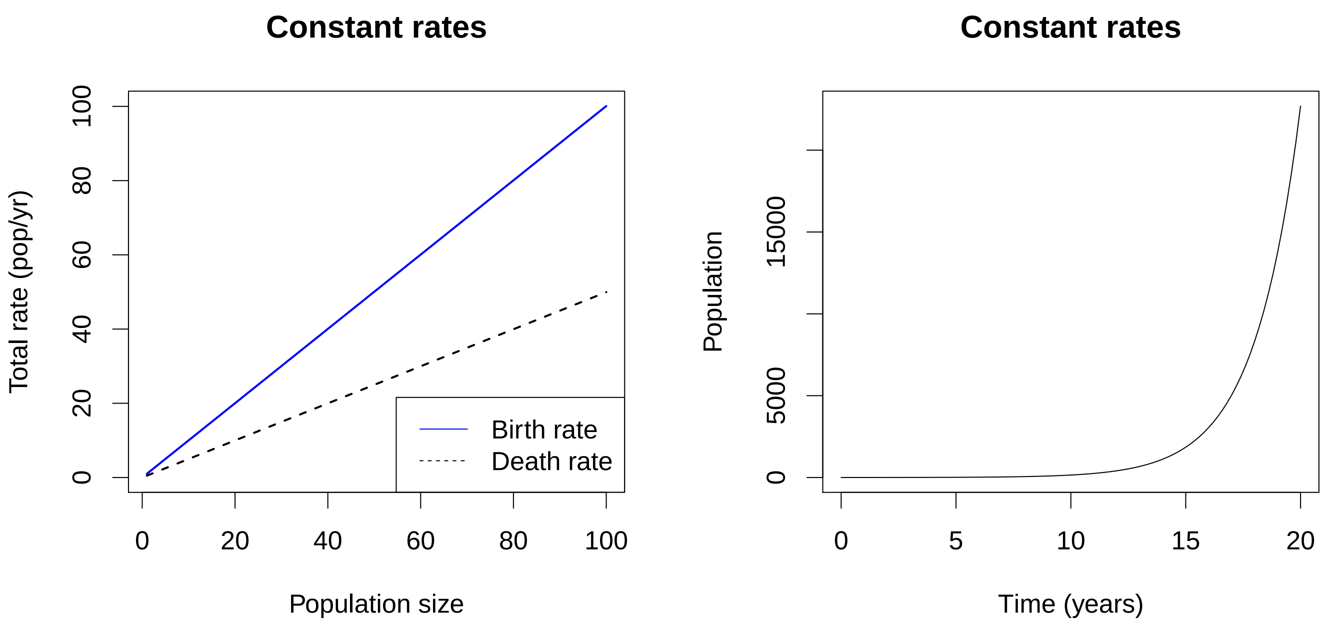
- Our linear population model is:
    - $\frac{dN}{dt} = (b - d)N$
- Per-capita rates are constant
- **Population-level rates are linear**
- Behaviour is exponential

Individual perspective



- Per capita rate shows birth and death per individual
- Corresponds to the time plot showing growth on a log scale
    - On the log scale we see *multiplicative* or *proportional* change

Population perspective



- Total rate shows birth and death for the whole population
- Corresponds to the time plot showing growth on a linear scale
  - On the linear scale we see *additive* or *absolute* change

Non-linear model

- Population has *per capita* birth rate $b(N)$ and death rate $d(N)$
  - Per-capita rates change with the population size
- Our non-linear model is: $\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$
  - Defines how fast the population is changing at any instant

Recruitment

- **Recruitment** is when an organism moves from one life stage to another:
  - Seed $\rightarrow$seedling $\rightarrow$sapling $\rightarrow$tree
  - Egg $\rightarrow$larva $\rightarrow$pupa $\rightarrow$moth
- In simple continuous-time population models, recruitment is included in birth:
  - b is the rate at which adults produce new adults; or seeds produce new seeds – we have to "close the loop"

Birth rates

- When a population is crowded, the birth rate will usually go down
  - Resources are limited: space, food, light
- But it may stay the same
- Or even go up
  - If individuals shift their resources to reproduction instead of survival

Death rates

- When a population is crowded, the death rate will often go up
  - Individuals are starving, or conflict increases
  - But it may stay the same
    * if reproduction is limited by competition for breeding sites, or by recruitment of juveniles
  - Or even go down
    * if organisms go into some sort of "resting mode"

Reproductive numbers

- Our model is: $\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$
- Reproductive number now also changes with N:
  - **Answer:** $\mathcal{R}(N) = b(N)/d(N)$
- When the population is crowded, individuals are stressed and the reproductive number will typically go down.

Carrying capacity

- If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- The population should increase
- Eventually, $\mathcal{R}$ will decrease, and eventually cross $\mathcal{R} = 1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying capacity**, K
  - $\mathcal{R}(K) \equiv 1$
  - $b(K) \equiv d(K)$
- When $N = K$:
  - **Answer:** Population stays the same, on average

Logistic model

- A popular model of density-dependent growth is the logistic model
- Per capita instantaneous growth rate r is a function of N
  - $r(N) = r_{\max}(1 - N/K)$
  - Consistent with various assumptions about $b(N)$ and $d(N)$
- Population increases to K and remans there
  - Units of N must match units of K
- Not a linear model, because *population-level* rates are not linear

Exponential-rates model

- In this course, we'll mostly use another simple model:
  - $b(N) = b_0 \exp(-N/N_b)$
  - $d(N) = d_0 \exp(N/N_d)$
- This is the simplest model that is smooth and keeps track of birth and death rates separately
  - Birth rate goes down with characteristic scale N_b
  - Death rate goes up with characteristic scale N_d

Exponential-rates vs. logistic

- The exponential-rates model is conceptually clearer
  - Birth and death rates are clearly defined
- Mathematically nicer
  - Rates always stay positive
- The logistic *looks* less scary

2.1 A simple, continuous-time model

Assumptions

- We model individual-level rates, but individuals are *not* independent: my rates depend on the number (or density) of individuals in the population
- The population can be censused at any time
- Population size changes continuously
- All individuals are the same all the time
- Population changes deterministically

Interpretation

- If we have N individuals at time t, how does the population change?
  - Individuals are giving birth at per-capita rate $b(N)$
  - Individuals are dying at per-capita rate $d(N)$
- Population dynamics follow:
  - $\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$

States and state variables

- What variable or variables describe the state of this system?
  - **Answer:** The same as before: population size (or density)
  - **Answer:** We are still assuming that's all we need to know
    * **Answer:** In other words, that all individuals are the same.

Parameters

- Poll: What quantities describe the rules for this system?
  - **Answer:** b_0 [1/time]
  - **Answer:** d_0 [1/time]
  - **Answer:** N_b [indiv] (or [indiv/area])
  - **Answer:** N_d [indiv] (or [indiv/area])

Characteristic *scale*

- A characteristic scale for density dependence is analogous to a characteristic time
- For example: $b(N) = b_0 \exp(-N/N_b)$
  - N_b is the characteristic scale of density-dependence in birth rate
  - If $N \ll N_b$, density dependence is linear (and relatively small)
  - If $N \gg N_b$, density dependence is exponential, and very large (virtually no births)

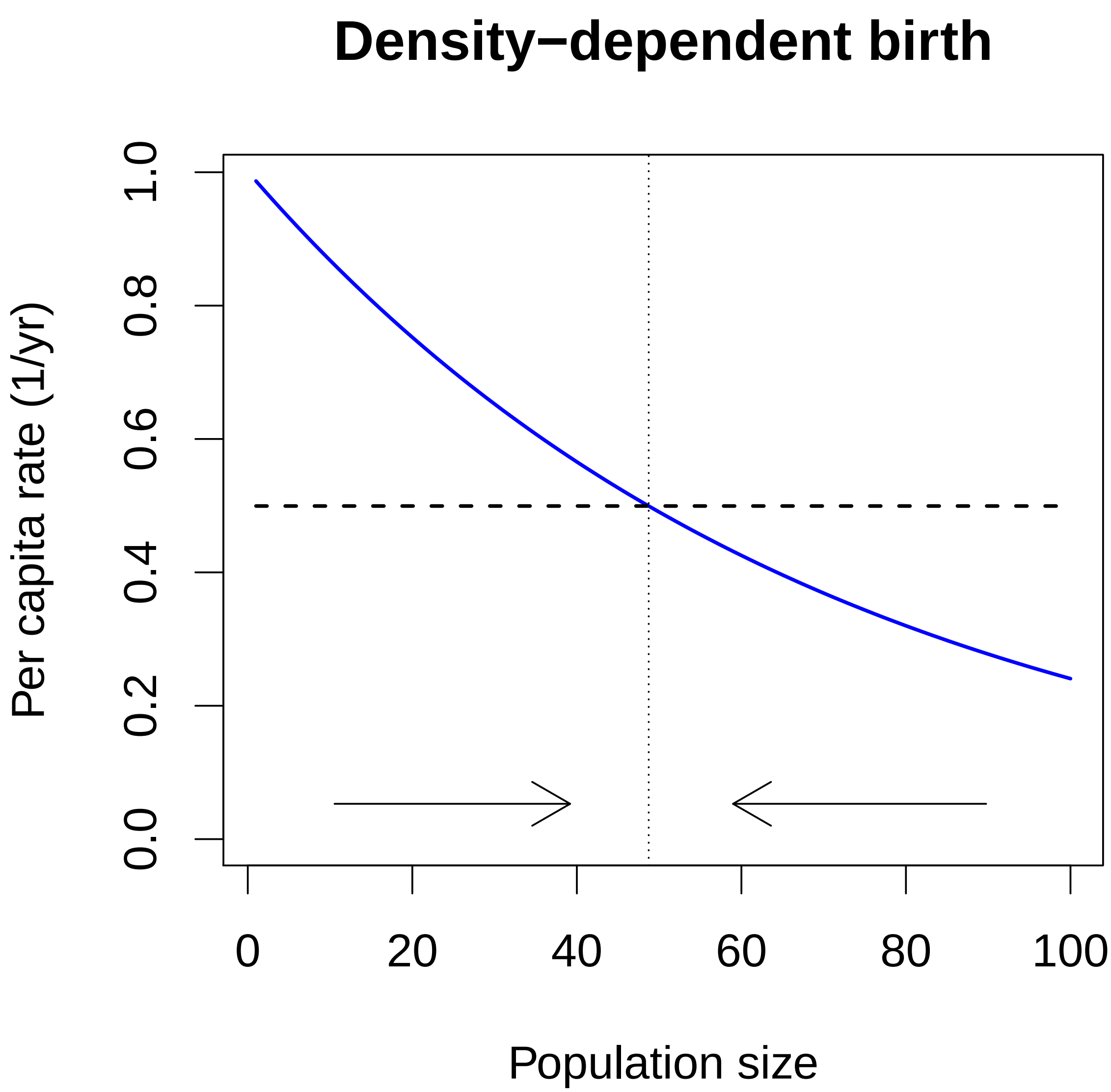
Model

- Dynamics:
  - $\frac{dN}{dt} = (b_0 \exp(-N/N_b) - d_0 \exp(N/N_d))N$
- Exact solution:
  - Insanely complicated
- Behaviour of the solution:
  - Pretty easy!

Dynamics

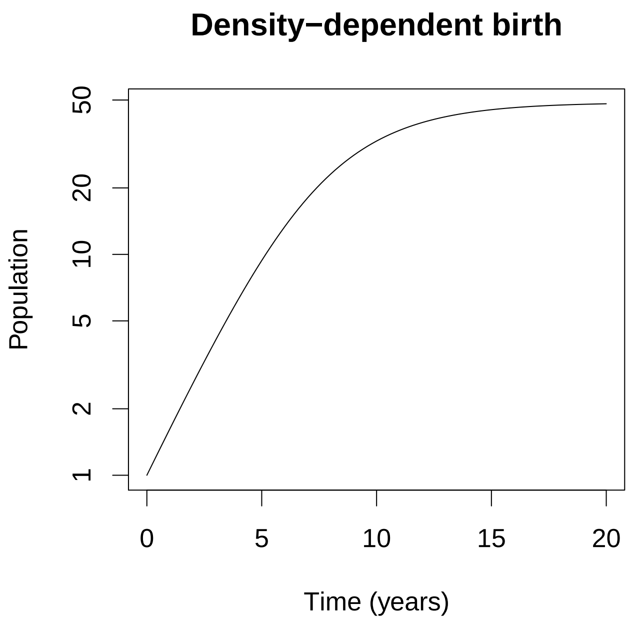
- What sort of **dynamics** do we expect from our conceptual model?
  - I.e., how will it change through time?
- What will the population do if it starts
  - near zero?
  - near the equilibrium?
  - at a high value?

What will this model do?



- Increase when population is below equilibrium
- Decrease when population is above equilibrium
- Converge

Examples



2.2 Simulating model behaviour

Simulations

- We will simulate the behaviour of populations in continuous time using the program R
- This program generates the pictures in this section by implementing our model of how the population changes instantaneously

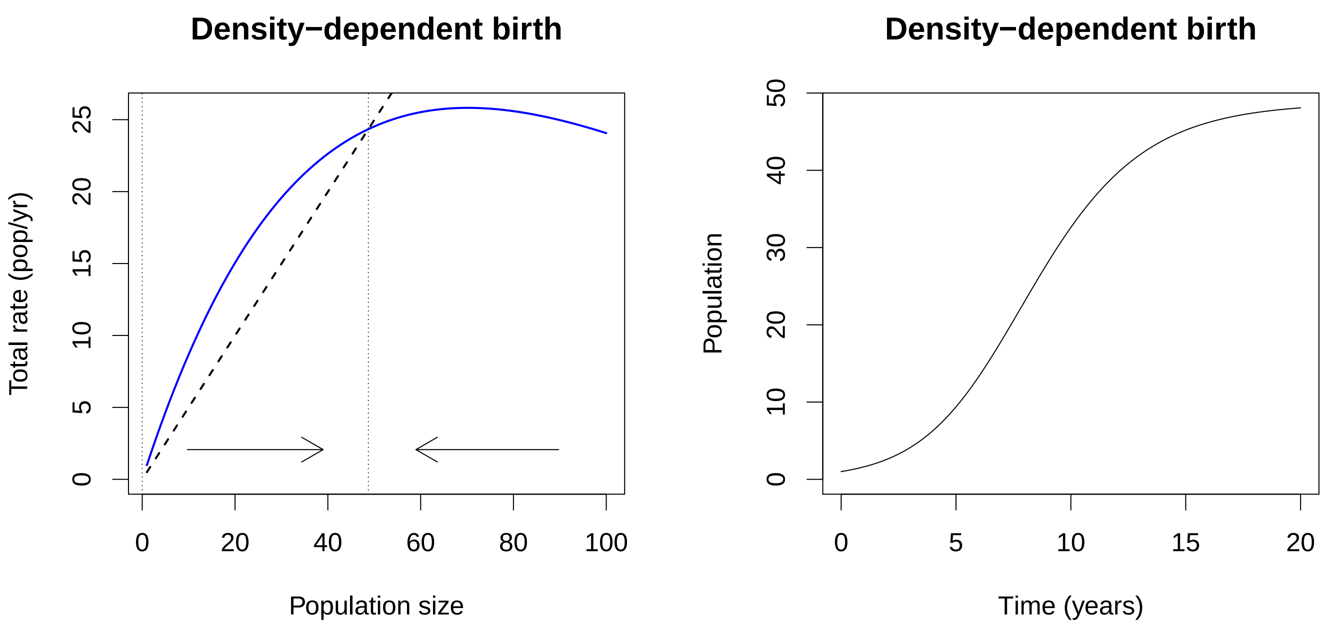
Individual-scale pictures

- We can view graphs of our population assumptions on the individual scale
  - per-capita birth and death rates
    - units [1/time]
  - what is each individual doing (on average)?
  - corresponds to the dynamics we visualize on a log-scale graph of the population
  - See above

Population-scale pictures

- We can view graphs of our population assumptions on the population scale
  - total birth and death rates
    * units [indiv/time]
    * or [density/time] = [(indiv/area)/time]
  - what is changing at the population level?
  - corresponds to the dynamics we visualize on a linear-scale graph of the population

Population perspective picture



Decreasing birth rate

- Decreasing birth rate (above) might be a good model for organisms that experience density dependence primarily in the recruitment stage

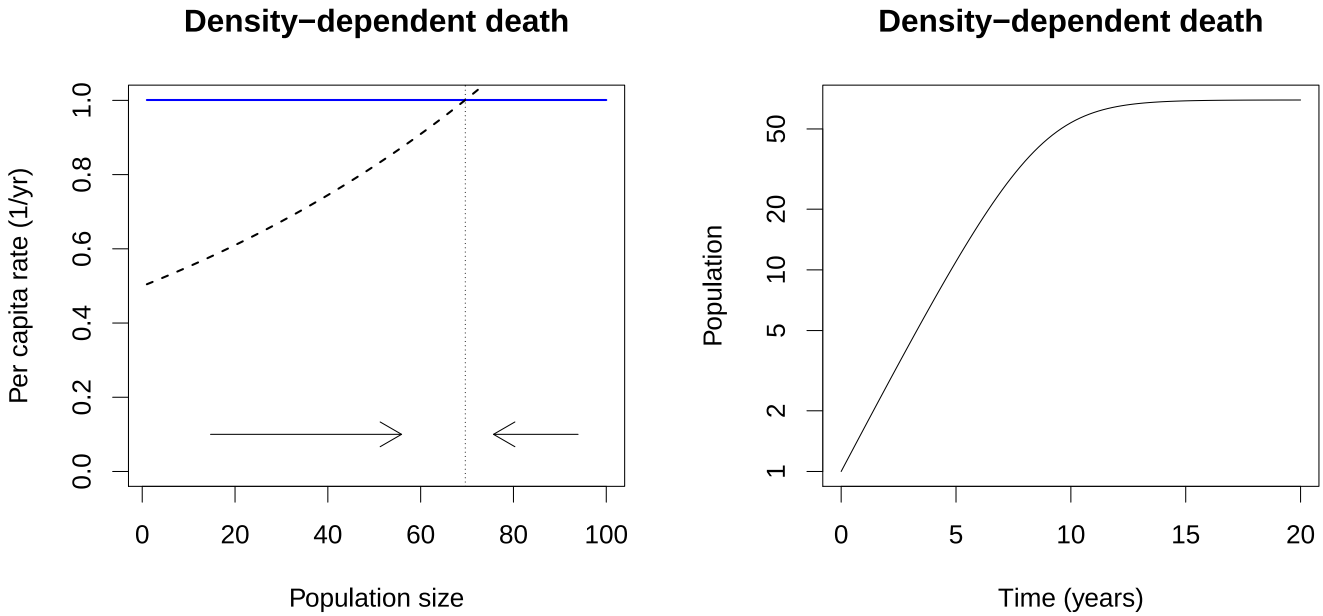
- For example, we might count adult trees, and these might not die more at high density – just fail to recruit younger ones

Increasing death rate

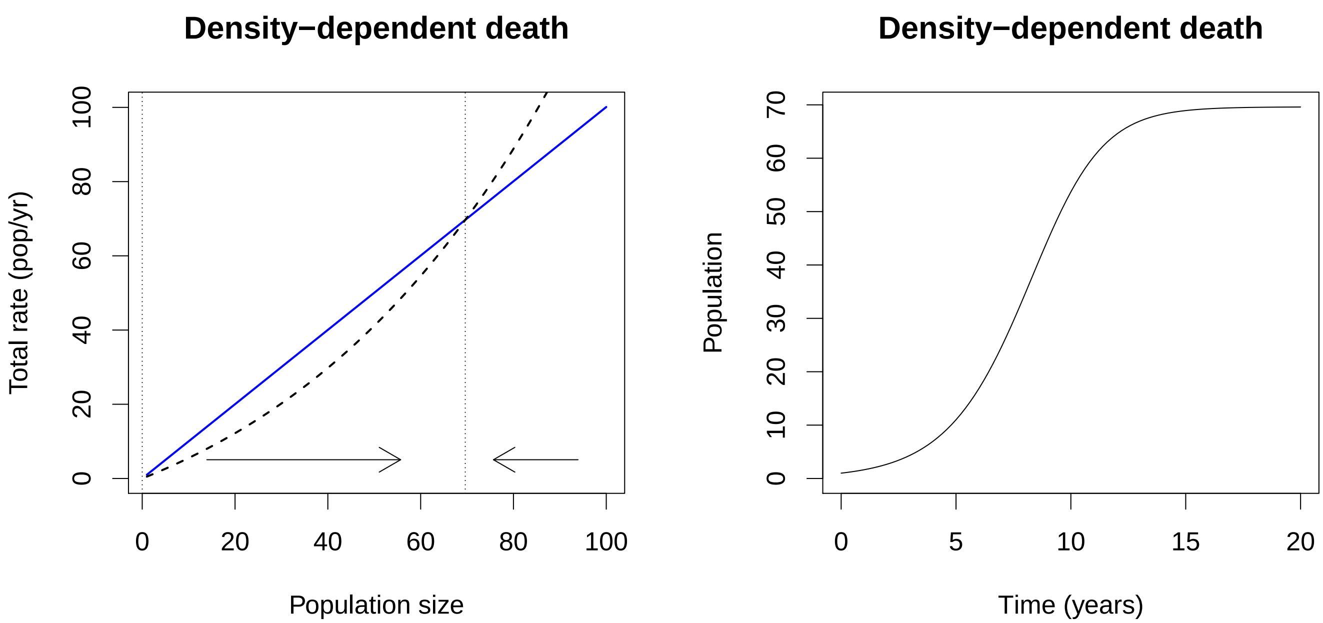
- Increasing death rate might be a good model for organisms that experience density dependence primarily as adults

- For example, in some environments, mussel density might be limited by adult crowding. Although juvenile mussels tend to have a hard time, this might not be density dependent

Individual perspective



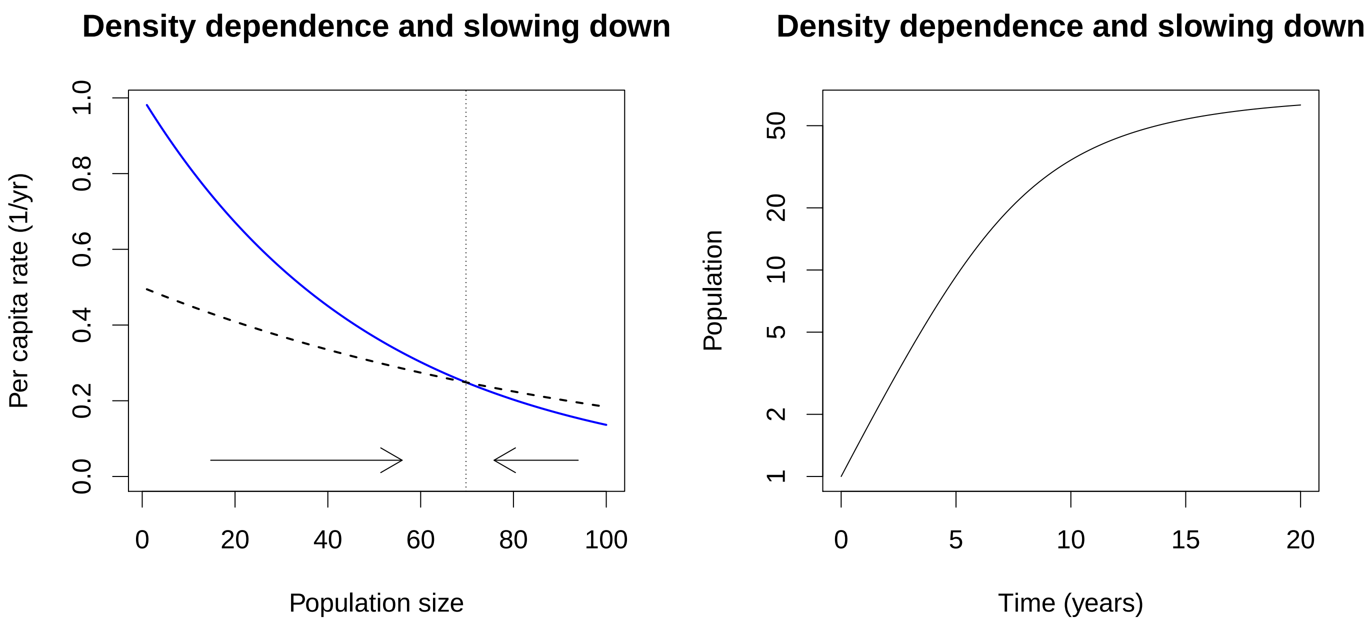
Population perspective



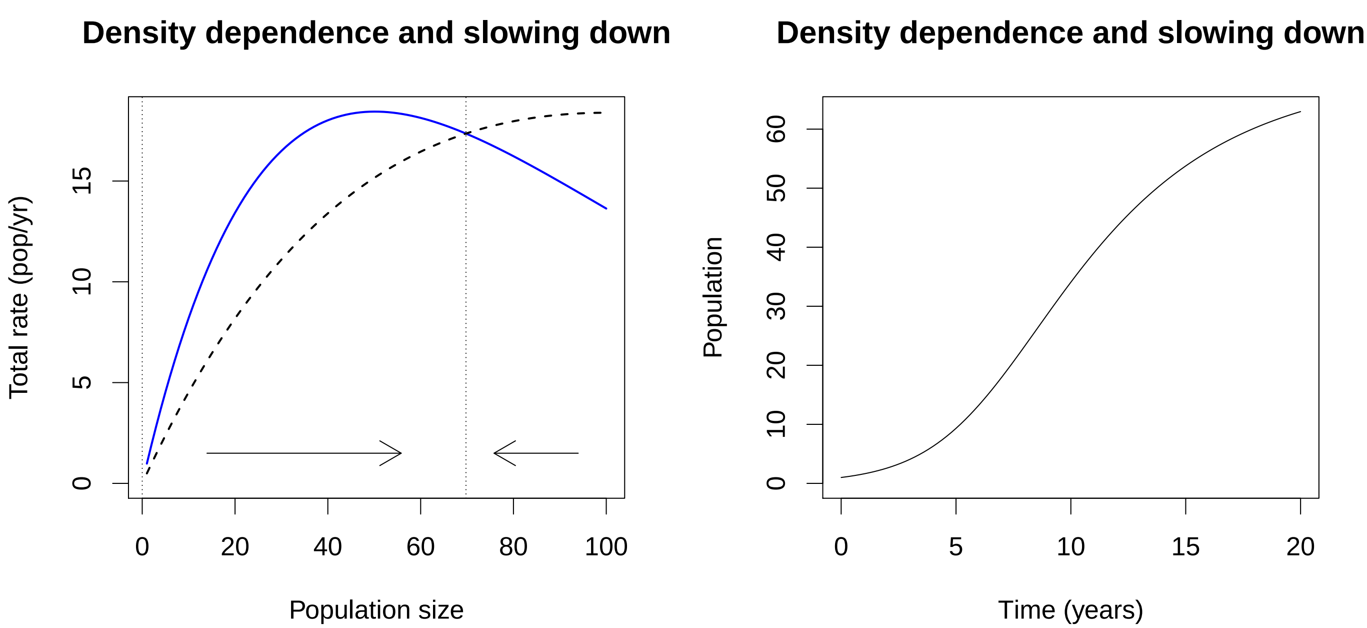
Decreasing death rate

- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate *decreases*
- How is this consistent with density dependence?
  - **Answer:** Birth rate must decrease even faster

Individual perspective



Population perspective



Other examples

- There are two other possible scenarios for density dependence
  - For fun, you can try to think of what they are
- But all of these examples have similar behaviour

  - Increase from low density
  - Decrease from high density
  - Approach carrying capacity

Maximum growth rates

- When does a population in this model have the fastest *per-capita* growth rate?
  - **Answer:** When density is low.
  - **Answer:** This is an assumption.
- When does a population in this model have the fastest *total* growth rate?
  - **Answer:** Intermediate between low density and the carrying capacity.
  - **Answer:** This is a something we learn from the model

2.3 Equilibria and time scales

- We define **equilibrium** as when the population is not changing
- Our simple model is $\frac{dN}{dt} = (b(N) - d(N))N$
- In this simple model, when does equilibrium occur?
  - **Answer:** $b(N) = d(N)$ (the carrying capacity)
  - **Answer:** $N = 0$ (the population is absent)

Stable and unstable equilibria

- Aren't equilibria always stable?
  - If we are at an equilibrium we expect to stay there
  - (in our simplified model, at least)
- An equilibrium is defined as stable if we expect to approach the equilibrium *when we are near it.*
- An equilibrium is defined as unstable if we expect to move away from the equilibrium *when we are near it.*

What kind of equilibrium?

- How can we tell an equilibrium is stable?
  - If population is just below the equilibrium:
    - **Answer:** It should increase ($b > d$)
  - If population is just above the equilibrium:
    - **Answer:** It should decrease ($d > b$)

Basic reproductive number

- The reproductive number of a population not affected by crowding is called the **basic reproductive number**
  - Written $\mathcal{R}_0$ or $\mathcal{R}_{\max}$.
- In this model, when $\mathcal{R}_0 < 1$ the population:
  - **Answer:** Always decreases
- When $\mathcal{R}_0 > 1$ the population:
  - **Answer:** Increases when it is small
  - **Answer:** Eventually $\mathcal{R}$ will decrease
- Poll: What is $\mathcal{R}_0$ in our current model?
  - **Answer:** $\mathcal{R}_0 = b(0)/d(0)$
- Does this make sene?
  - **Answer:** Not really; nothing actually grows or dies when $N = 0$
  - **Answer:** we resolve this by think of $\mathcal{R}_0$, $b(0)$, and $d(0)$ as limits
    * **Answer:** What are the values when density is very low?

Invasion

- We say a species can "invade" a system if its rate of change is positive when the population is small.
- In other words, population can invade if the extinction equilibrium is not stable
- In this conceptual model, this is the same as saying $b(0) > d(0)$
- Which is the same as saying $\mathcal{R}_0 > 1$

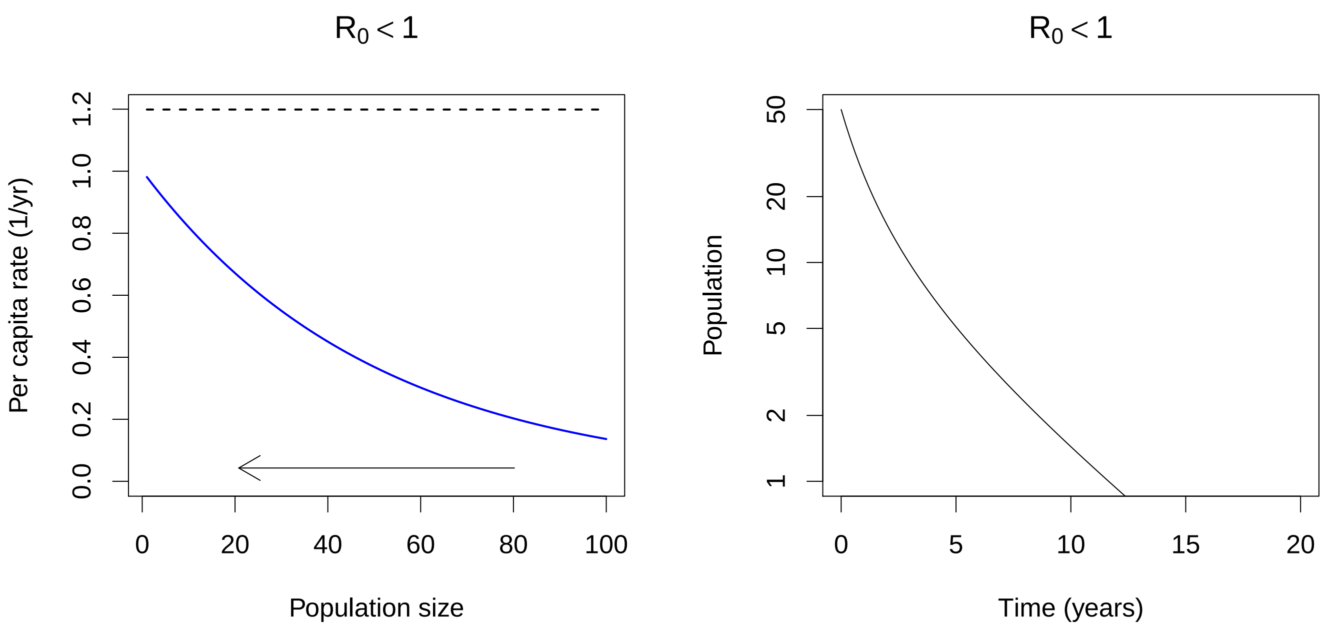
Invasion examples

- Poll: What are some examples of biological invasions?
  - **Answer postponed:**
  - **Answer postponed:**
  - **Answer postponed:**
  - **Answer postponed:**

Different behaviours

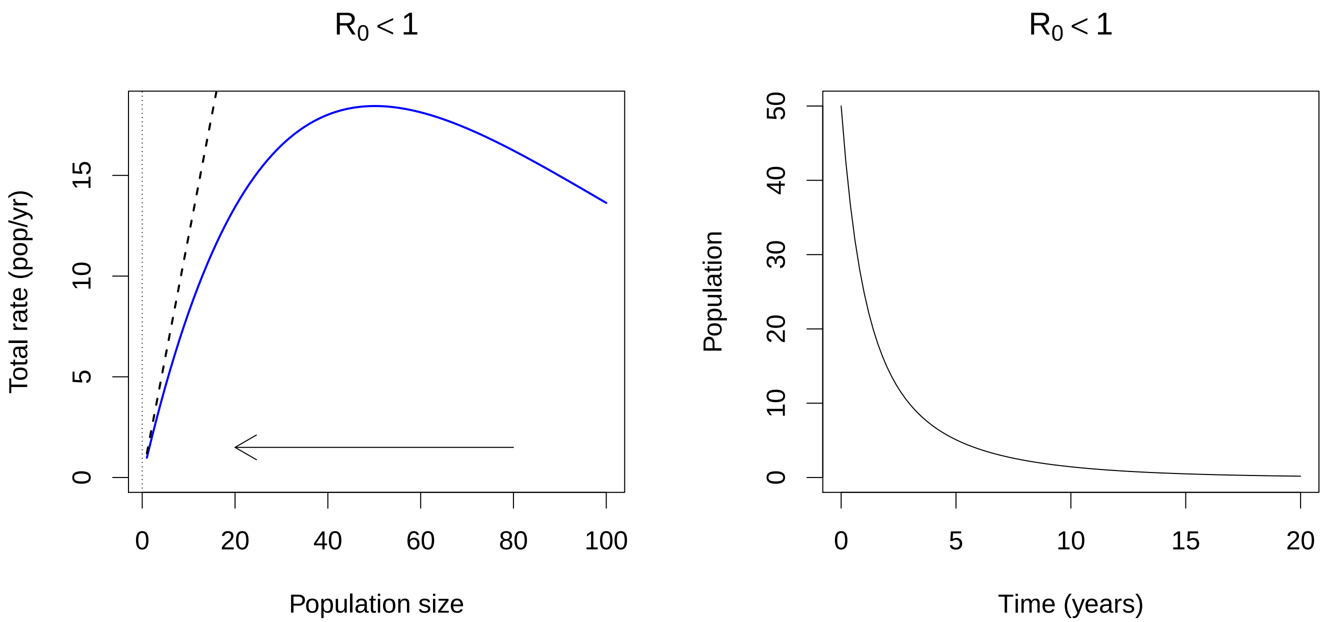
- When $\mathcal{R}_0 > 1$, the population invades
  - Zero equilibrium is unstable, carrying capacity equilibrium is stable
- When $\mathcal{R}_0 < 1$, the population fails to invade
  - Zero equilibrium is stable, carrying capacity equilibrium does not exist

Individual perspective



- When $\mathcal{R}_0 < 1$ population always decreases

Population perspective



- When $\mathcal{R}_0 < 1$ population always decreases

$\mathcal{R}_0$ and thresholds

- A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
  - It will suddenly disappear at the population level
  - Even while it can still survive and reproduce at an individual level
- This is why there are no white spruce trees in Cootes Paradise
- And no malaria in the mainland United States

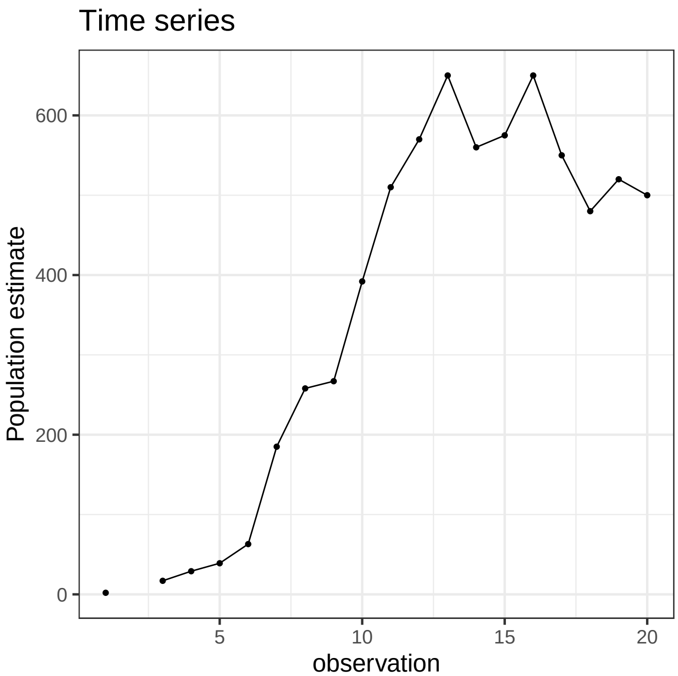
Characteristic times

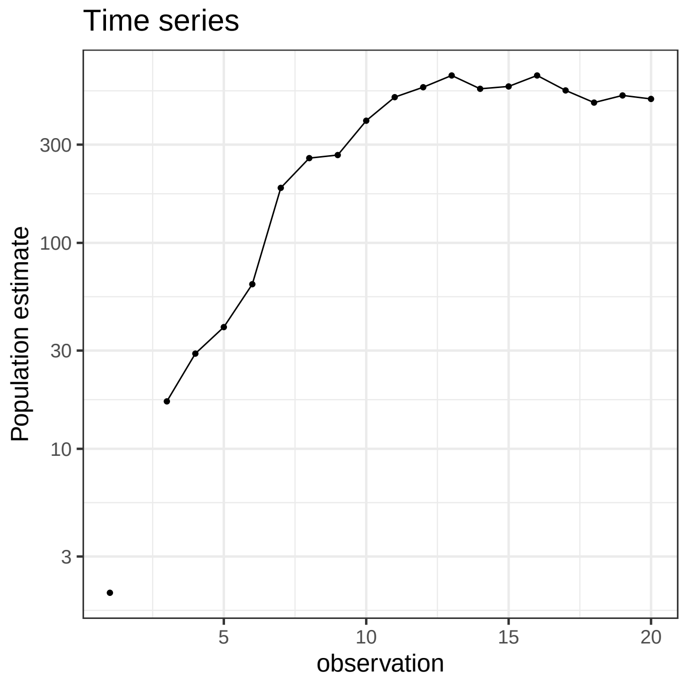
- Just like in the simple model, an equilibrium will have a characteristic time
- If I'm close to an equilibrium, how long would it take:
  - to go the distance to the equilibrium at my current "speed"
  - to actually get e times closer, or e times farther

Dynamics of density-dependent populations

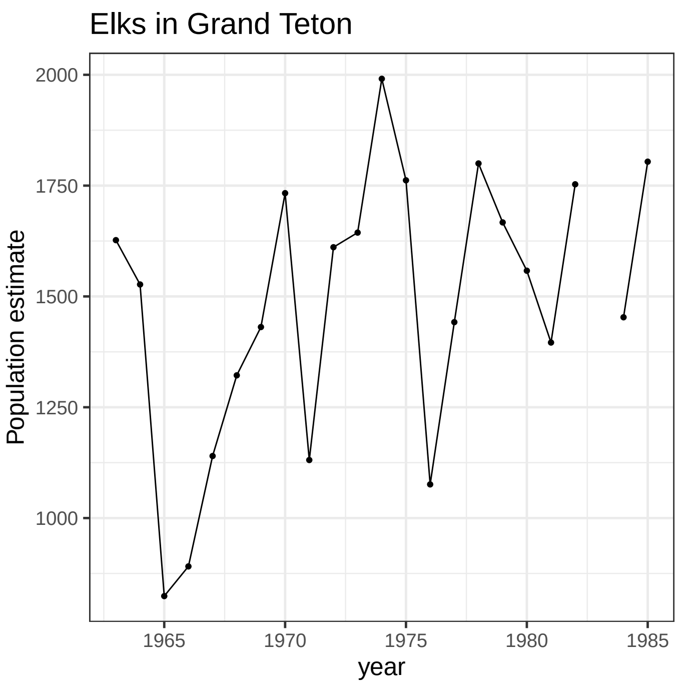
- Populations following this model change *smoothly*
  - Equations tell how the population will change at each instant
- They have no memory
  - Birth rate and death rate are determined by population size alone
- Cycling is impossible
  - **<u>Answer:</u>** If I went from A to B, I can't go from B to A by following the same rules

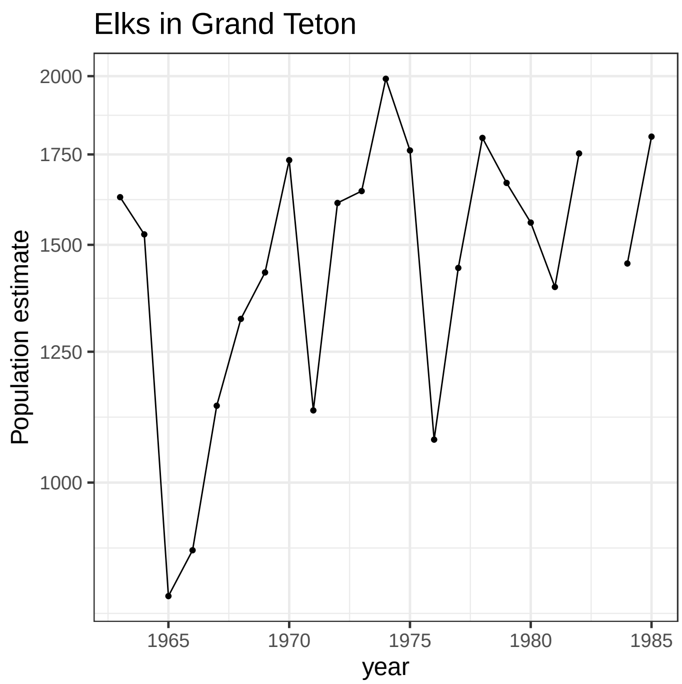
Paramecia





Elk





Dynamics of real-world populations

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe
  - Real populations are subject to **stochastic** (random) effects
  - Real populations are subject to changing conditions
- Some species seem to cycle predictably

Continuous-time regulation

- Continuous-time regulation in simple models makes useful predictions:
  - Threshold value for populations to survive
  - Greatest population-level growth at intermediate density
  - Greatest individual-level growth at low density
- Cannot explain complicated dynamics
  - More mechanisms are needed