

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, 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.
- What is an example of a density-dependent mechanism that affects growth rate?

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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?

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

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1.1 Population Examples

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

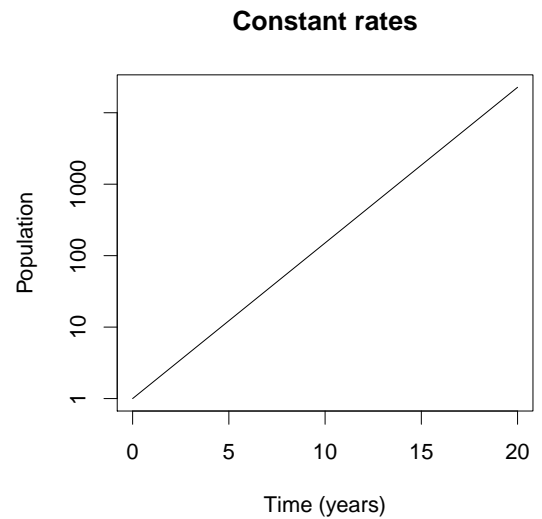
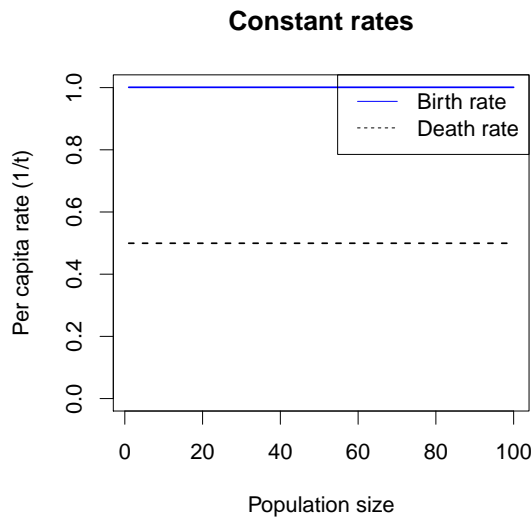
Build on the linear model

- Our linear population model is:

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

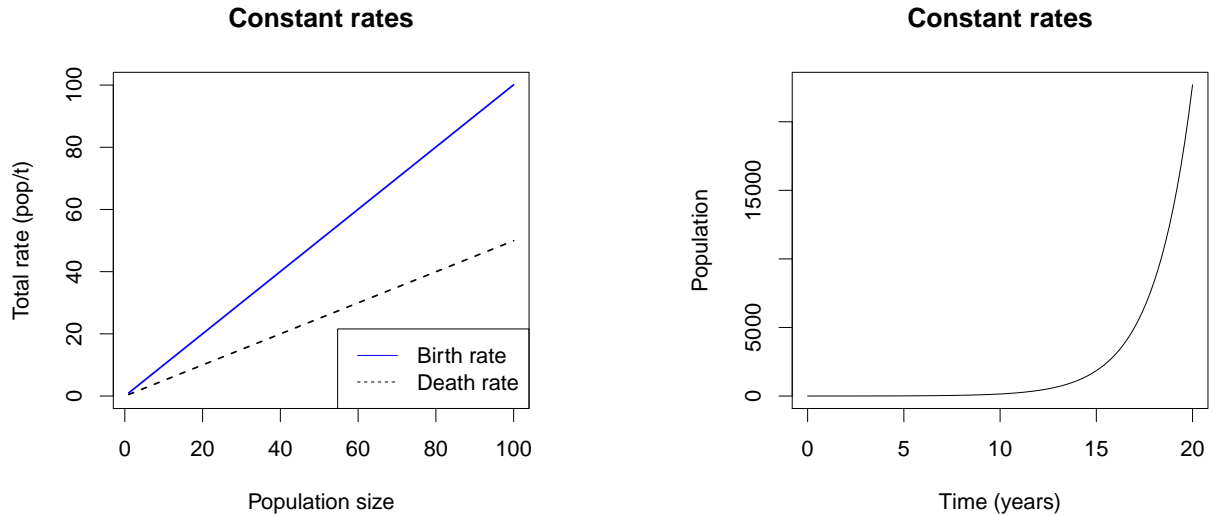
- Per-capita rates are constant
- **Population-level rates are linear**
- Behaviour is exponential

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 :
 -
- 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
- 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 remains 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 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?

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Parameters

- What quantities describe the rules for this system?

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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!

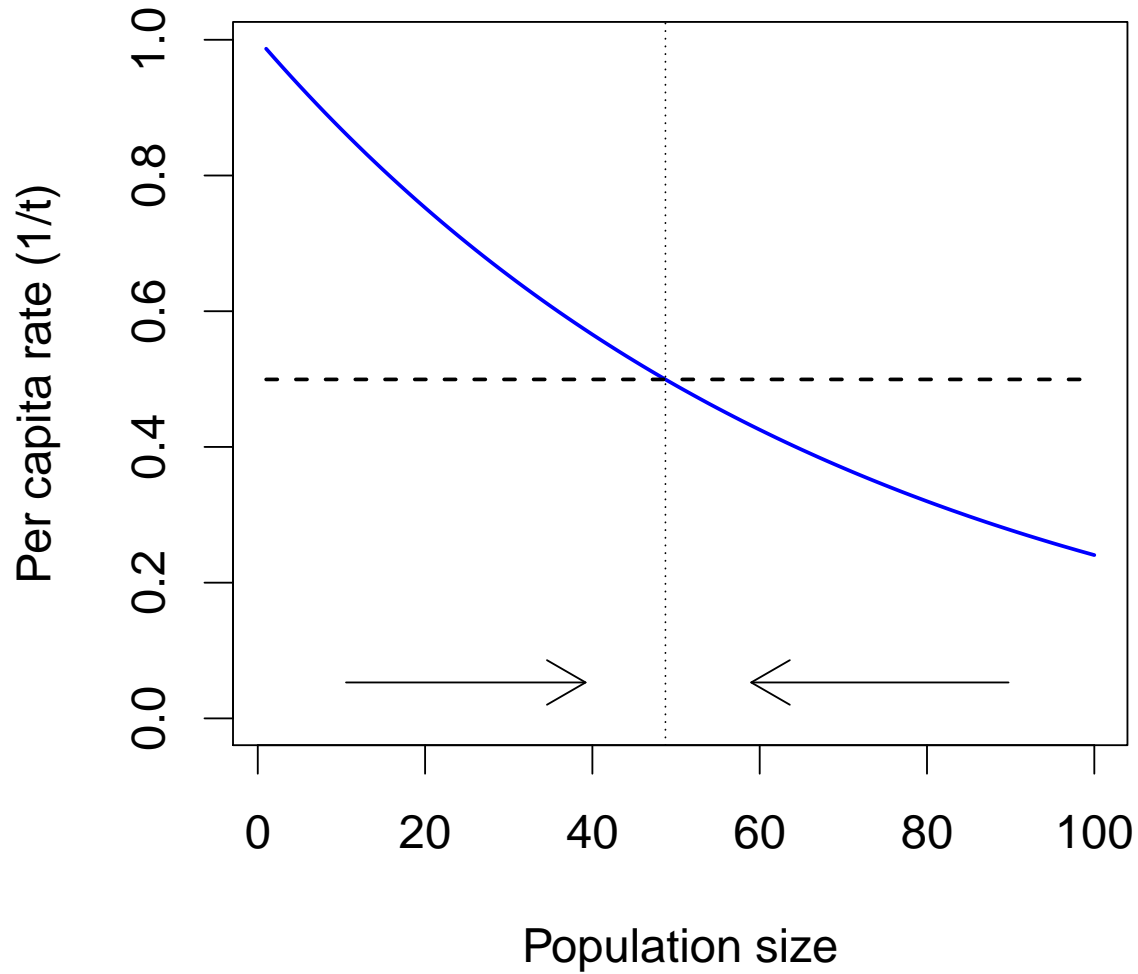
Dynamics

- 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?

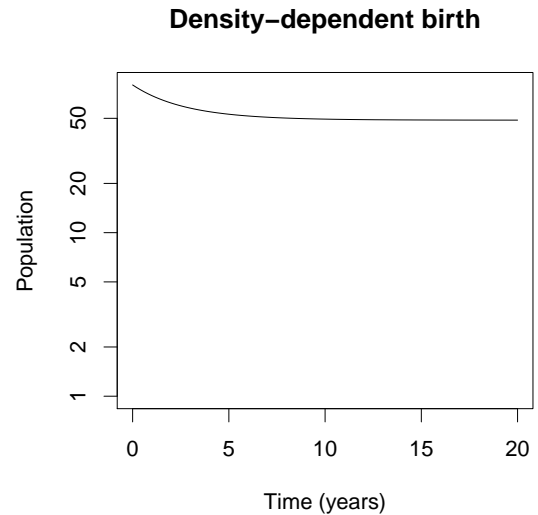
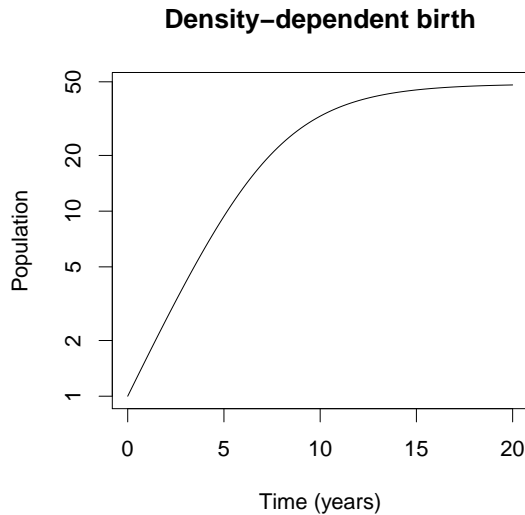
Density-dependent birth



- 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

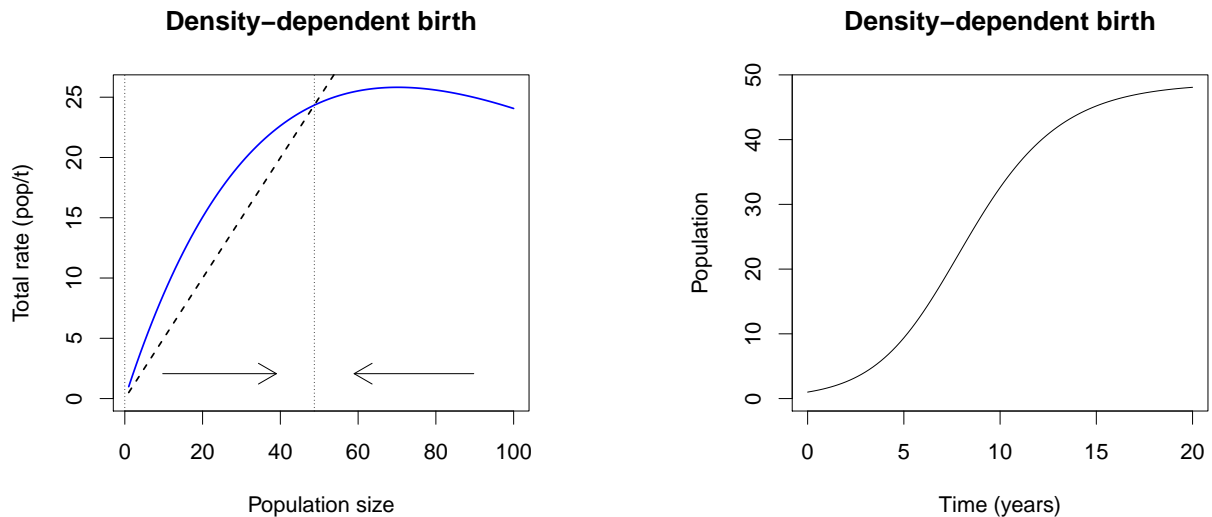
Individual-scale pictures

- We can view graphs of our population assumptions on the individual scale
 - per-capita birth and death rates
 - * units $[1/\text{time}]$
 - 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 $[\text{indiv}/\text{time}]$
 - * or $[\text{density}/\text{time}] = [(\text{indiv}/\text{area})/\text{time}]$
 - what is changing at the population level?
 - corresponds to the dynamics we visualize on a linear-scale graph of the population

Population perspective picture



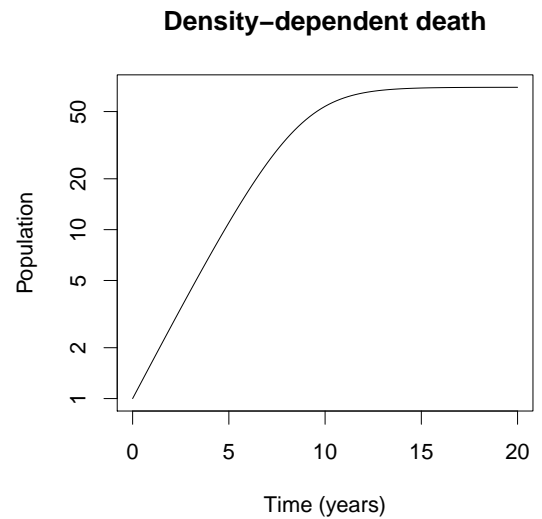
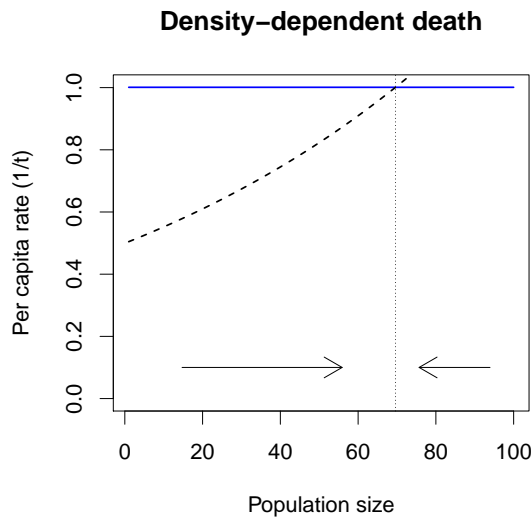
Decreasing birth rate

- 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

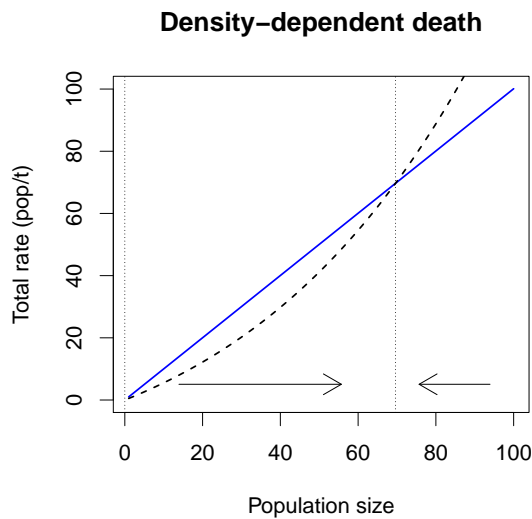
Increasing death rate

- 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

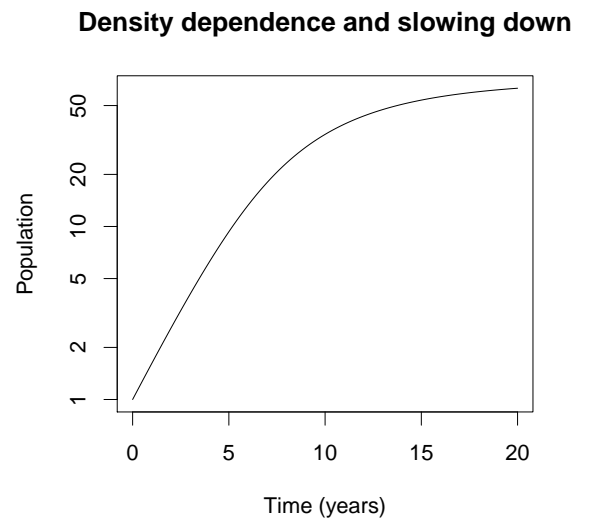
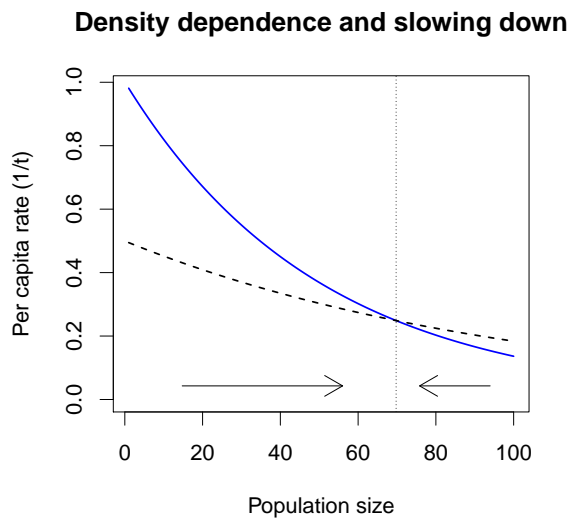
- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate

decreases

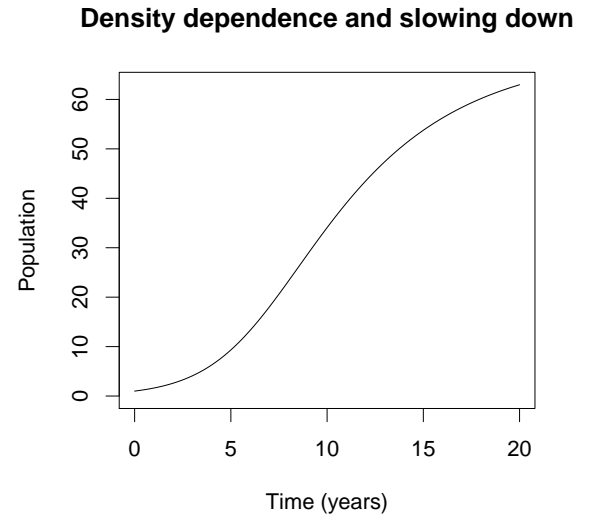
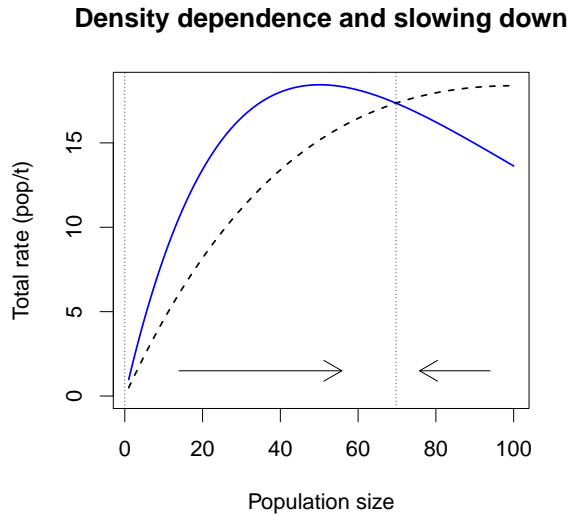
- How is this consistent with density dependence?

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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?

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- 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?
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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:
 - *
 - 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:
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- When $\mathcal{R}_0 > 1$ the population:

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- What is \mathcal{R}_0 in our current model?
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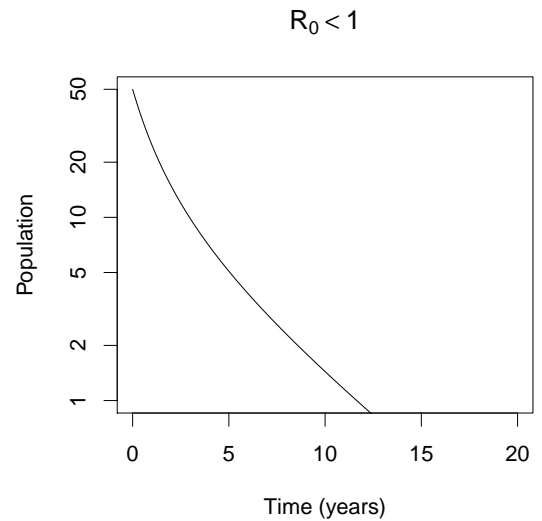
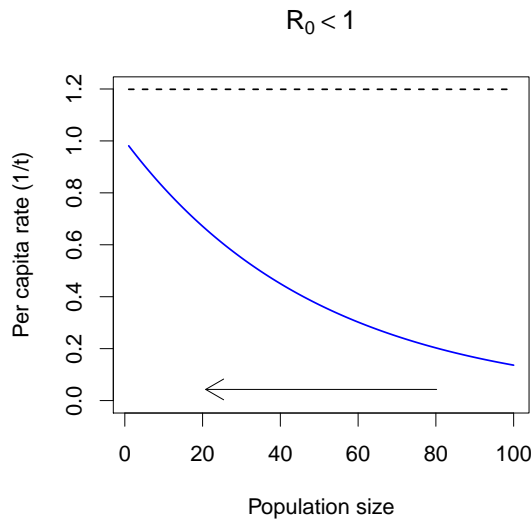
Invasion

- 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 $\mathcal{R}_0 > 1$

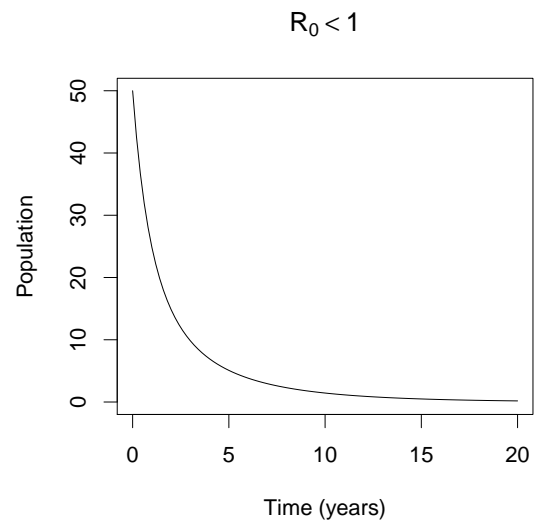
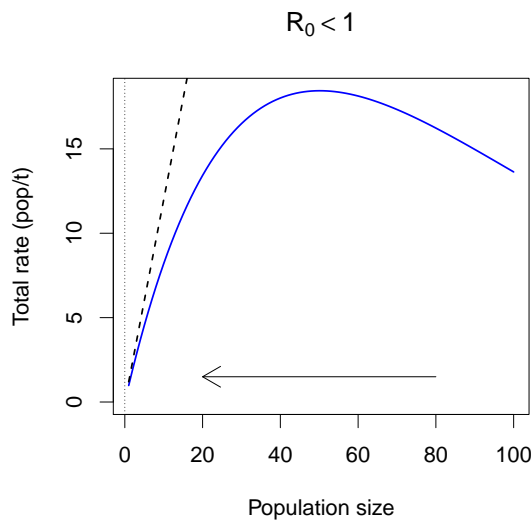
Different behaviours

- 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

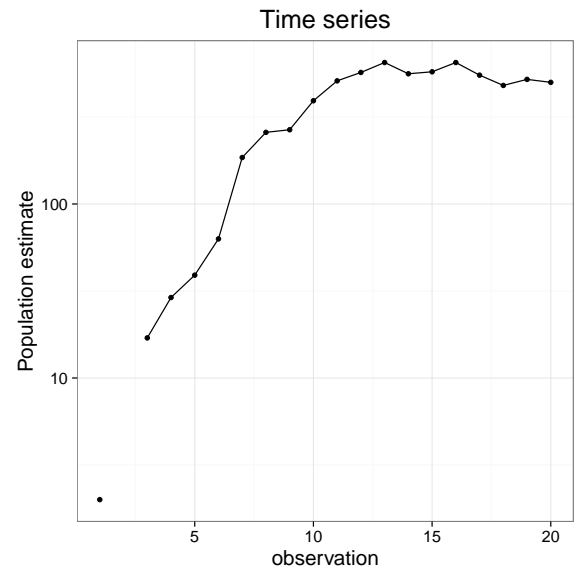
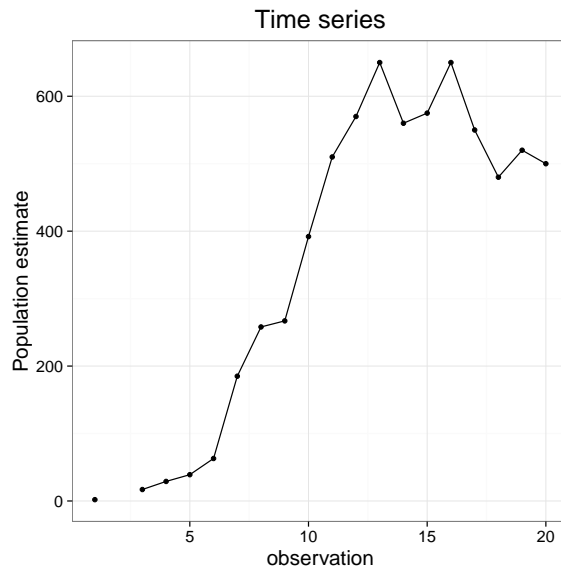
Dynamics of density-dependent populations

- Populations following this model change *smoothly*
 - Equations tell how the population will change at each instant
- They have no memory

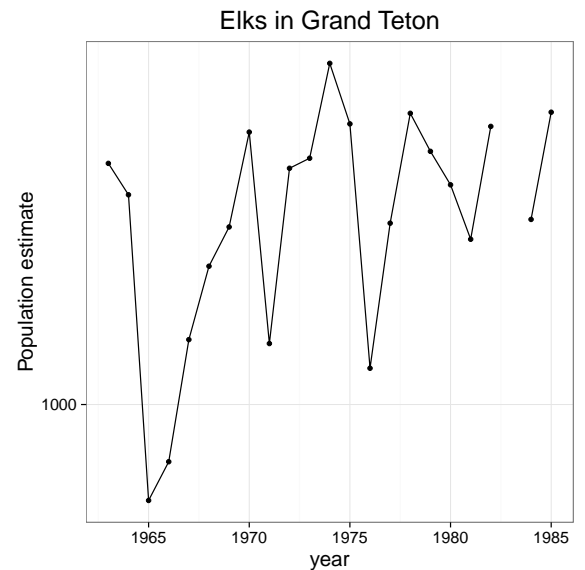
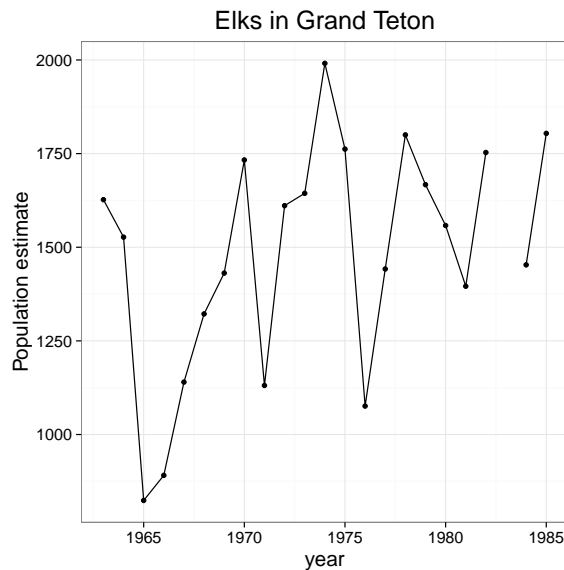
- Birth rate and death rate are determined by population size alone
- Cycling is impossible

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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

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).
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Our model

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

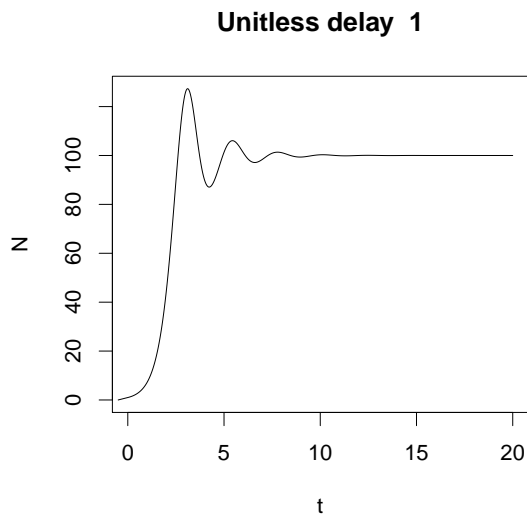
- If a population is growing, what will happen as it approaches the equilibrium?

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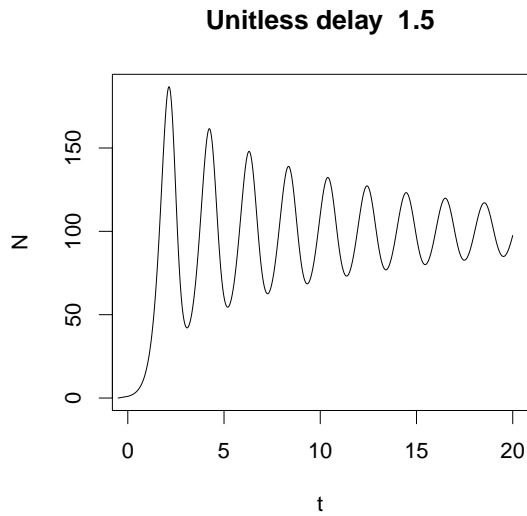
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- So what happens in the long term?

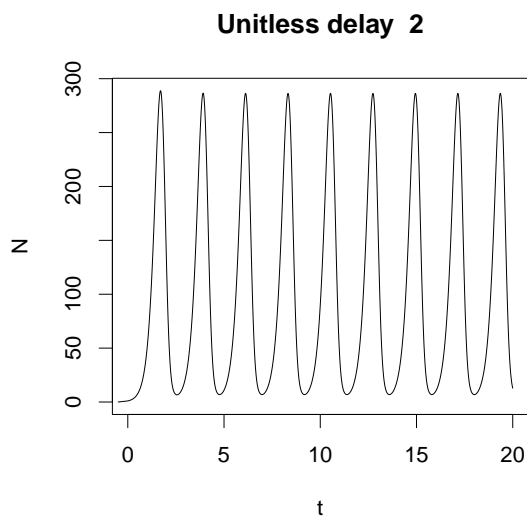
Time-delayed dynamics



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?
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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:
 - $N_{T+1} = (p(N_T) + f(N_T))N_T \equiv \lambda(N)N_T$

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:
 - $f(N) = f_0 \exp(-N/N_f)$
 - $p(N) = p_0 \exp(-N/N_p)$
- 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?
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What is \mathcal{R}_0 ?

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

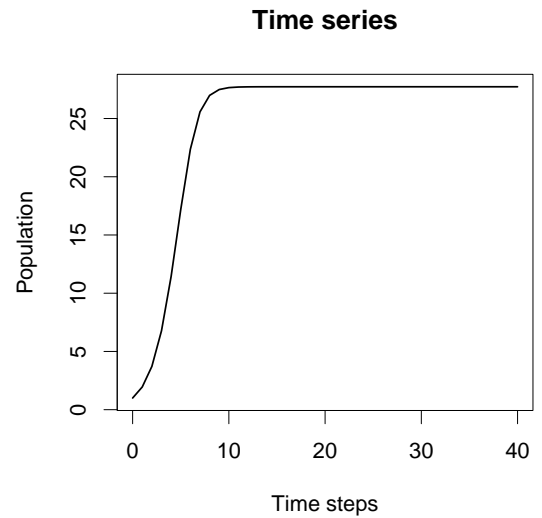
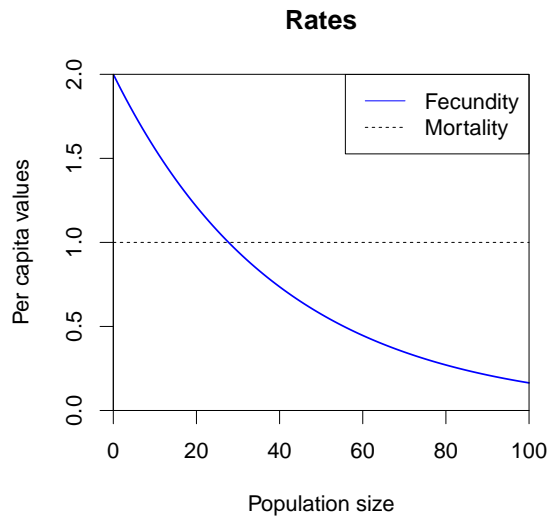
Behaviours

- 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

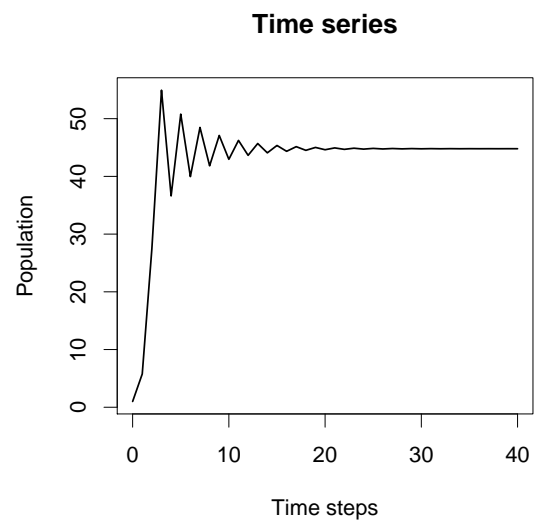
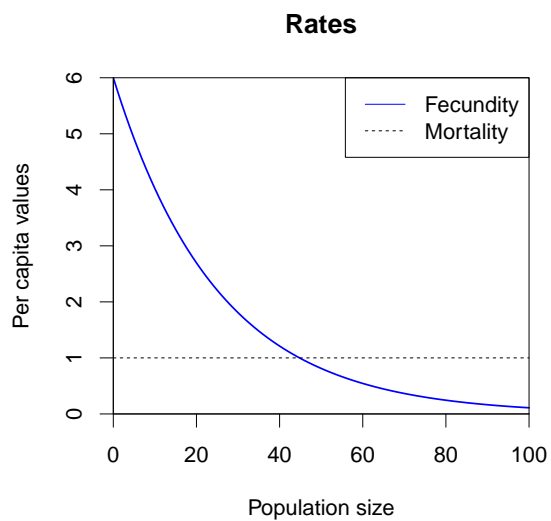
4.2 Simulating this system

- 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

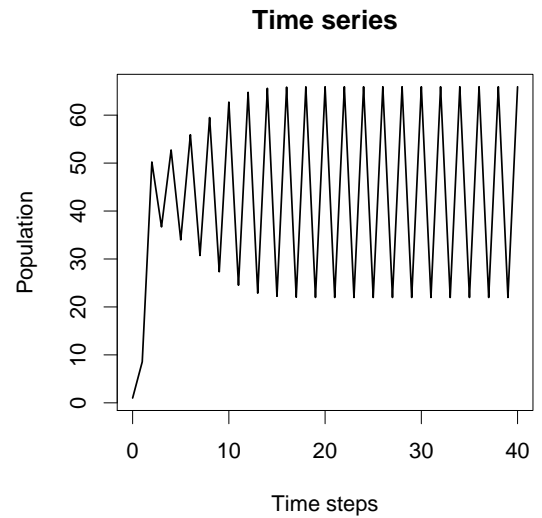
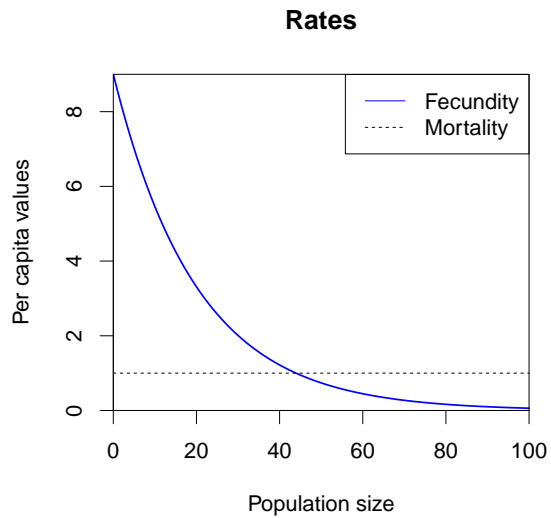
We expect simple dynamics



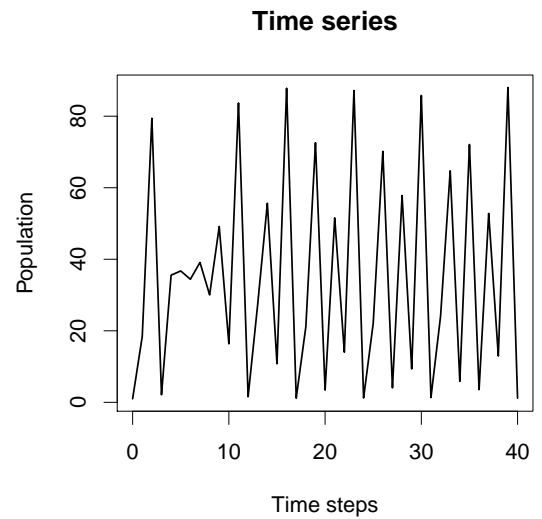
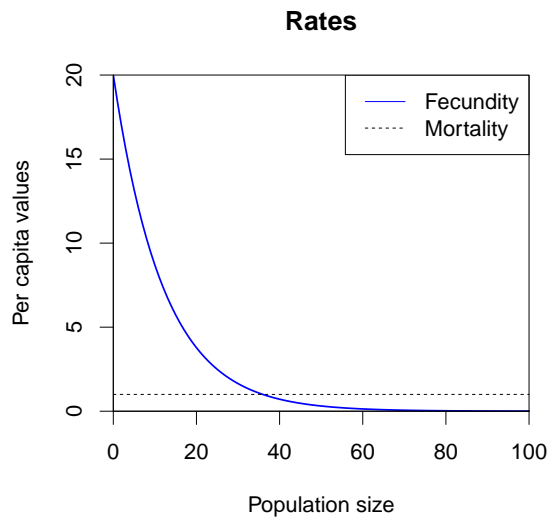
Damped oscillations



Persistent oscillations



Lots of other behaviours



4.3 Interpreting complex behaviour

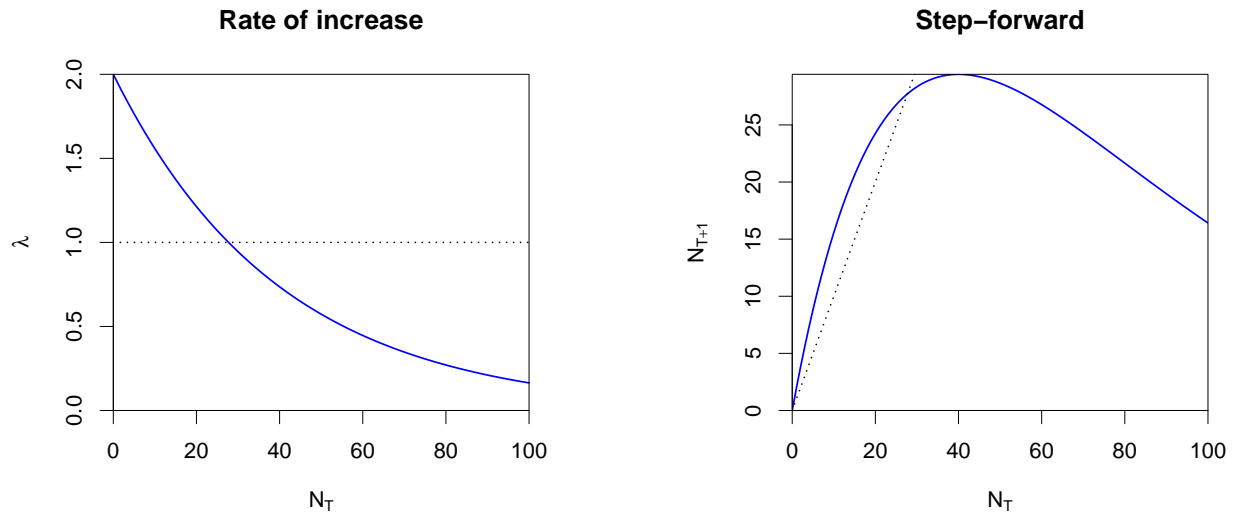
- In a simple cycle:

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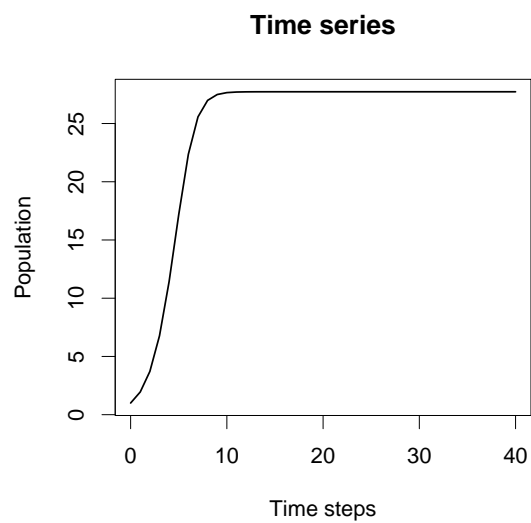
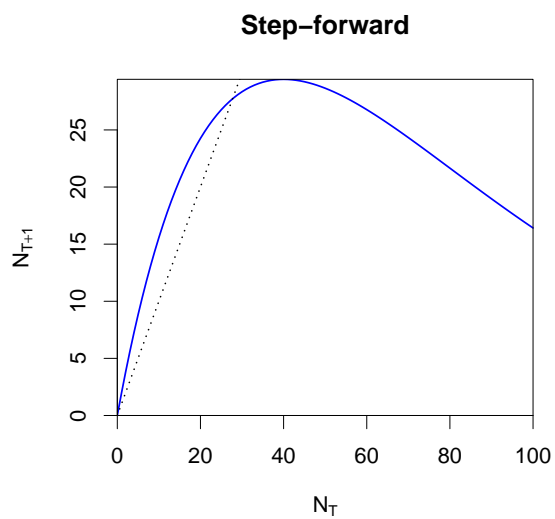
Response to population increase



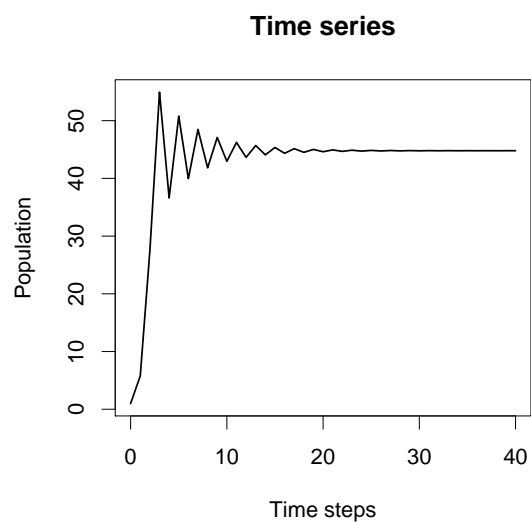
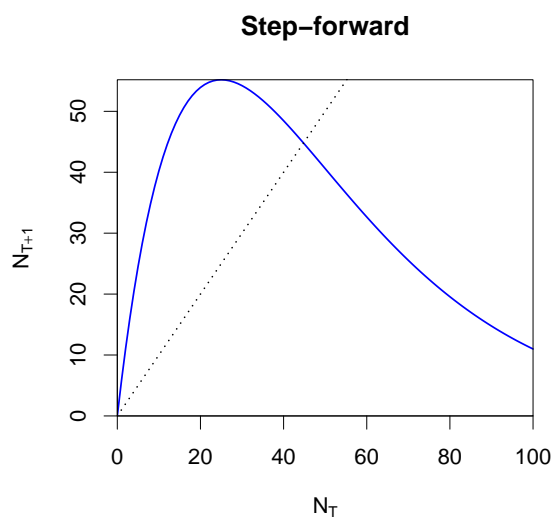
Turnover

- 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

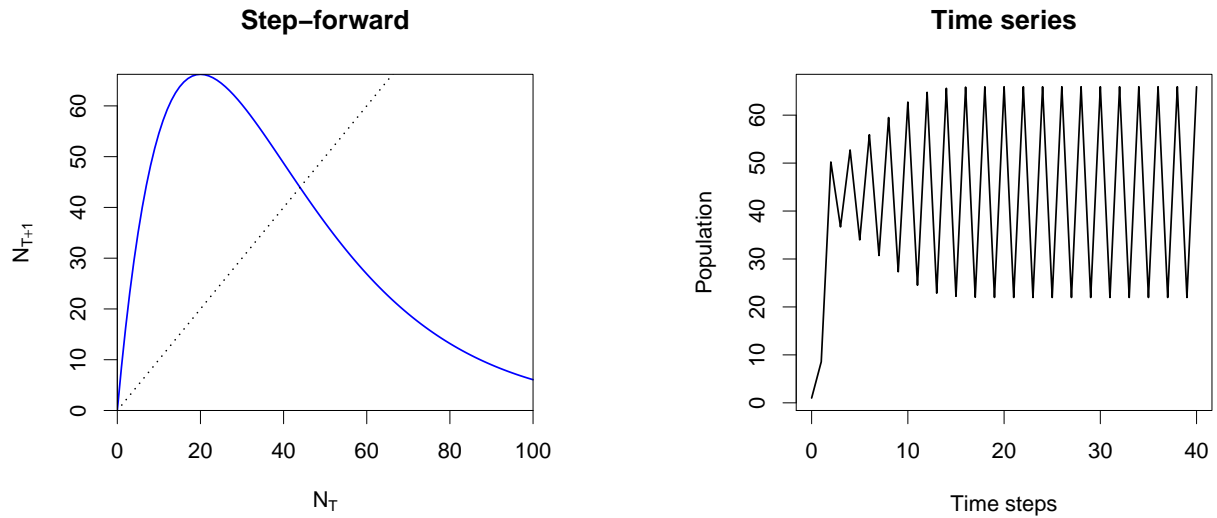
Simple dynamics



Damped oscillations



Persistent oscillations



Complex behaviour in our conceptual model

- Biologically, when might we expect N_{T+1} to “turn over”?

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- When should the mapping *not* turn over?

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Scramble competition

- **Scramble** competition refers to the case where all individuals in a crowded population are gathering resources at similar

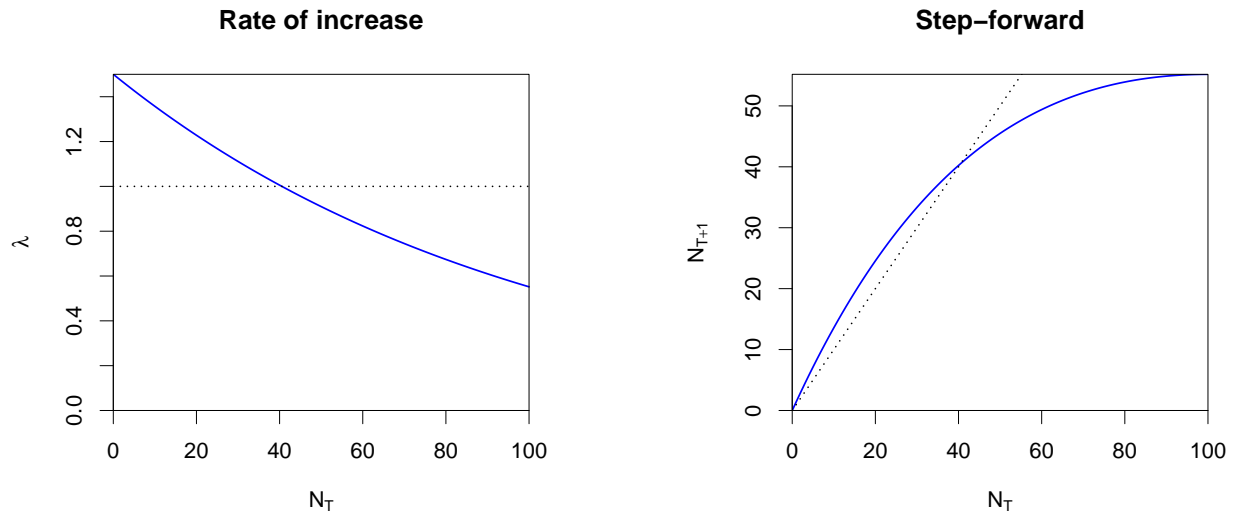
rates: as the density goes up there is less resource for everyone, and everyone does less well

- 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?
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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

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Plants

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

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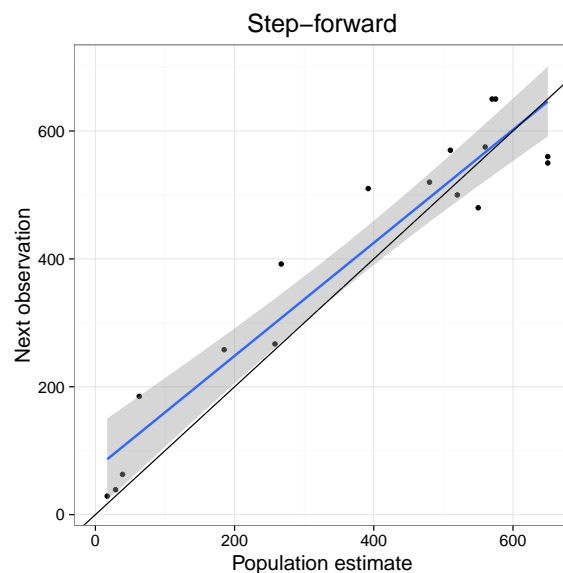
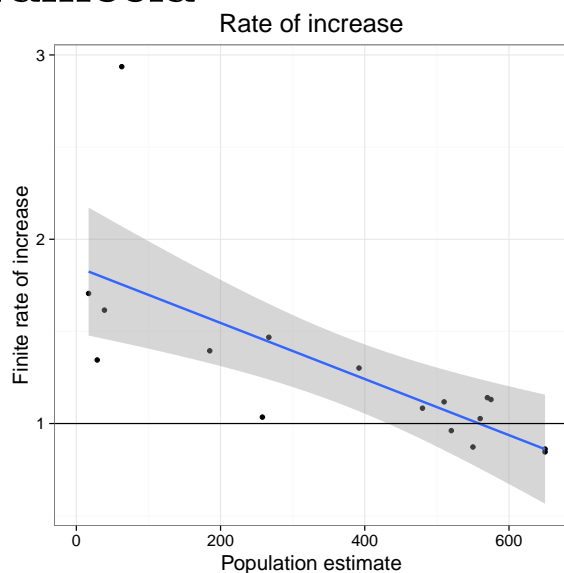
Complex behaviour from a simple model

- 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

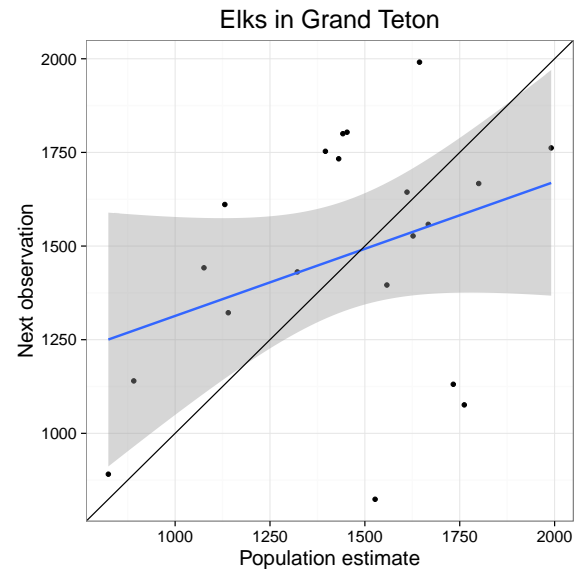
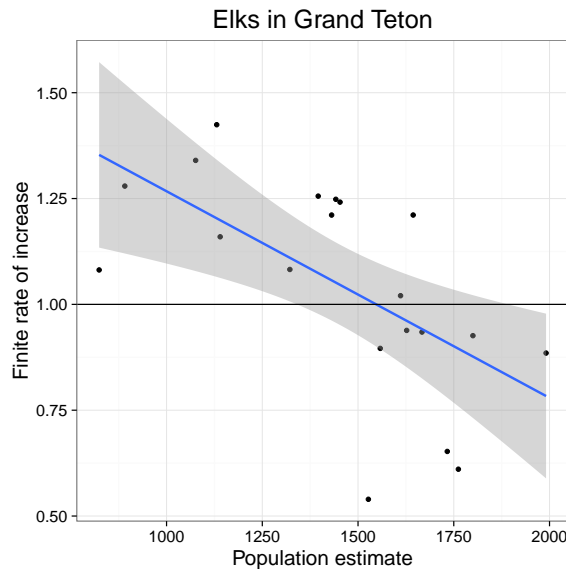
Complex behaviour in real populations

- 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?

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- What about two butterflies?

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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?
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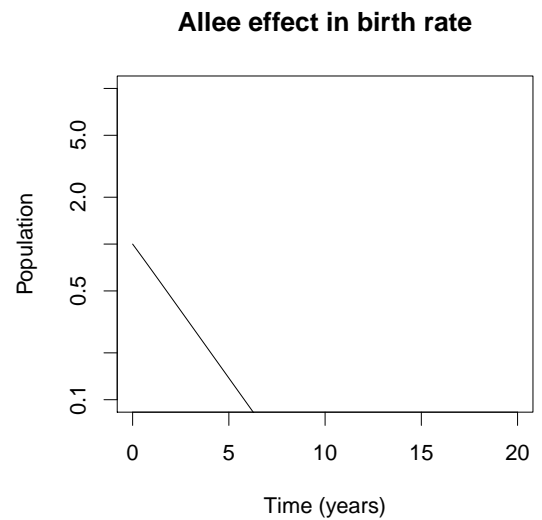
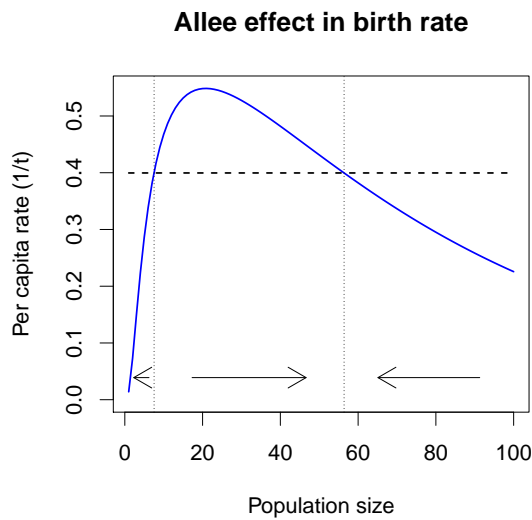
Types of Allee effect

- Allee effects can affect the birth rate
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- ... or the death rate
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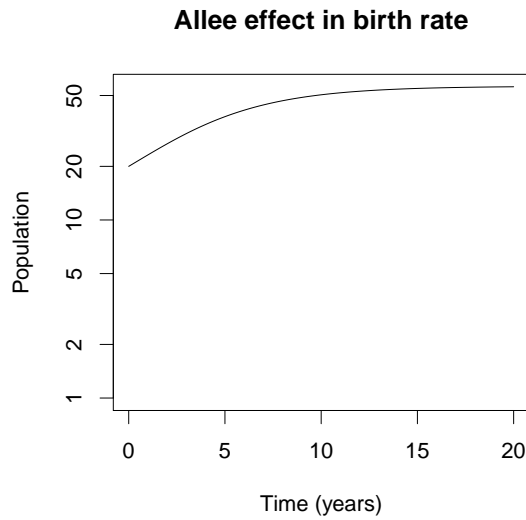
Allee effect models

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

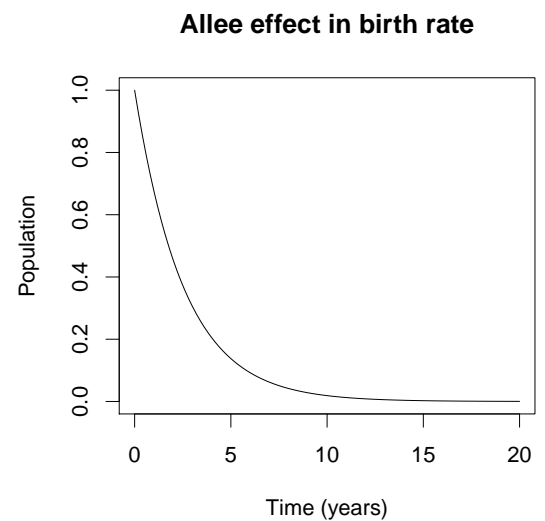
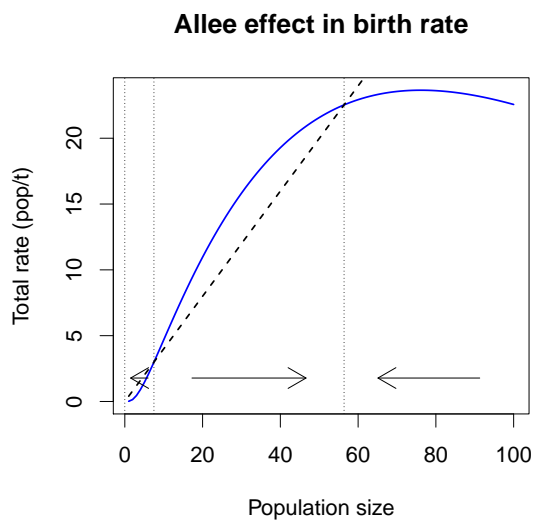
Individual perspective



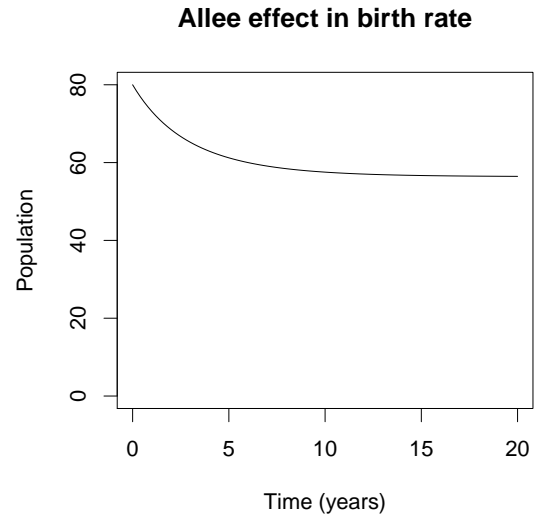
Individual perspective



Population perspective



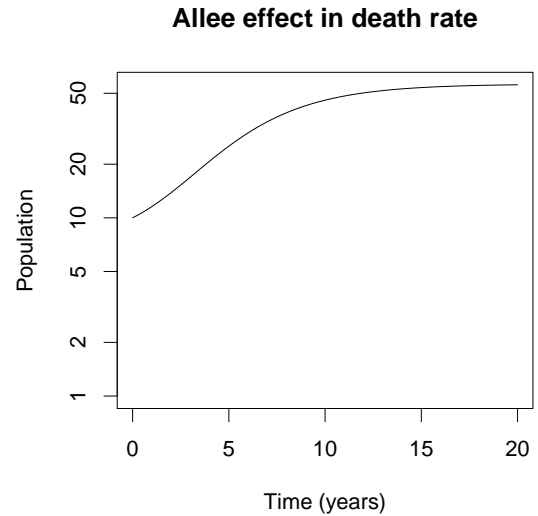
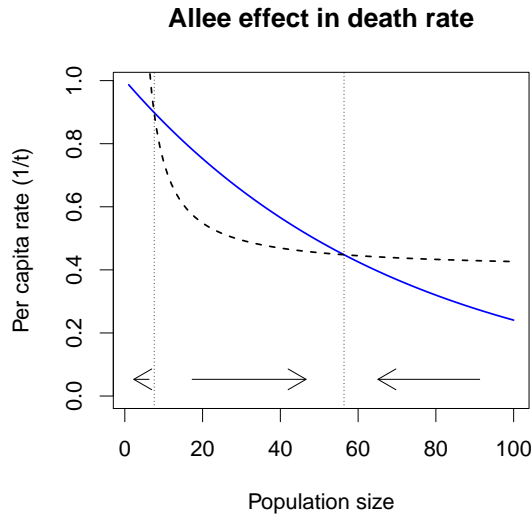
Population perspective



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}_{\max} : \mathcal{R} at whatever level is the peak

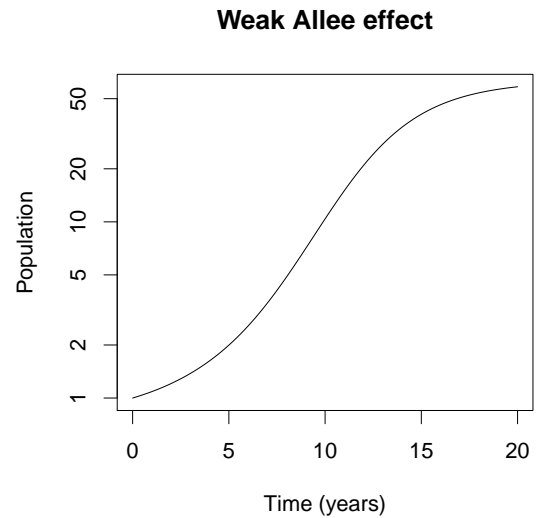
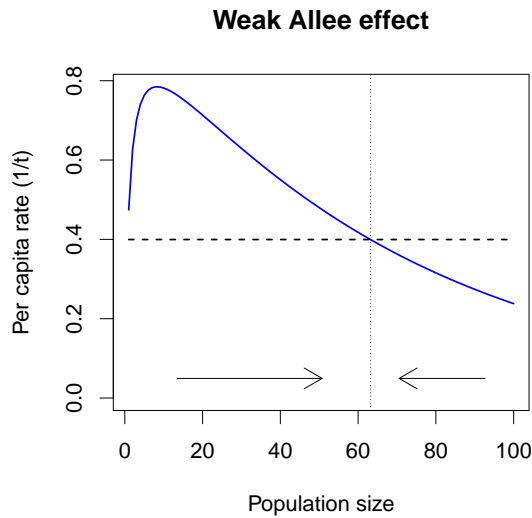
Invasion

- 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
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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?

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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?
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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

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- What if $\lambda < 1$?

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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
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- But small populations are the ones in danger of going extinct
 -
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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