UNIT 2 Non-linear population models

1 Introduction

- In linear population models, per capita rates are independent of population size
- Now we'll discuss why large and small populations might have different birth or death rates
  - and what this implies 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, liimiting 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.
- What is an example of a density-dependent mechanism that affects growth rate?
  -
    *
  -
    *
  -

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 food limitation at bad times (e.g., during regular droughts)

Regulation works over the long term

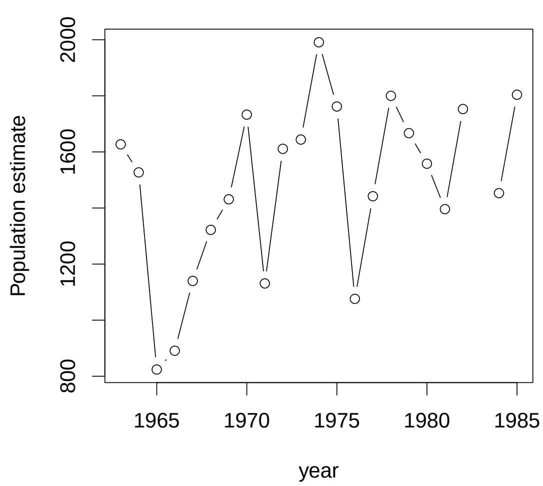
- Not every species is experiencing population regulation at every time
- A species that we see now may be expanding into a niche (e.g., because of climate change)
- Some species are controlled by big outbreaks of disease
- Some species have big outbreaks into marginal habitat, and spend most of their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

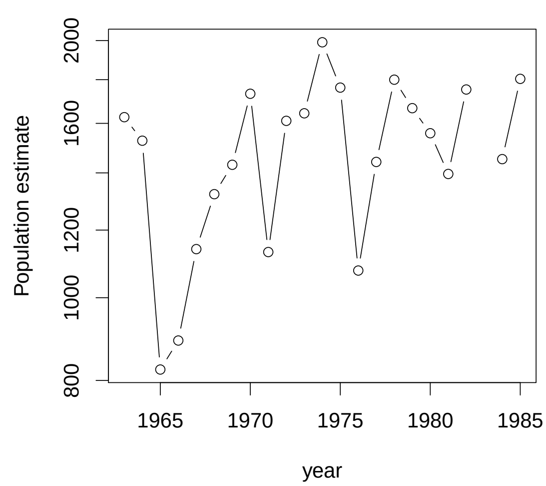
How do we know it's regulation?

- Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
  -
  -
  -
  -

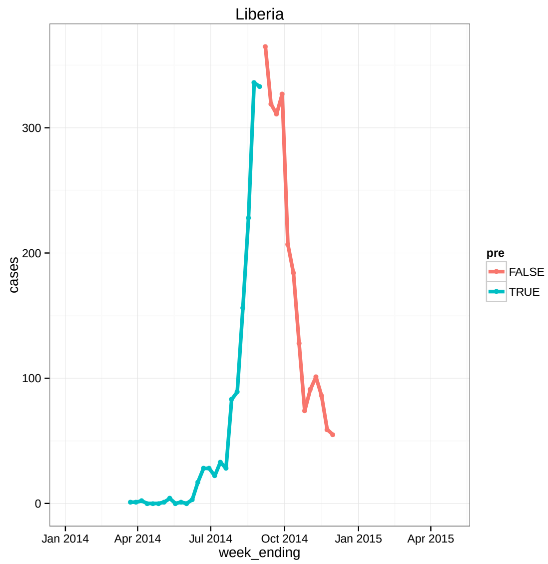
1.1 Population Examples

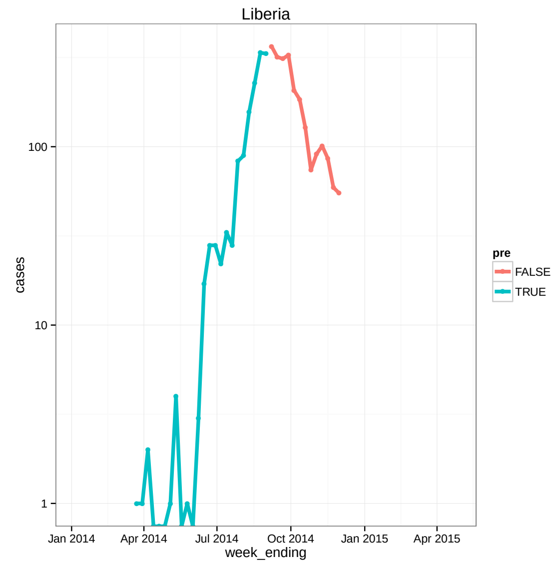
Elk



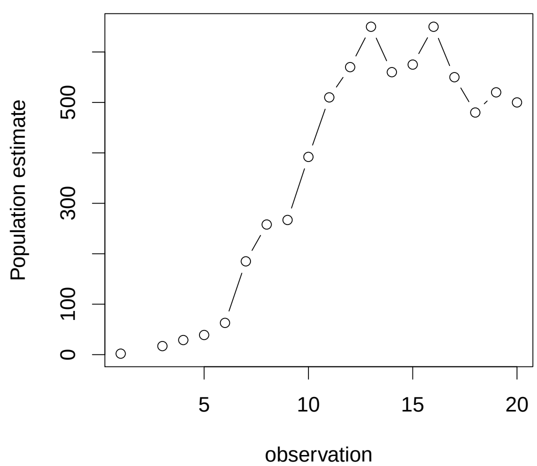


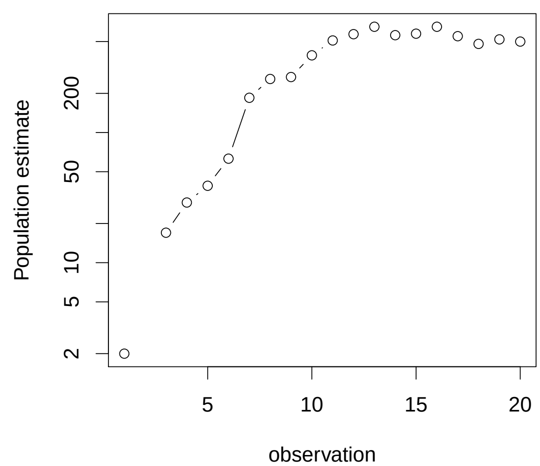
Ebola





Paramecia





Gypsy moths

- 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

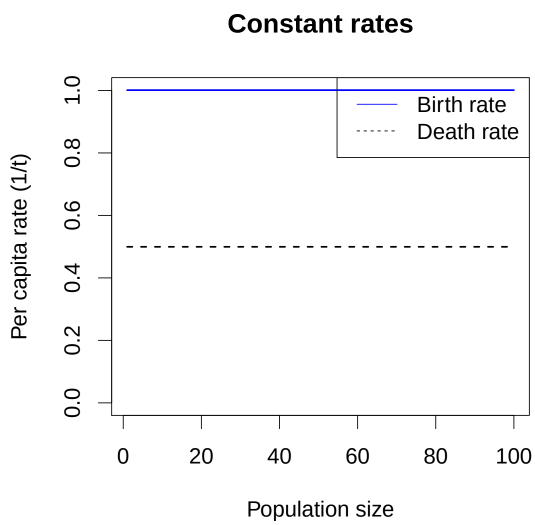
Build on the linear model

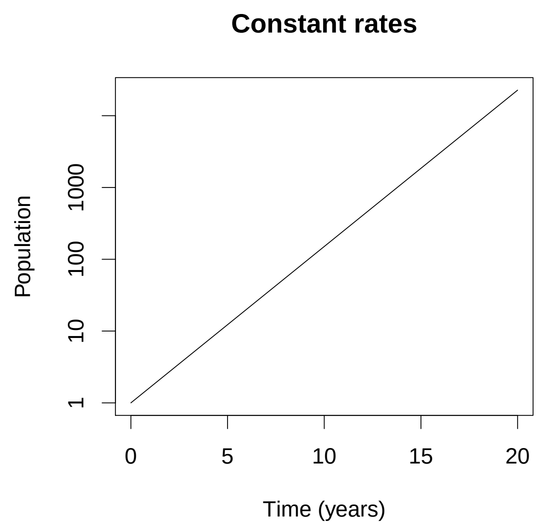
- Our linear population model is:

$$-\quad \frac{dN}{dt} = (b - d)N$$

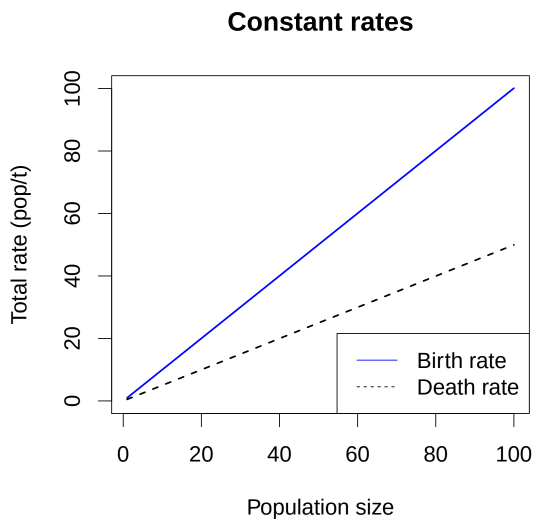
- Per-capita rates are constant
- **Population-level rates are linear**
- Behaviour is exponential

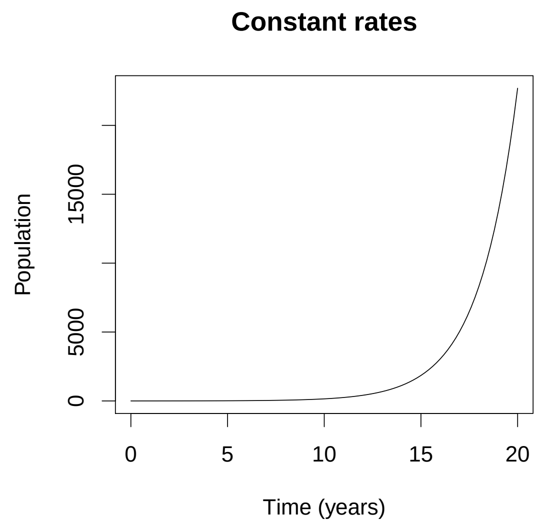
Individual perspective





Population perspective





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: $\dfrac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$
  - Defines how fast the population is changing at any instant

Recruitment

- **Recruitment** is when an organism moves from one life stage to another:
  - Seed →seedling →sapling →tree
  - Egg →larva →pupa →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:
  -
- 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 until it becomes crowded
- Then $\mathcal{R}$ will go down until $\mathcal{R} = 1$
  - Birth rate is equal to death rate
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying capacity**, K
  - $\mathcal{R}(K) \equiv 1$
  - $b(K) \equiv d(K)$

Logistic model

- A popular model of density-dependent growth is the logistic model
  - $r(N) = r_{\max}(1 - N/K)$
  - 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:
  - $b(N) = b_0 \exp(-N/N_b)$
  - $d(N) = d_0 \exp(-N/N_d)$
- N_b and N_d have the same units as N
- This is the simplest model that is perfectly smooth and keeps track of birth and death rates separately

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?
  -
  -

Parameters

- What quantities describe the rules for this system?
  -
  -
  -
  -

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)

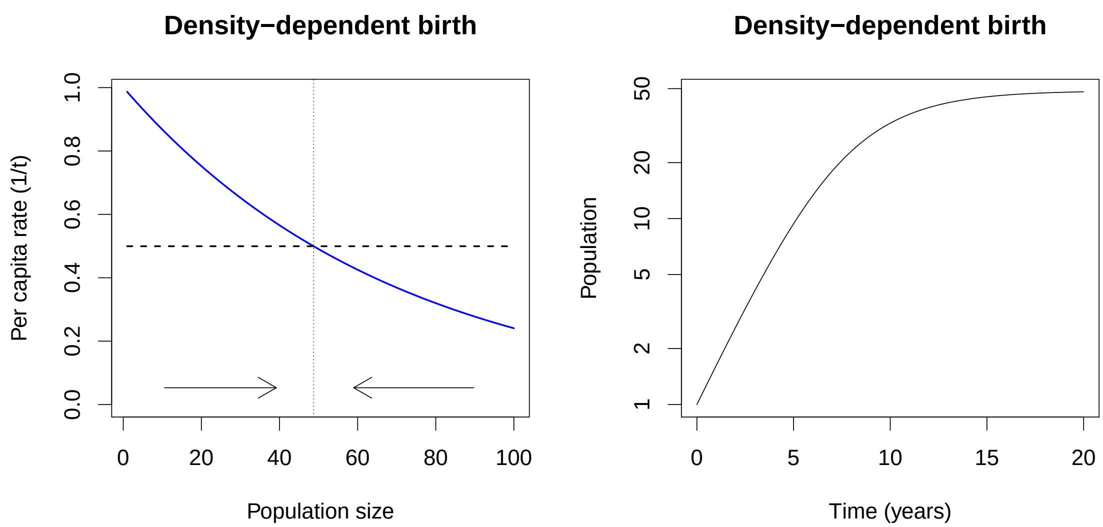
Model

- 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!

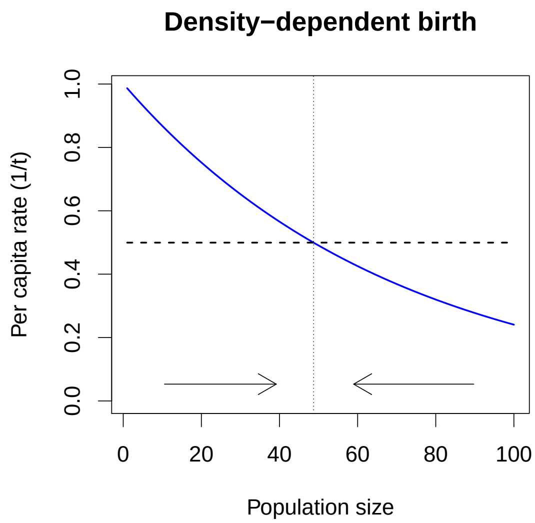
Dynamics

- 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?



High starting population



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

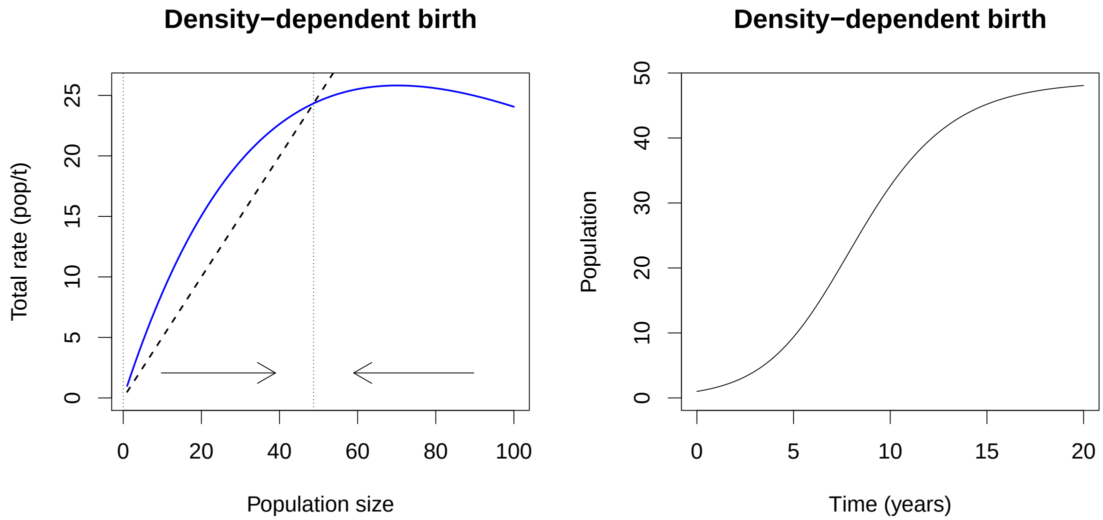
Individual-scale pictures

- 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



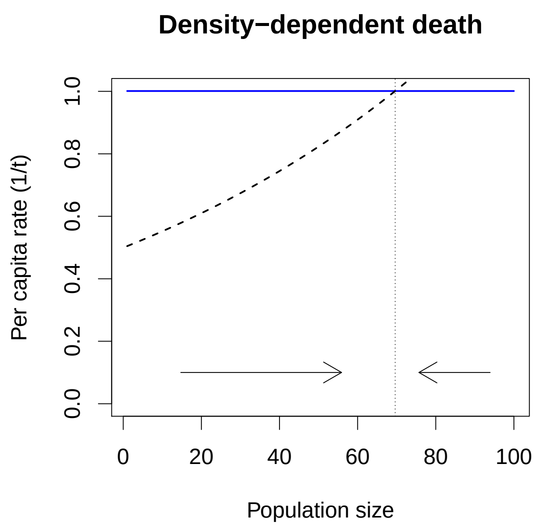
Decreasing birth rate

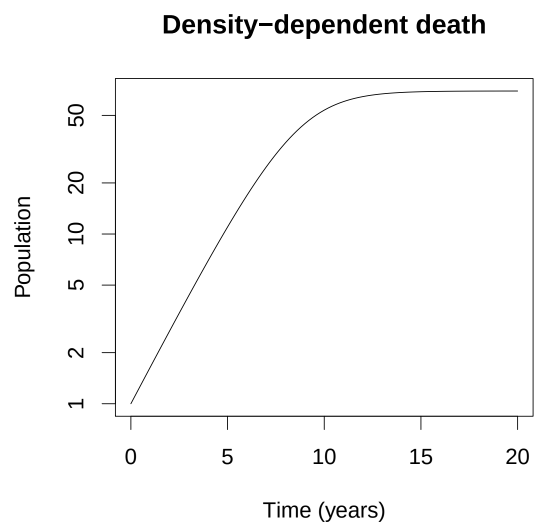
- Decreasing birth rate (above) might be a good model for organisms that experience density dependence primarily in the recruitment stage
- For example, we might count adult trees, and these might not die more at high density – just fail to recruit younger ones

Increasing death rate

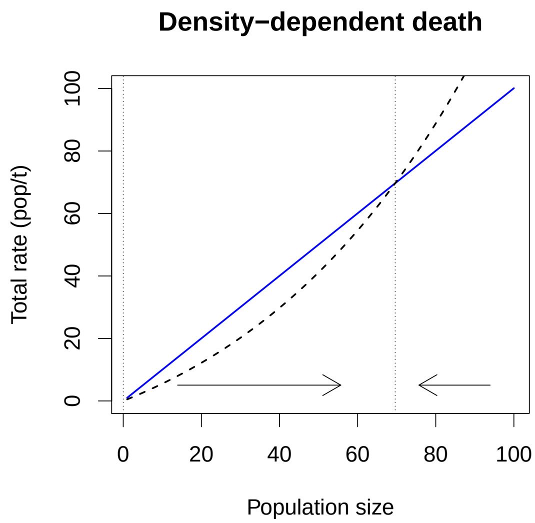
- Increasing death rate might be a good model for organisms that experience density dependence primarily as adults
- For example, in some environments, mussel density might be limited by adult crowding. Although juvenile mussels tend to have a hard time, this might not be density dependent

Individual perspective





Population perspective



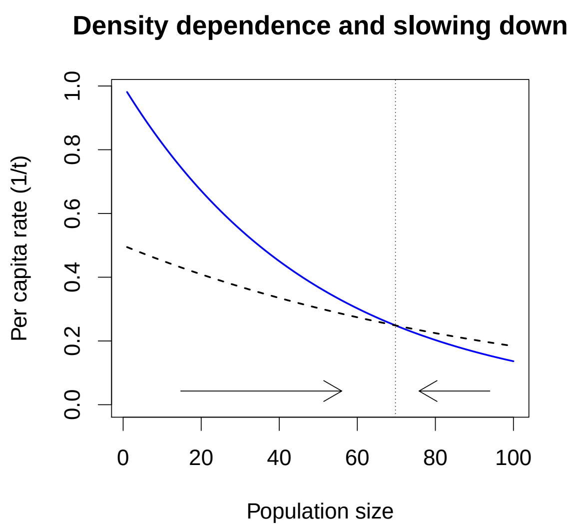
Decreasing death rate

- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate *decreases*

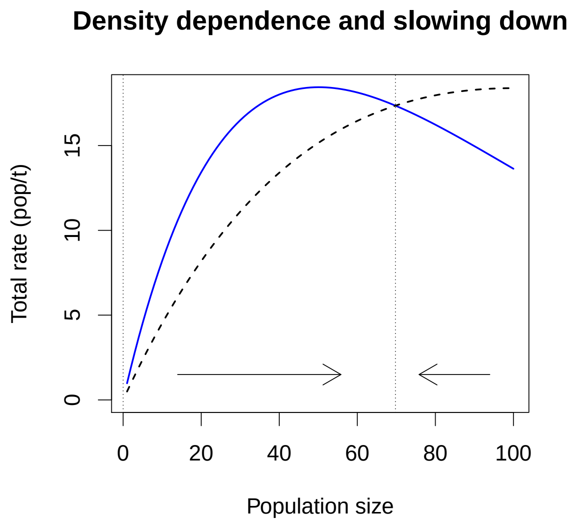
- How is this consistent with density dependence?

  –

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?
  -
- When does a population in this model have the fastest *total* growth rate?
  -

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?
  -
  -

Stable and unstable equilibria

- If we are at an equilibrium we expect to stay there
  - At least in our simplified model
- 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:
    *
  - If population is just above the equilibrium:
    *

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:
  -

- When $\mathcal{R}_0 > 1$ the population:
  -
- What is $\mathcal{R}_0$ in our current model?
  -

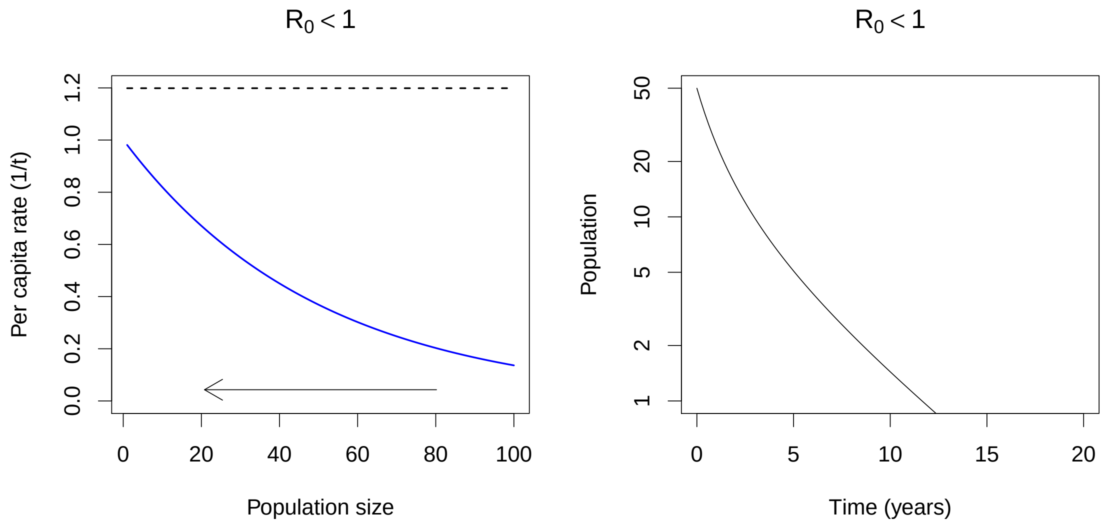
Invasion

- 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 $\mathcal{R}_0 > 1$

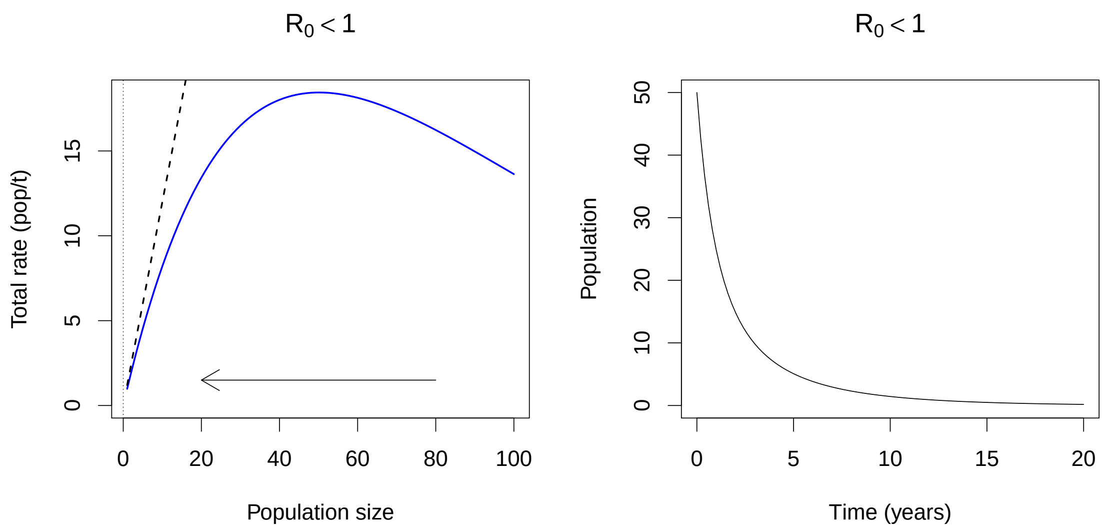
Different behaviours

- 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



Population perspective



$\mathcal{R}_0$ 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

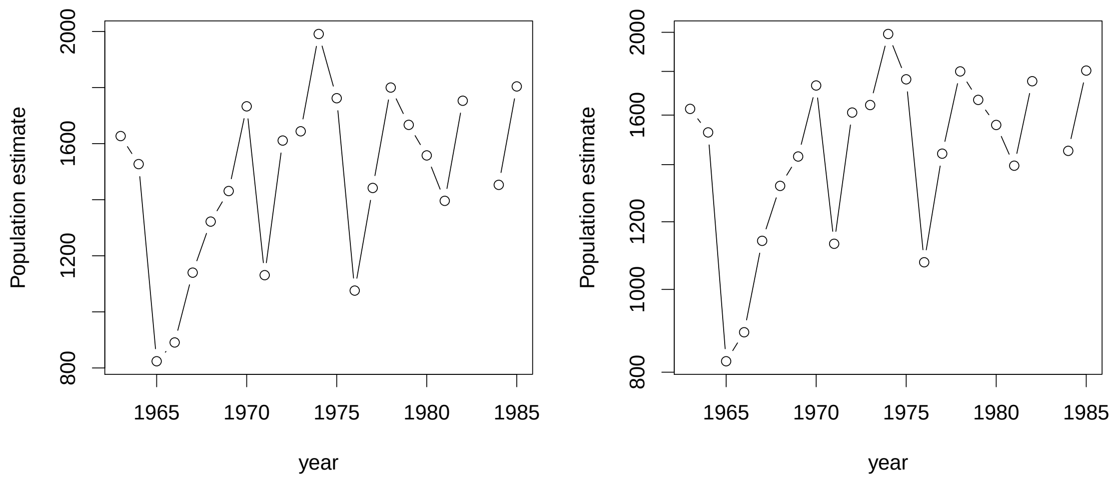
Characteristic times

- 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

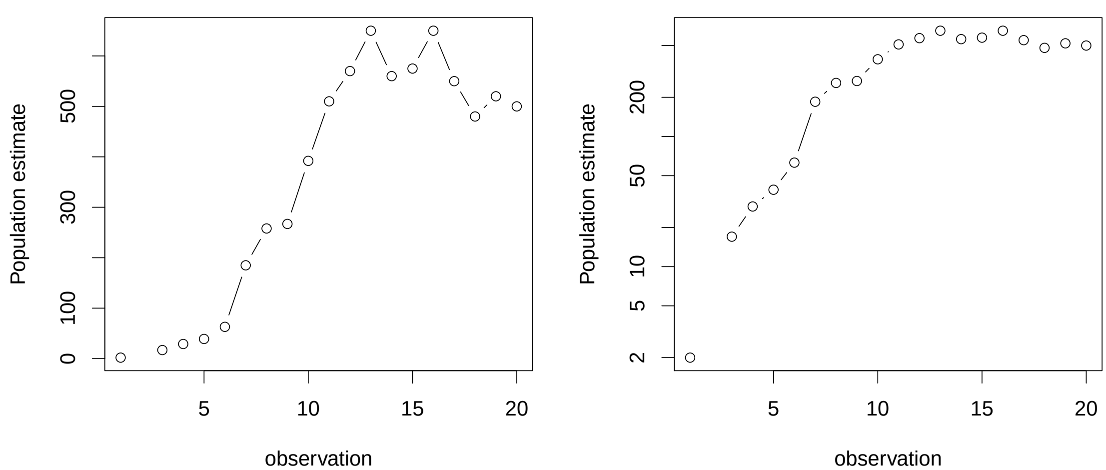
Dynamics of density-dependent populations

- 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
  -

Elk



Paramecia



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

3 Delayed regulation

- One mechanism for population cycles might be if regulation is *delayed* in time
  - It takes time for individuals to complete their life cycle
    - Recall that the life cycle is implicit in our simple models
  - It takes time for the population to damage its resources or build up natural enemies

Time-delayed continuous models

- How would change a simple continuous-time model into a (relatively) simple time-delayed model?
- Original model: $\frac{dN}{dt} = (b(N) - d(N))N$
- Be explicit about time: $\frac{dN(t)}{dt} = (b(N(t)) - d(N(t)))N(t)$
- Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
  -
  -
  -

Our model

- $\dfrac{dN(t)}{dt} = (b(N(t-\tau)) - d(N(t-\tau)))N(t)$

- For simplicity, we assume that both rates are delayed by the same amount of time

- More realistic models might have different delays

  - or delay in only one quantity

  - or *distributed* delays, so that the rate is some kind of average

Model dynamics

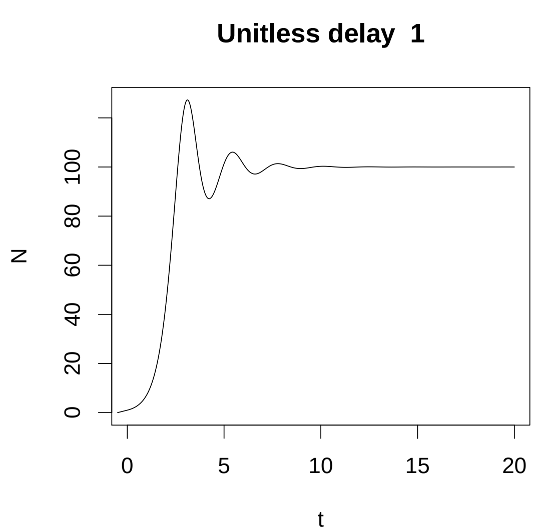
- If a population is growing, what will happen as it approaches the equilibrium?

  -

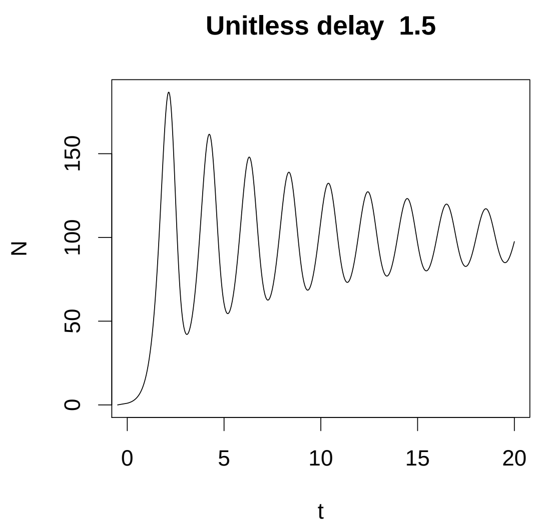
  -

- So what happens in the long term?

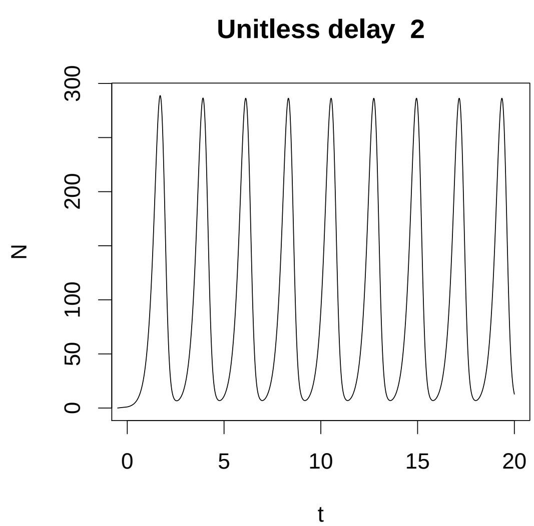
Time-delayed dynamics



Time-delayed dynamics



Time-delayed dynamics



Time-delayed population models

- Delayed population models show:
  - **Damped** oscillations (growing smaller and smaller) for shorter delays

    * These could be so small that you wouldn't expect to notice them
  - **Persistent** oscillations for longer delays

Time scales

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- Long compared to what?
  -
  -
  -

Unitless quantities

- The behaviour of any particular delay system is determined by one or more unitless quantities
- Our simple model is controlled by the ratio τ/t_c, where t_c is the characteristic time of approach to the carrying capacity in the absence of delay
- In fact, cycles are persistent when $\tau/t_c > \pi/2$!

Time-delayed regulation

- Time-delayed regulation produces simple cycles
  - Damped when delay is short ...
  - Persistent when delay is long ...
- ... compared to characteristic time of approach to equilibrium

4 Discrete-time regulation

4.1 A simple, discrete-time model

- We extend our discrete-time model from the previous unit:
  - $N_{T+1} = (p + f)N_T \equiv \lambda N_T$
  - $t_{T+1} = t_T + \Delta t$ (does not change)
- To:
  - $N_{T+1} = (p(N) + f(N))N_T \equiv \lambda(N)N_T$

Assumptions

- The population is censused at regular time intervals Δt
- All individuals are the same at the time of census
- Population changes deterministically

Specific assumptions

- For our examples, we will assume:
  - $f(N) = f_0 \exp(-N/N_f)$
  - $p(N) = p_0 \exp(-N/N_p)$
- Good for organisms where competition is mostly felt by the young
- As in the continuous case, other formulations will give similar results

States and state variables

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

Parameters

- What quantities describe the rules for this system?
  -
  -
  -
  -

What is $\mathcal{R}_0$?

- $\mathcal{R}$ is the fecundity multiplied by the lifespan
  -
  -
- $\mathcal{R}_0$ is $\mathcal{R}$ in the limit where density is low
  -

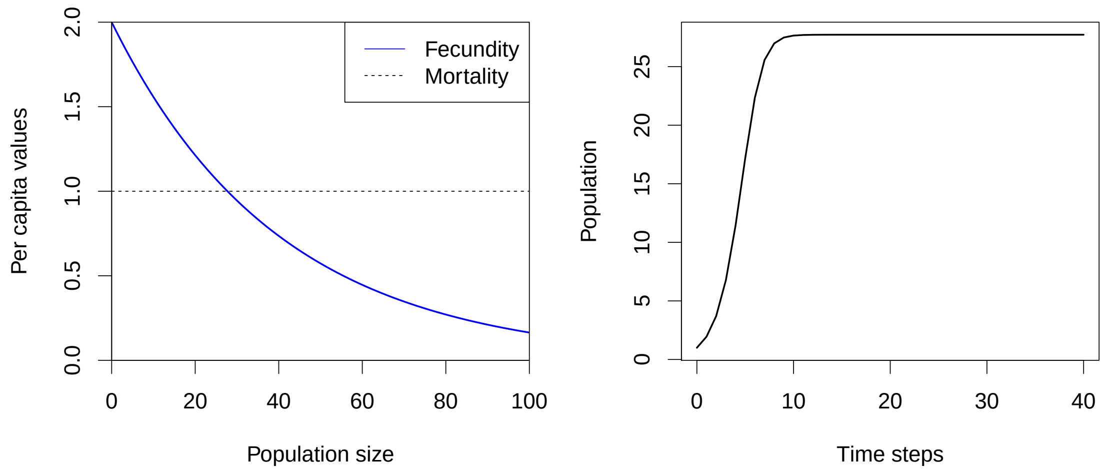
Behaviours

- When $\mathcal{R}_0 < 1$ population always declines
- When $\mathcal{R}_0 > 1$, population can show:
  - Smooth behaviour (like the continuous-time model)
  - Damped oscillations (like the delayed model)
  - Two-year cycles (high $\rightarrow$low $\rightarrow$high $\rightarrow$low)
  - All kinds of other stuff

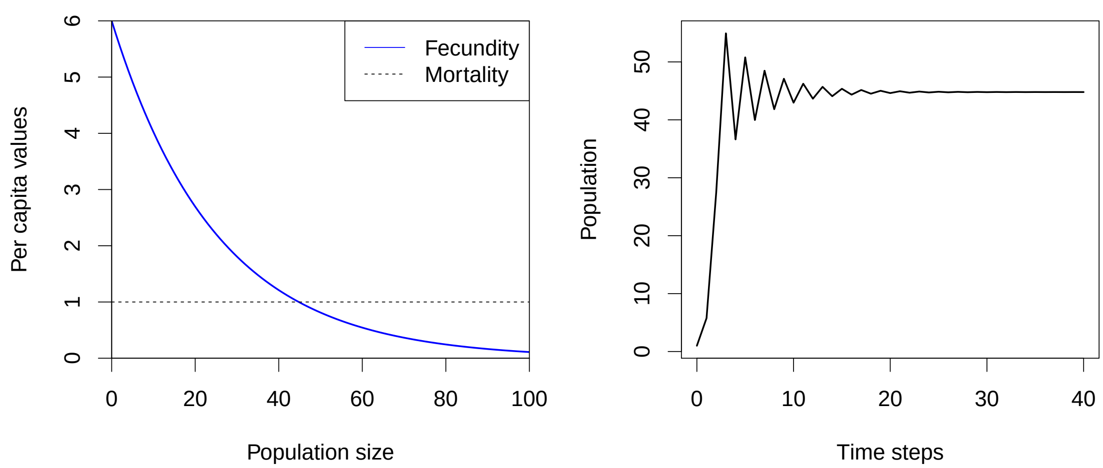
4.2 Simulating this system

- This system can be simulated very easily by following the rule for N_{T+1} as a function of N_T
- We can even do it in the spreadsheet if we have time

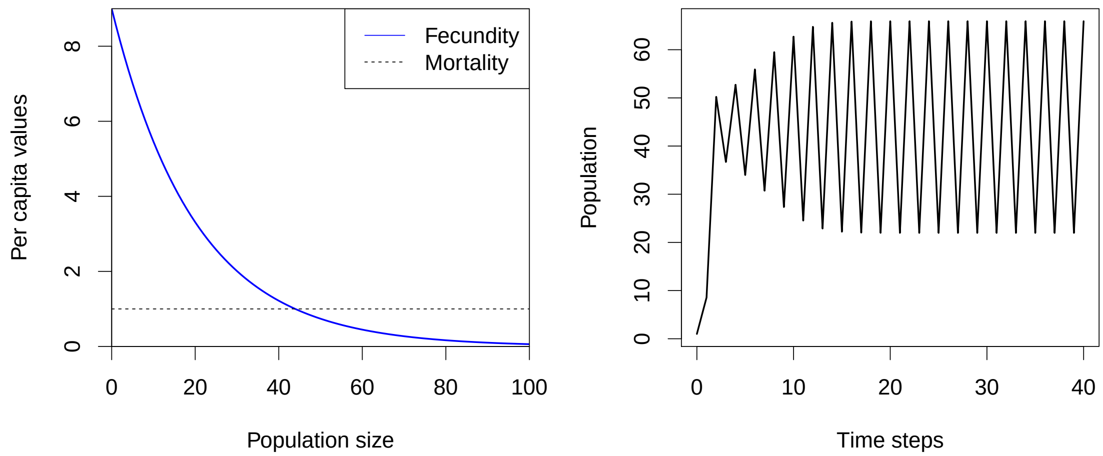
We expect simple dynamics



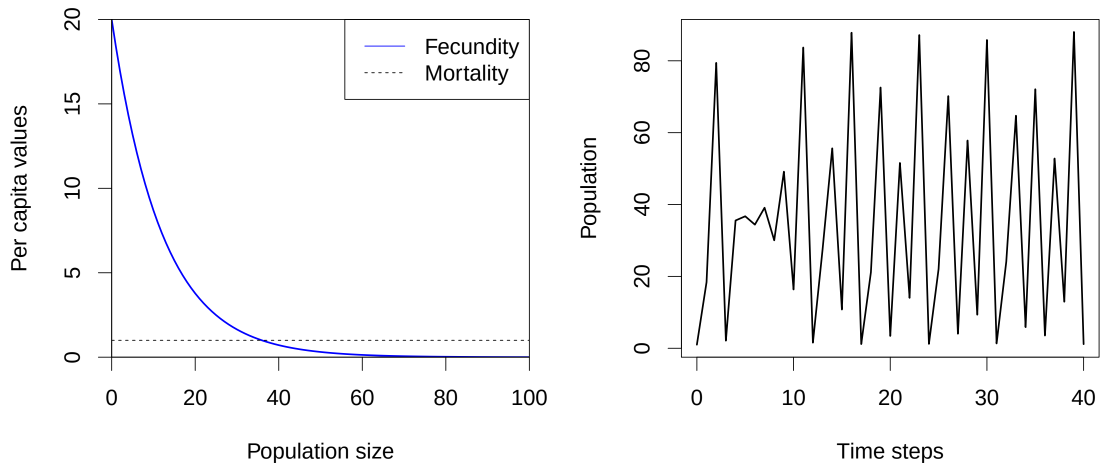
Damped oscillations



Persistent oscillations



Lots of other behaviours



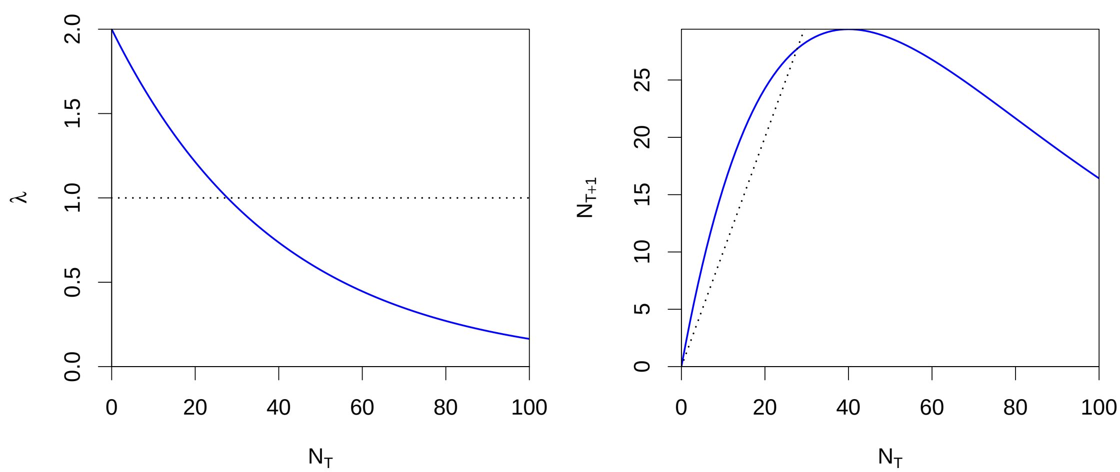
4.3 Interpreting complex behaviour

- In a simple cycle:
  - Low populations this year mean high populations next year
  - and vice versa

Complex behaviour in our simulations

- In our simple models, as N_T increases, what happens to λ?
  -
- In our simple models, as N_T increases, what happens to next year's population?
  -
  -
  -

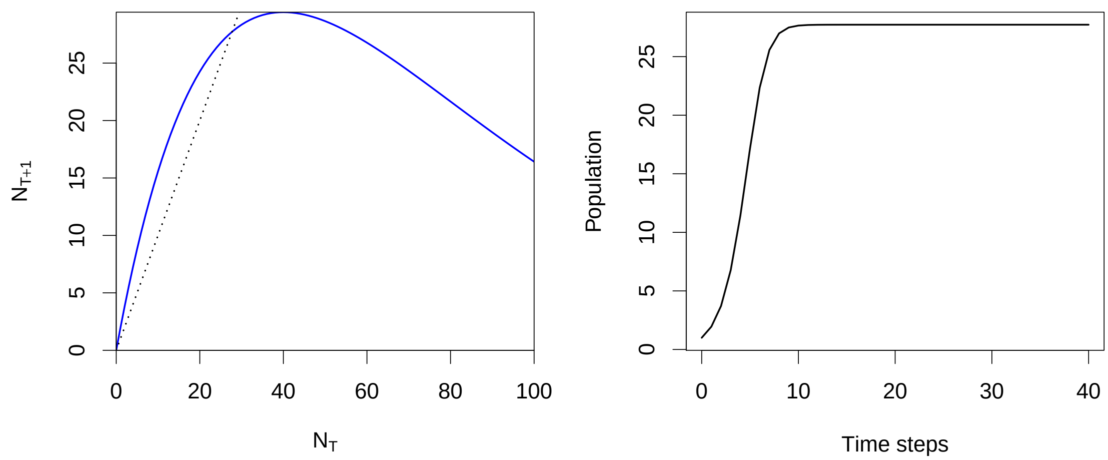
Response to population increase



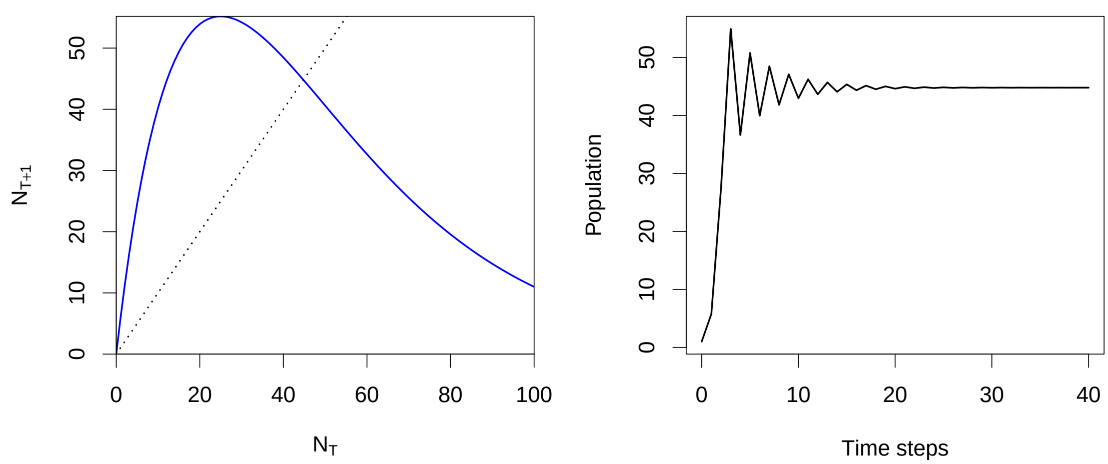
Turnover

- When N_T is small, N_{T+1} increases with N.
- Complex behaviour arises when the relationship between N_T and N_{T+1} **turns over** below the equilibrium value
  - A small population this year leads to a large population next year

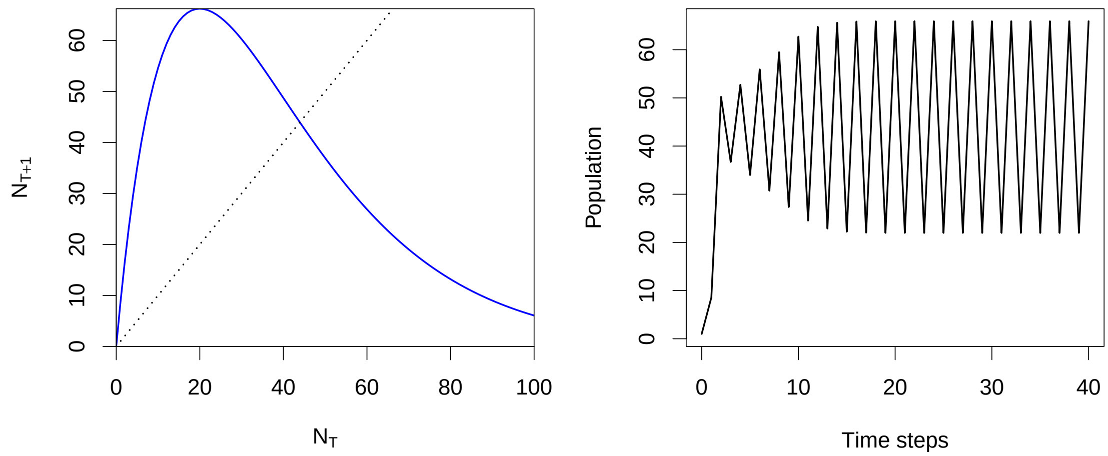
Simple dynamics



Damped oscillations



Persistent oscillations



Complex behaviour in our conceptual model

- Biologically, when might we expect N_{T+1} to "turn over"?
  -
  -
- When should the mapping *not* turn over?
  -
  -
  -

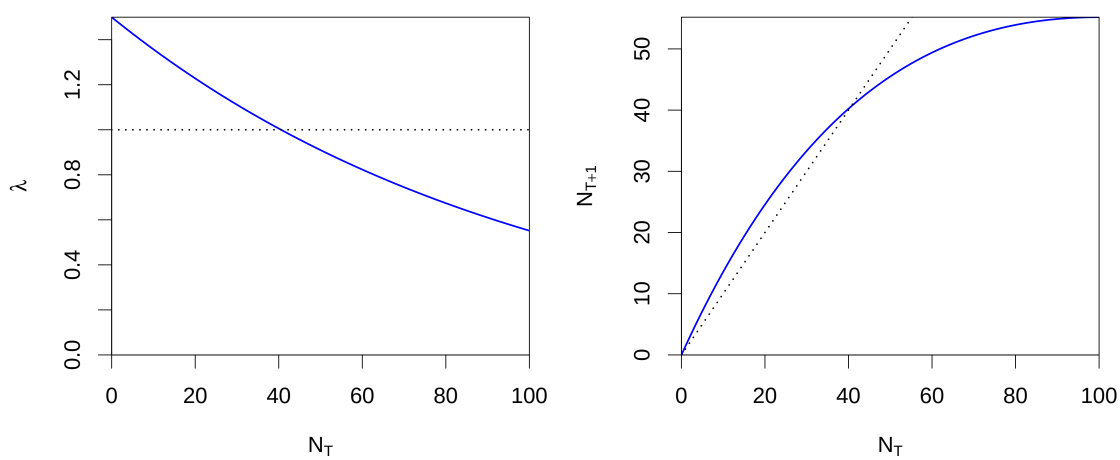
Scramble competition

- **Scramble** competition refers to the case where all individuals in a crowded population are gathering resources at similar rates: as the density goes up there is less resource for everyone, and everyone does less well
  - If there is any kind of delay, scramble competition can lead to turning over

Contest competition

- **Contest** competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
  - Contest competition doesn't usually lead to turning over, even with delay
- How does contest competition square with regulation?
  -

Contest regulation



Songbirds

- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
  -

Plants

- Some plant populations are limited by water, and some by light
- Which is more likely to work out as a scramble?
  -
  -

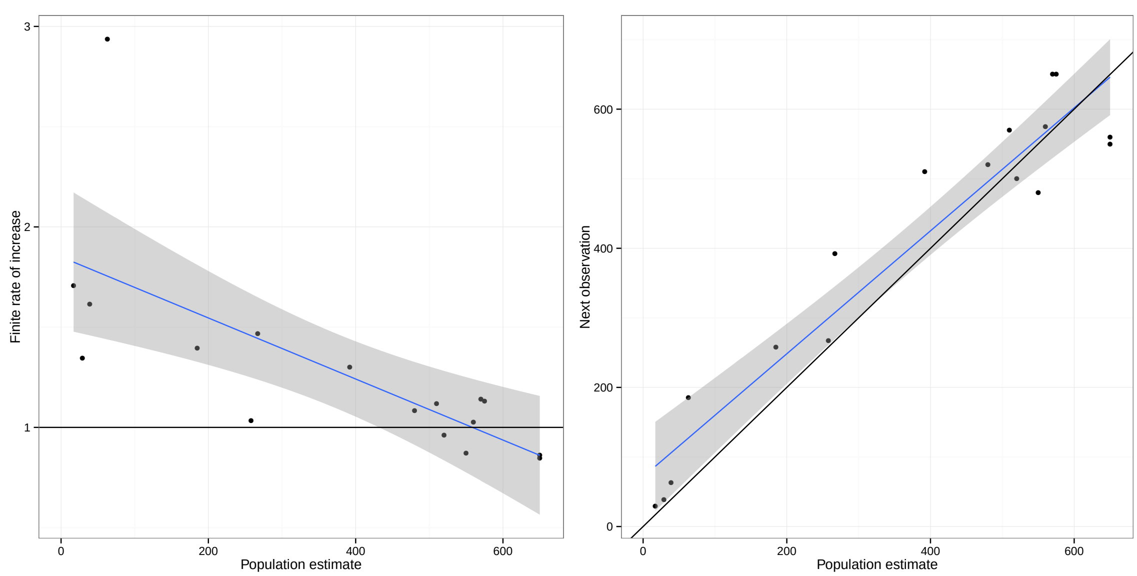
Complex behaviour from a simple model

- It's interesting that we can get complicated behaviour from such a dead-simple model
- Complex dynamics may have simple causes
- People always tend to look for specific reasons, but sometimes the changes we observe are just natural dynamics

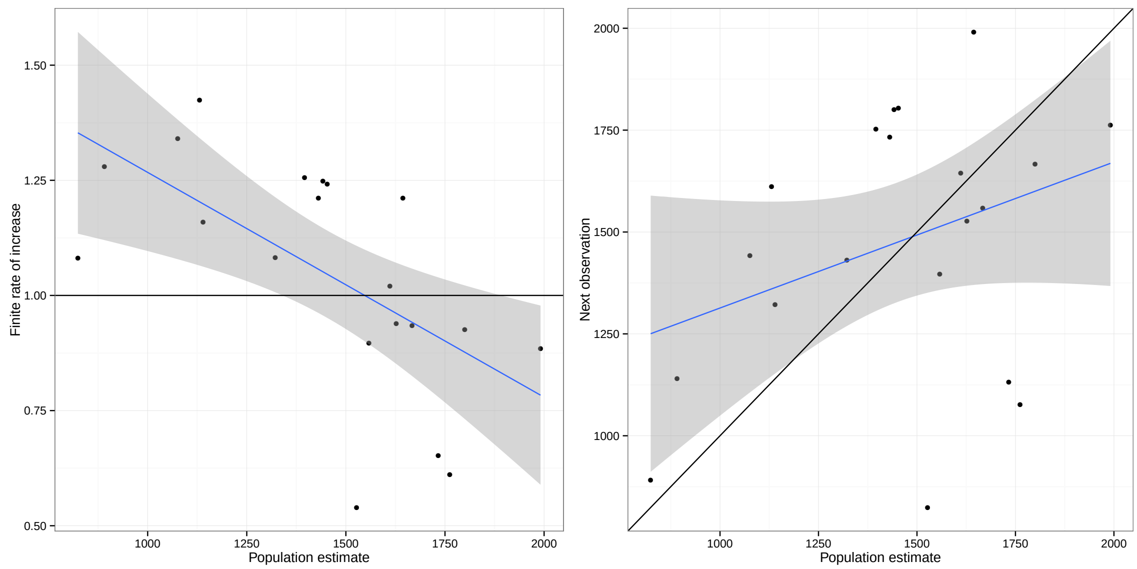
Complex behaviour in real populations

- We can plot λ and N_{T+1} vs. N for real population data
- We expect λ to decrease (on average)
- We're curious about N_{T+1}.

Paramecia



Elk



Real populations

- It's hard to find examples of turnover from real population data.
- So how do we explain real population cycles?
  - Regulation may happen on a longer time scale
  - May be hard to see because of "noise" – i.e., other sources of variation
  - Cycles may be due to more complicated mechanisms

5 Small populations and stochasticity

Example

- What would happen if I released one butterfly into a new, highly suitable habitat?
  -
- What about two butterflies?
  -

Small populations

- Population success (reproductive number) may be lower for very small populations
  - We've already assumed reproductive numbers are low for very large populations
- Small populations are likely to be harder to predict
  - More affected by stochasticity

5.1 Allee effects

- Effects which cause small populations to have low per-capita growth rates are called Allee effects
  - Equivalent to saying that medium-sized populations have larger per-capita growth rates than small ones
- Why might growth rates be low when populations are small?
  -
  -
  -
  -

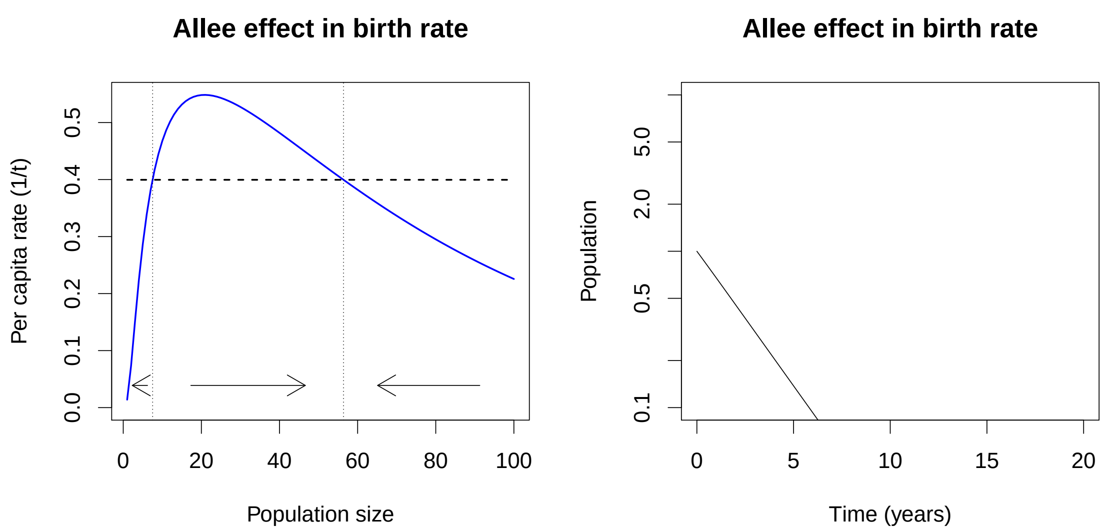
Types of Allee effect

- Allee effects can affect the birth rate
  –
- ... or the death rate
  –

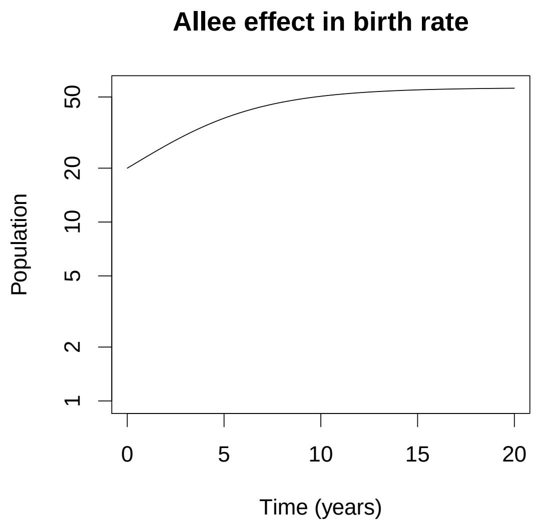
Allee effect models

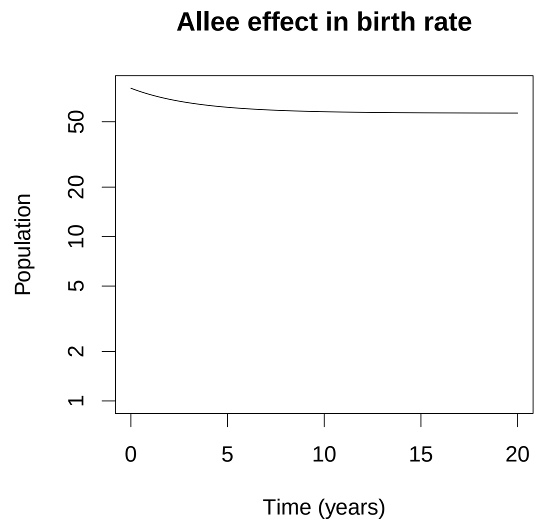
- What will this model do, if the initial population is:
  - low, medium or high?

Individual perspective

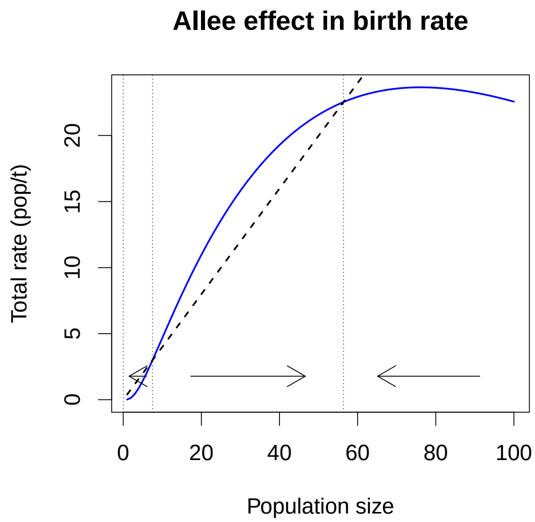


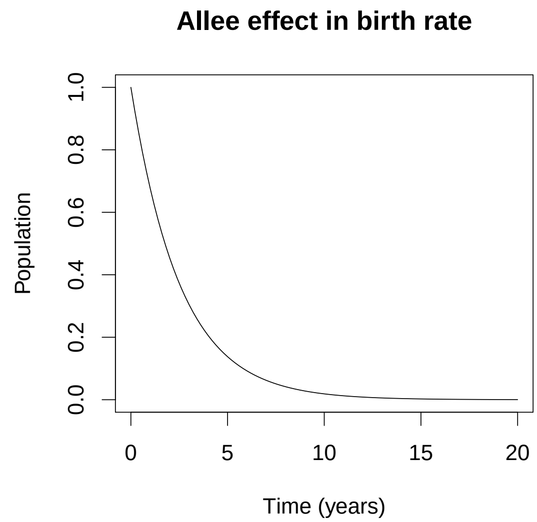
Individual perspective



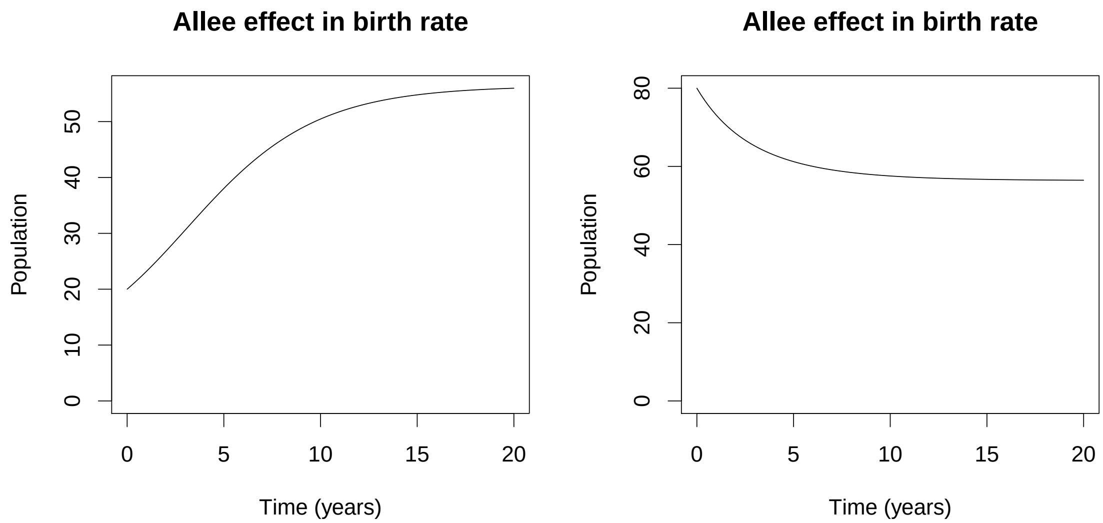


Population perspective





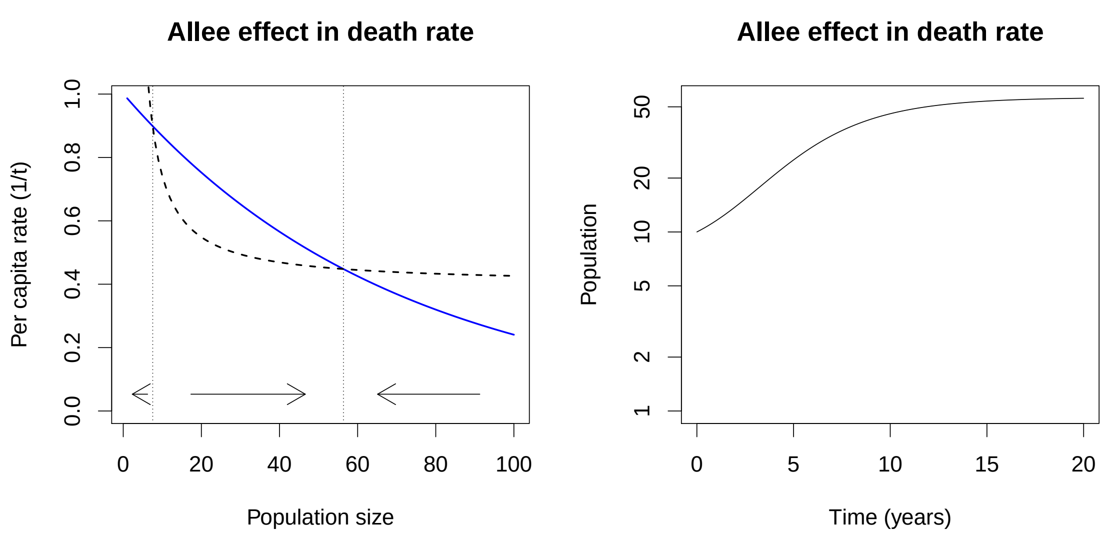
Population perspective



Allee effect in death rate

- What is the difference between this example and the previous one?
- What will this model do, if the initial population is:
  - low, medium or high?

Individual perspective



More reproductive numbers

- The reproductive number $\mathcal{R}$ means the average lifetime number of offspring per individual
  - Should be unitless, so we consider offspring at the same stage as the individual.
- We can apply $\mathcal{R}$ in general for any set of conditions, or we can distinguish:
  - the **basic reproductive number** $\mathcal{R}_0$: $\mathcal{R}$ in the limit when the population is small, and
  - the **maximal reproductive number** $\mathcal{R}_{\mathbf{max}}$: $\mathcal{R}$ at whatever level is the peak

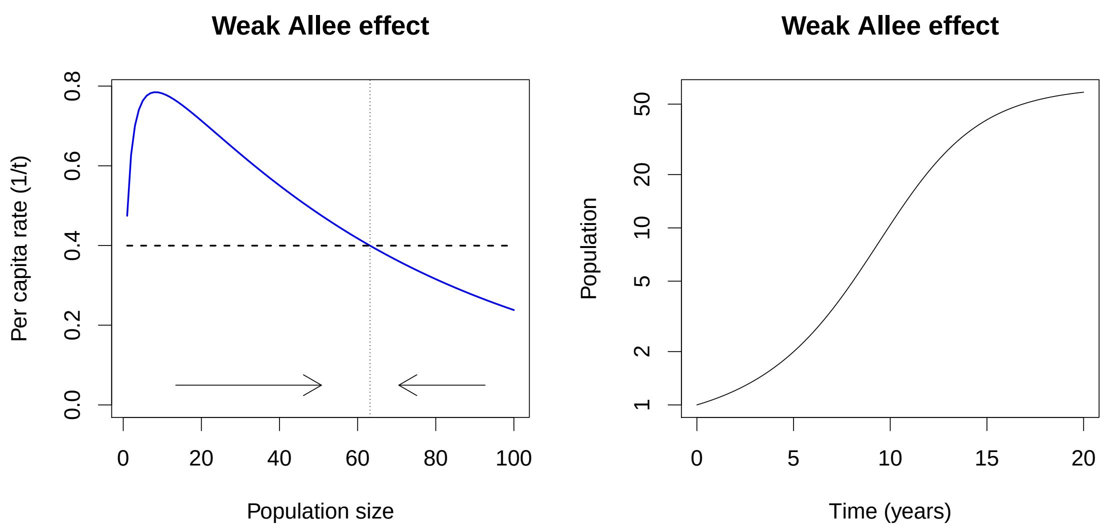
Invasion

- We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct
  - A population that can't invade can never replace itself on average
- When Allee effects are present, it's no longer true that a species that can't invade can't persist
  -

Weak Allee effects

- If birth rates go down or death rates go up at low density, we consider this an Allee effect
- This doesn't always mean $Ro < 1$

Individual perspective



Allee effect summary

- Population may go extinct if it drops below a certain threshold
- How come the population is there in the first place if there's an Allee effect?
  -
  -
  -

5.2 Stochastic effects

- The world is complicated and biological populations are not perfectly predictable
- Real populations don't go smoothly to equilibria, instead they bounce around (or sometimes do other wild stuff)
- We divide stochastic (or random) effects into demographic and environmental stochasticity

Example

- Female butterflies of a certain species lay 200 eggs on average, of which:
  - Half are female
  - 50% hatch successfully into larvae
  - 10% of larvae successfully pupate
  - 60% of pupae become adults
  - Half of adult females successfully reproduce
- A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?
  -
  -

Butterfly example

- Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the *probabilities*, that would not guarantee an exact result
  -
- What if $\lambda < 1$?
  -

Demographic stochasticity

- **Demographic** stochasticity is stochasticity that operates at the level of individuals
  - Individuals don't increase gradually, they die or give birth
  - Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 . . .

- Even if we control conditions perfectly, we can't exactly predict the dynamics of small populations
- Demographic stochasticity averages out in large populations

Environmental stochasticity

- **Environmental** stochasticity is stochasticity that operates at the level of the population
  - E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
  -
- But small populations are the ones in danger of going extinct
  -
  -

Simulations

- We can simulate stochastic systems very easily
- But if we do the same simulation twice, we can get different answers
- Realistic, but not always easy to interpret

Summary

- Stochasticity is very important in real populations, but hard to study
  - Mathematical analysis is very difficult
  - Simulations are useful, but hard to interpret
    - Each time you simulate, you get a different answer
- Ecologists need to learn to recognize and communicate our uncertainty about the future