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?

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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?
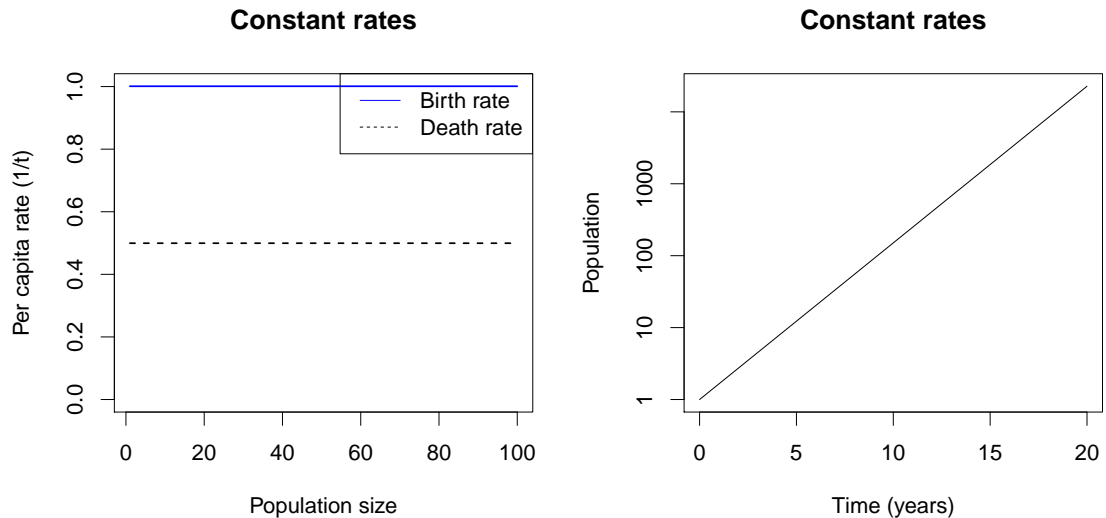
2 Continuous-time regulation

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

Constant rates **Constant rates**

- 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

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Population perspective

Constant rates **Constant rates**
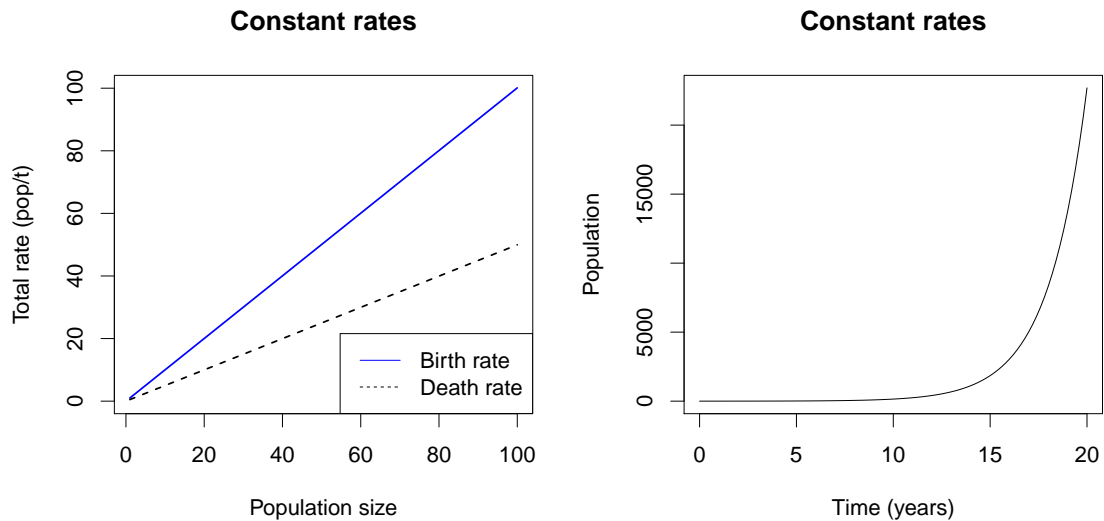
- Total rate shows birth and death for the whole population

- 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: $\dfrac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$

  - 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

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- 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: $\dfrac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$

- Reproductive number now also changes with N:

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- 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 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 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
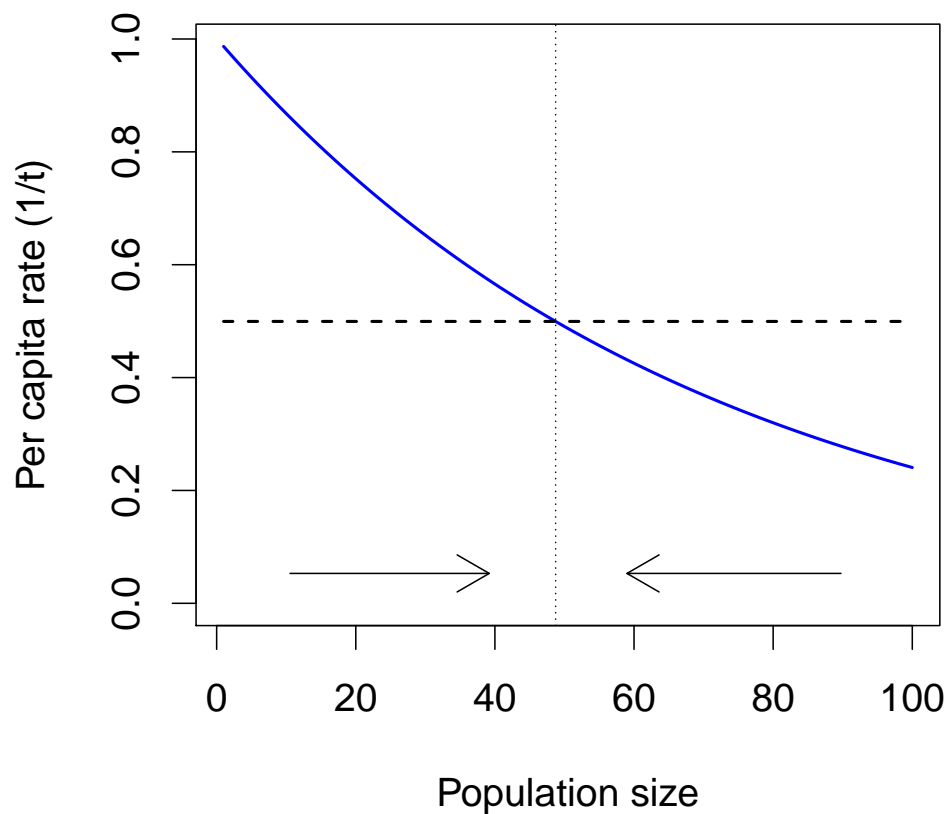
- Increase when population is below equilibrium

- Decrease when population is above equilibrium

- Converge

Examples

Density–dependent birth

Density–dependent birth

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

Density−dependent birth   **Density−dependent birth**
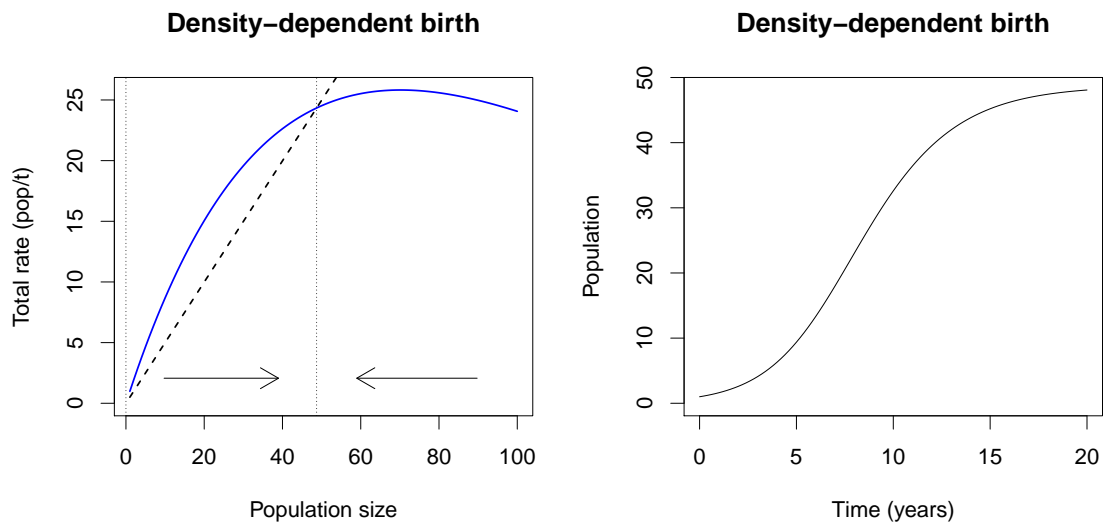
Decreasing birth rate

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

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- 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
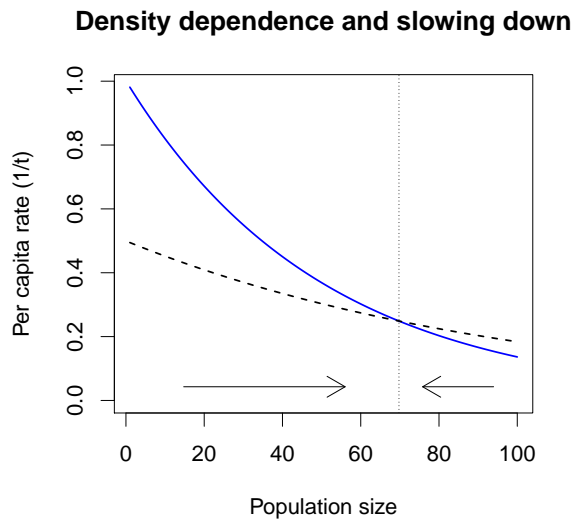
Individual perspective

Population perspective

Density−dependent death (left plot)

Total rate (pop/t) vs Population size

Density−dependent death (right plot)

Population vs Time (years)
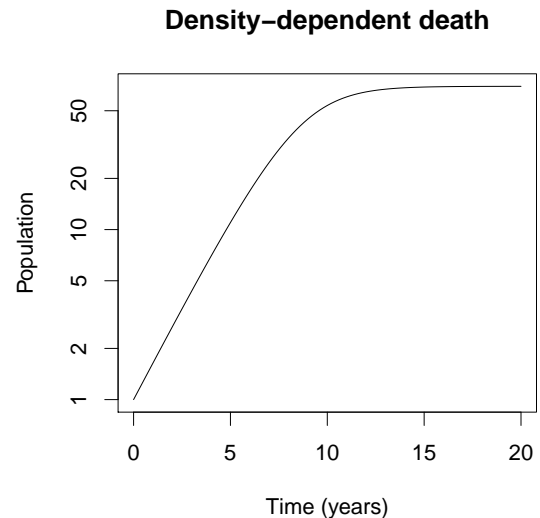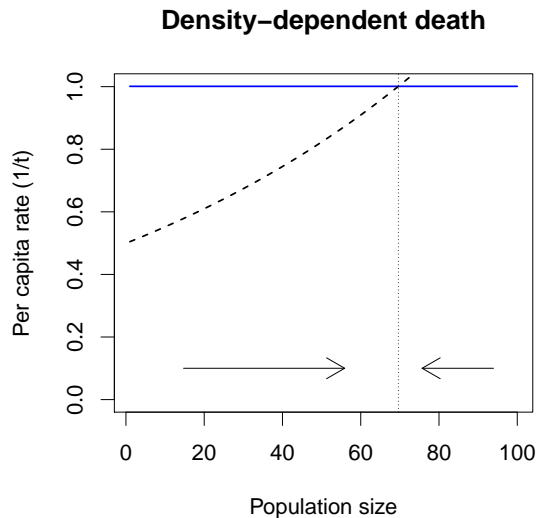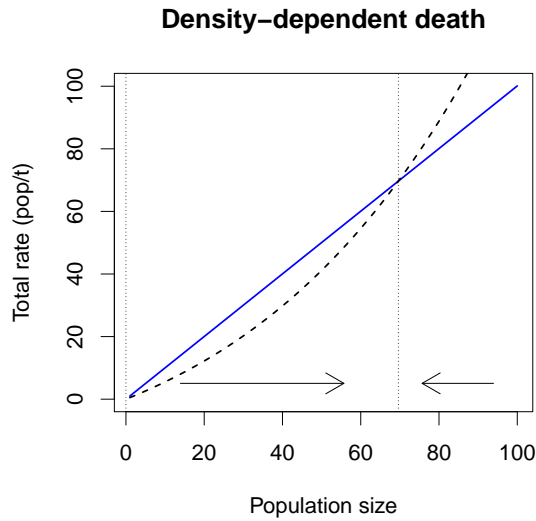
Decreasing death rate

- 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

Density dependence and slowing down (left plot)

Per capita rate (1/t) vs Population size

Density dependence and slowing down (right plot)

Population vs Time (years)

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Population perspective

Density dependence and slowing down   **Density dependence and slowing down**
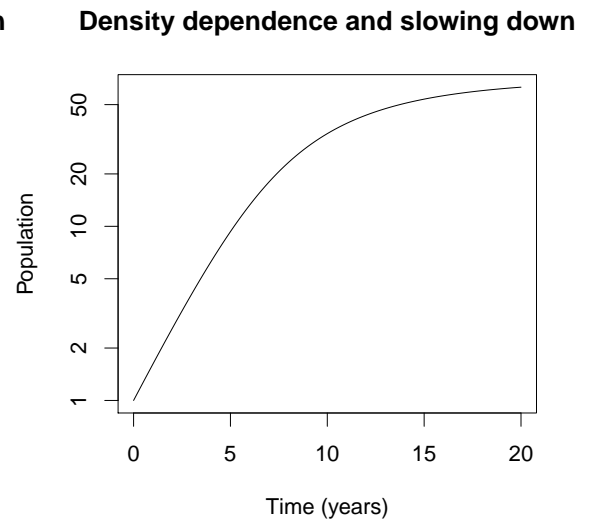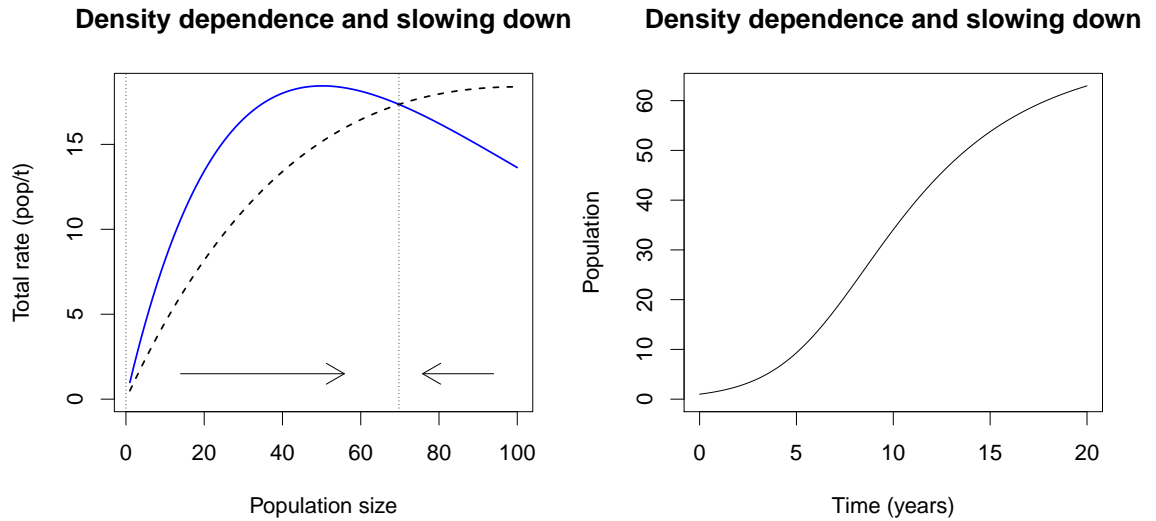
Other examples

- 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?

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2.3 Equilibria and time scales

- We define **equilibrium** as when the population is not changing

- Our simple model is $\dfrac{dN}{dt} = (b(N) - d(N))N$

- 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:

    -

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

    -

- 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

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Individual perspective
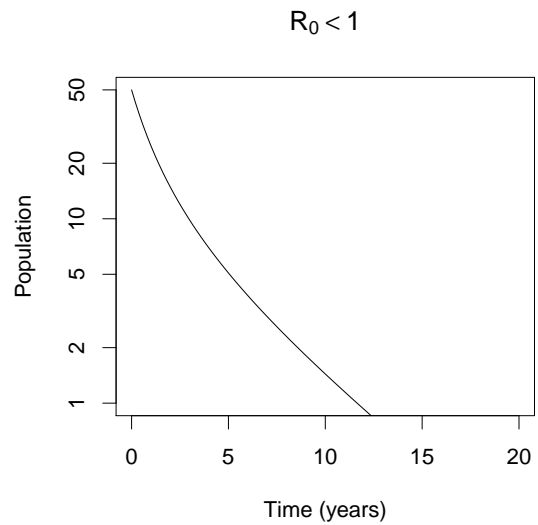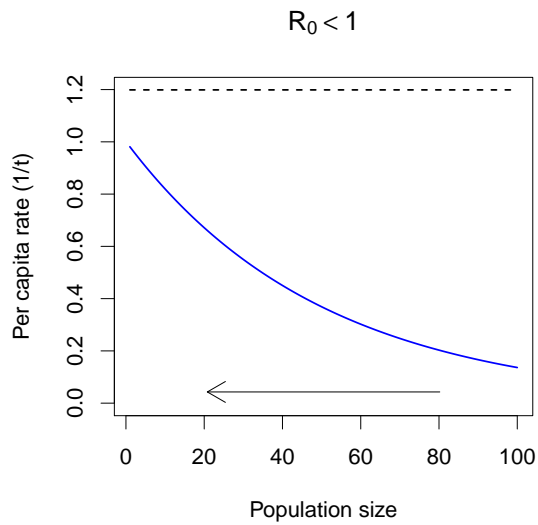
Population perspective
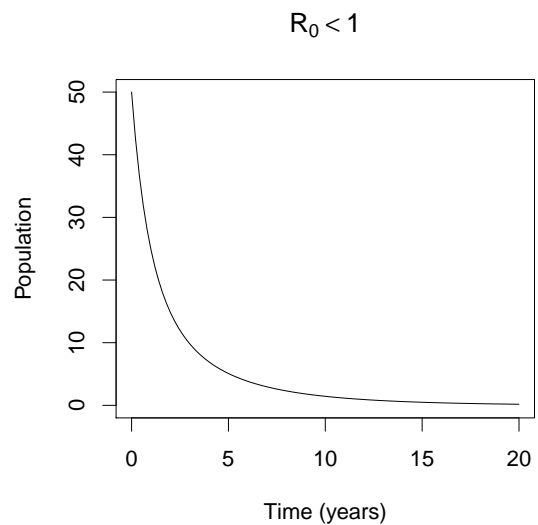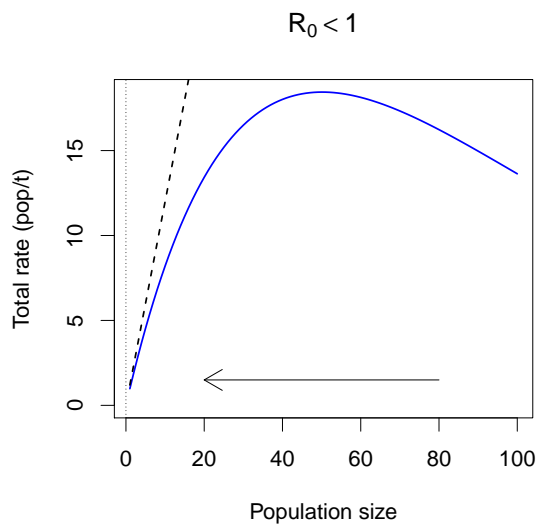
$\mathcal{R}_0$ and thresholds

- 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:

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- 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
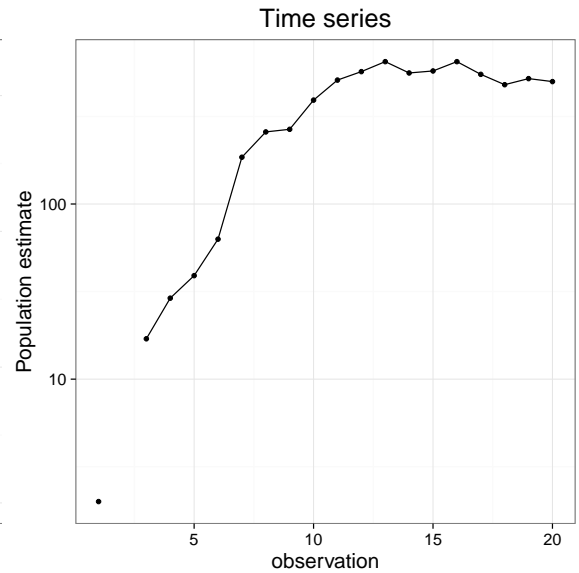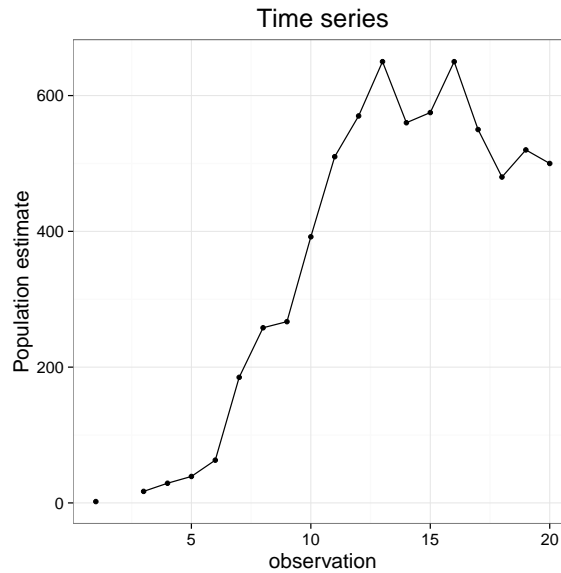
Elk
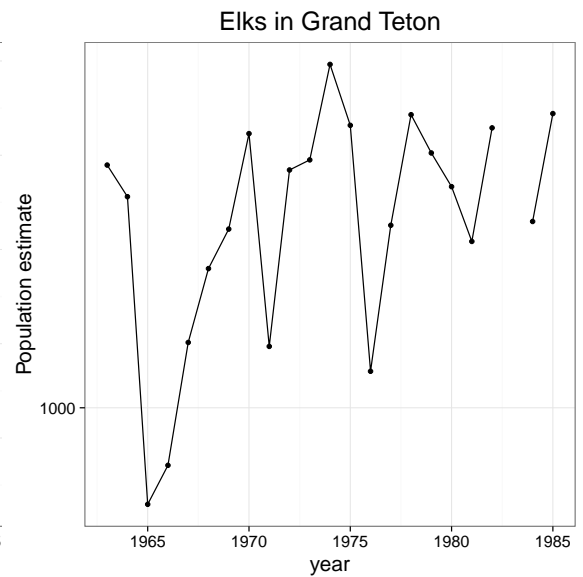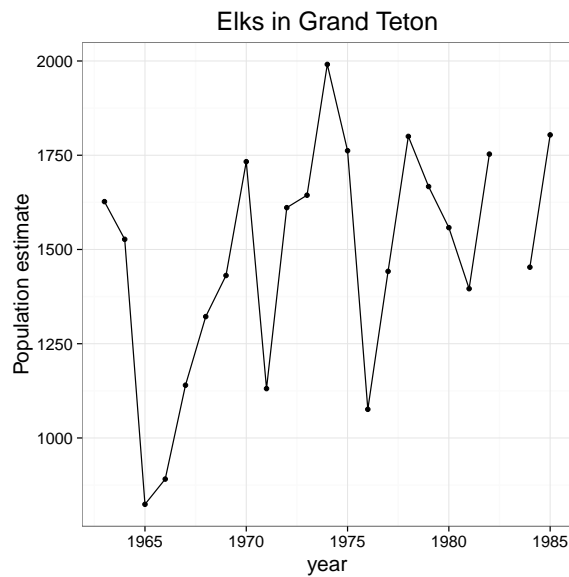
Dynamics of real-world populations

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

- Be explicit about time: $\dfrac{dN(t)}{dt} = (b(N(t)) - d(N(t)))N(t)$

- 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

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

- 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

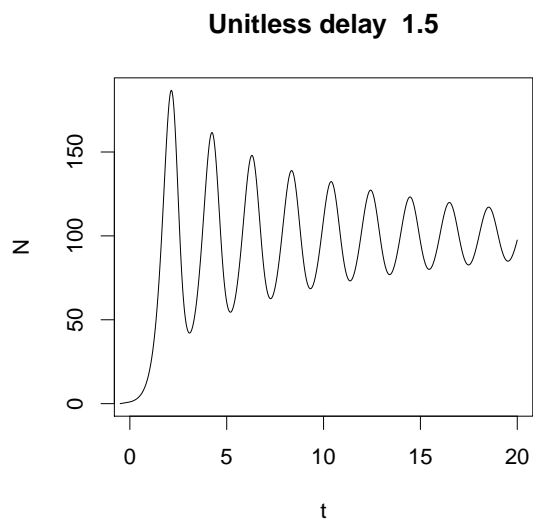   – or *distributed* delays, so that the rate is some kind of average

Model dynamics

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

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- So what happens in the long term?

Time-delayed dynamics

Unitless delay 1

Time-delayed dynamics

Unitless delay 1.5

Time-delayed dynamics

Unitless delay 2
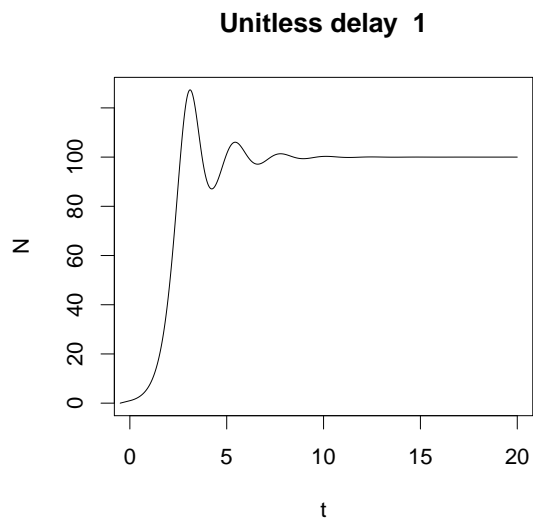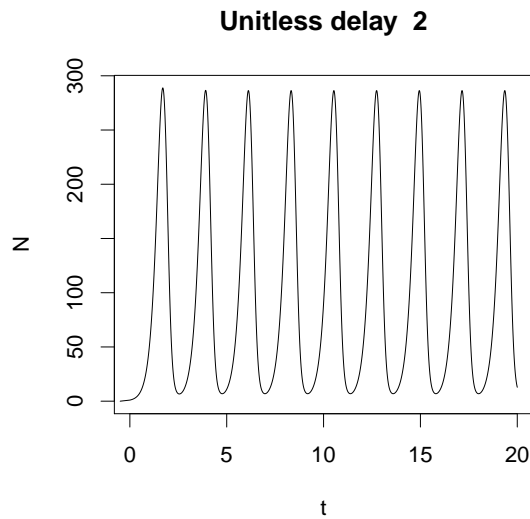
Time-delayed population models

- 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

    -

    -

- $\mathcal{R}_0$ 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 →low →high →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
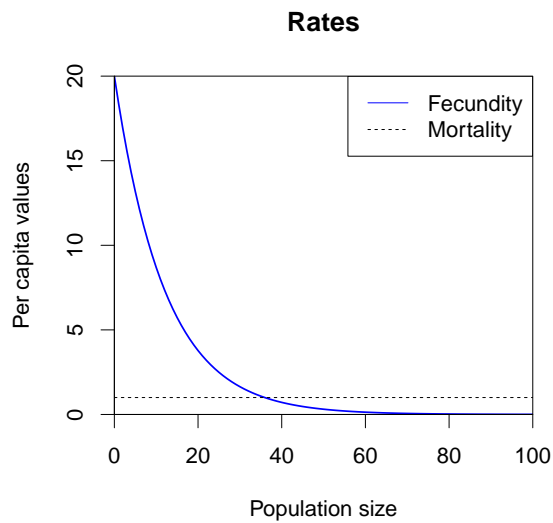
We expect simple dynamics
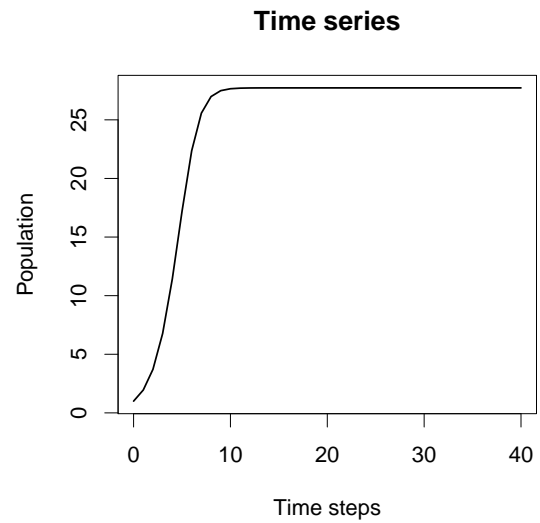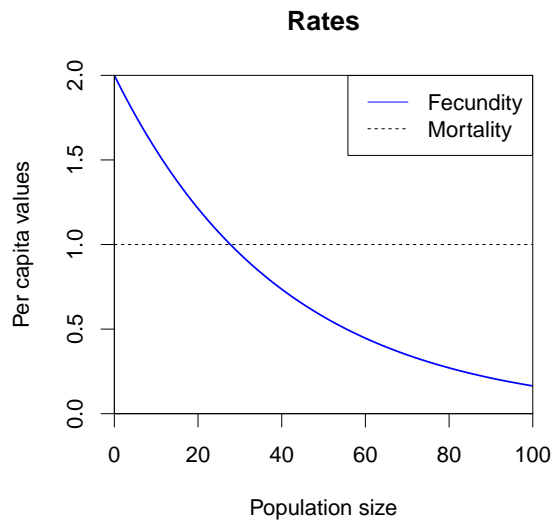
Damped oscillations

Persistent oscillations

Rates
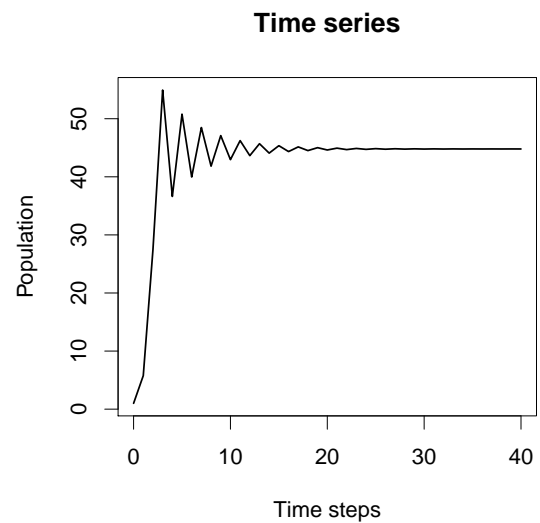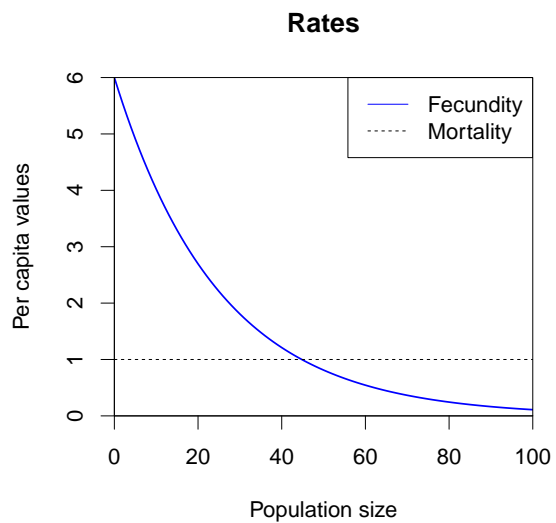
Time series
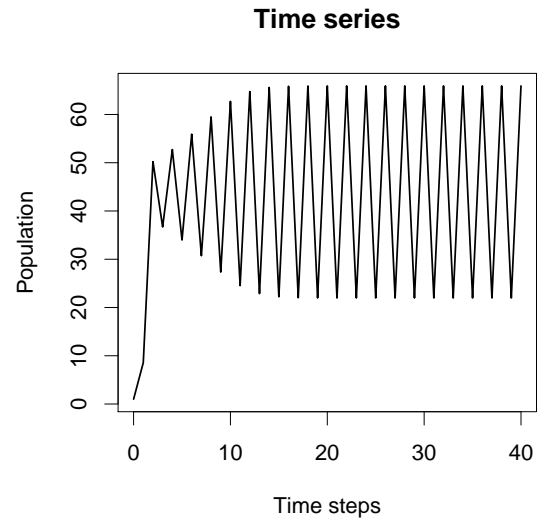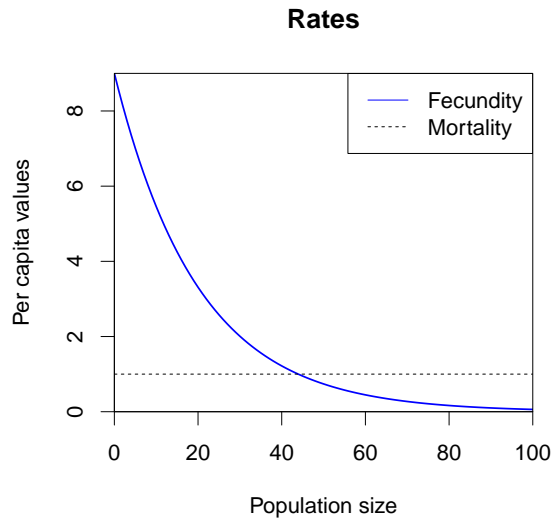
## Lots of other behaviours

Rates

Time series
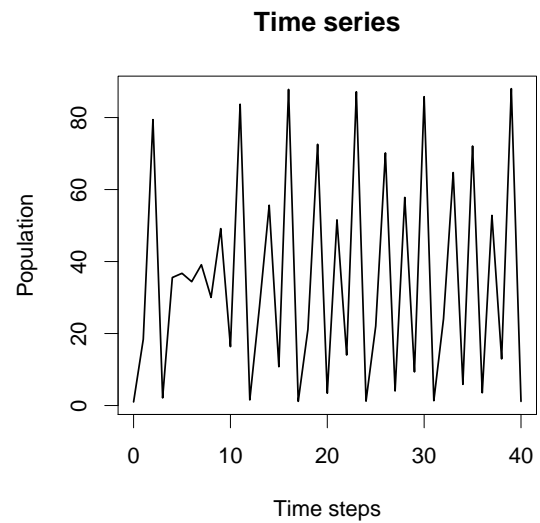
4.3   Interpreting complex behaviour

- 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?

  –

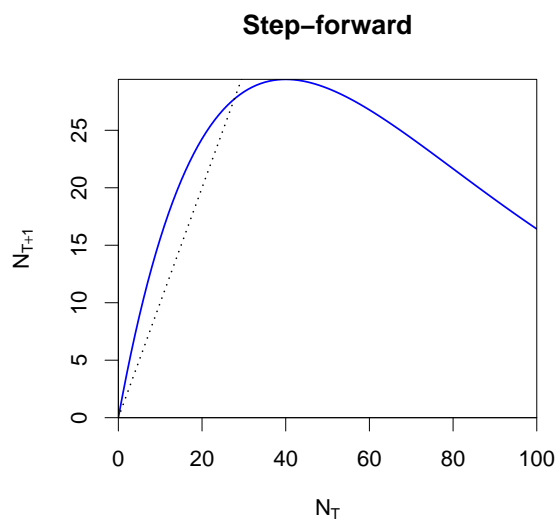- In our simple models, as N_T increases, what happens to next year's population?

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Response to population increase
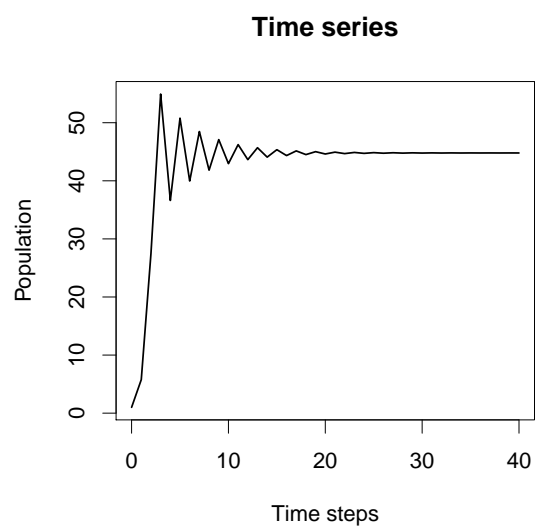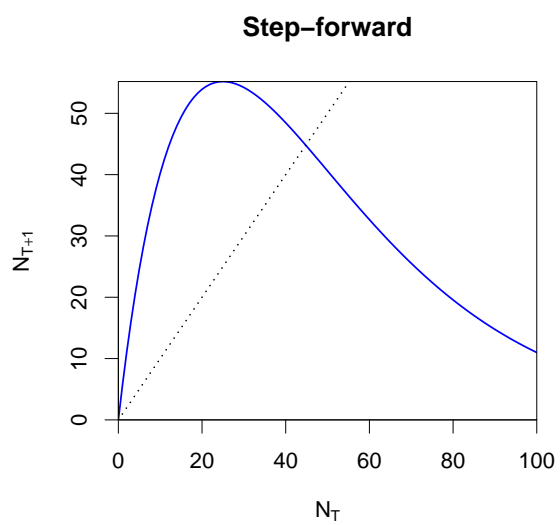

Rate of increase   **Step–forward**
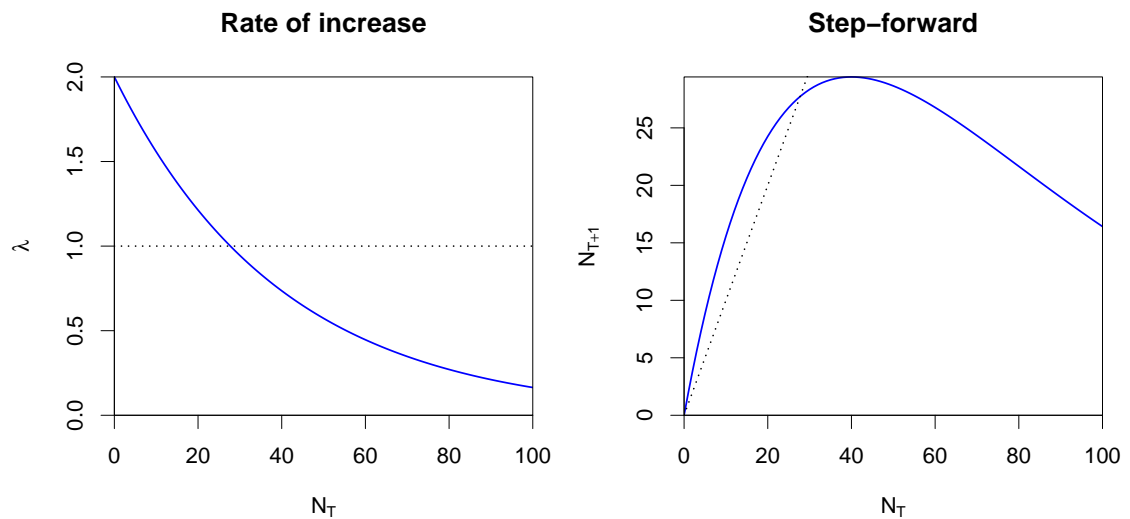
Turnover

- 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

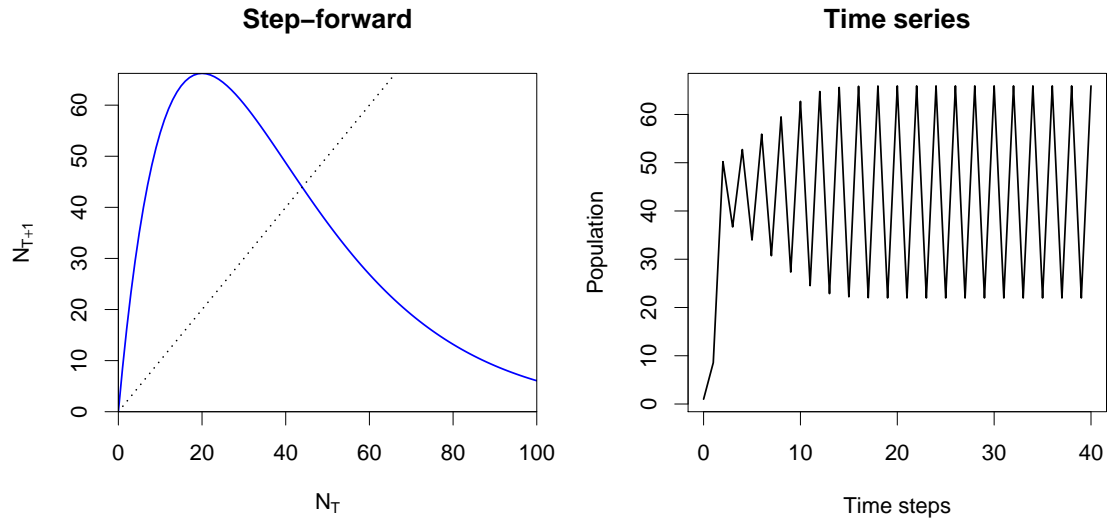 – A small population this year leads to a large population next year

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Simple dynamics

Step–forward

Time series

Damped oscillations

Step–forward

Time series

Persistent oscillations

Step–forward   **Time series**

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

Rate of increase   **Step–forward**
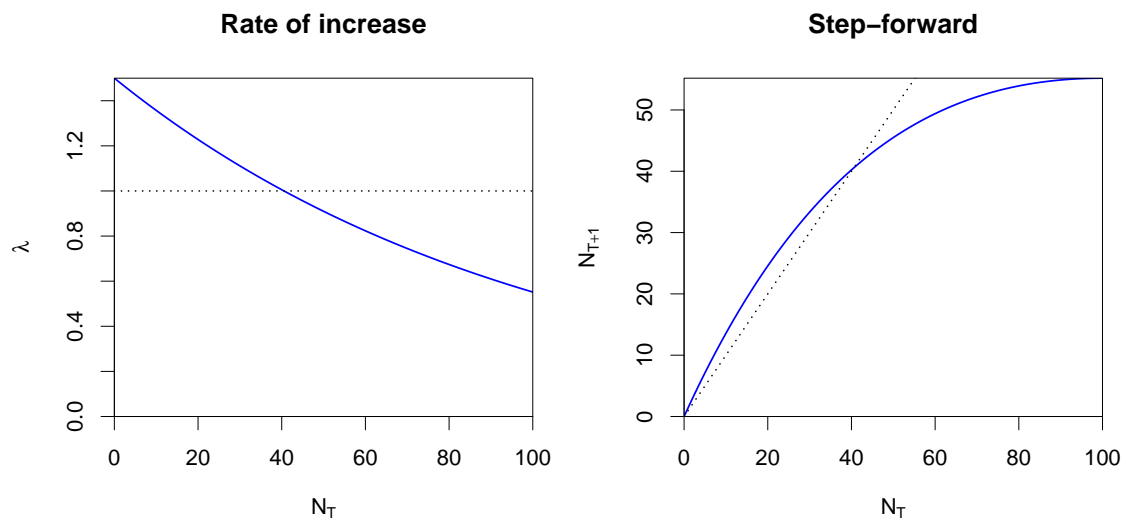
Songbirds

- 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
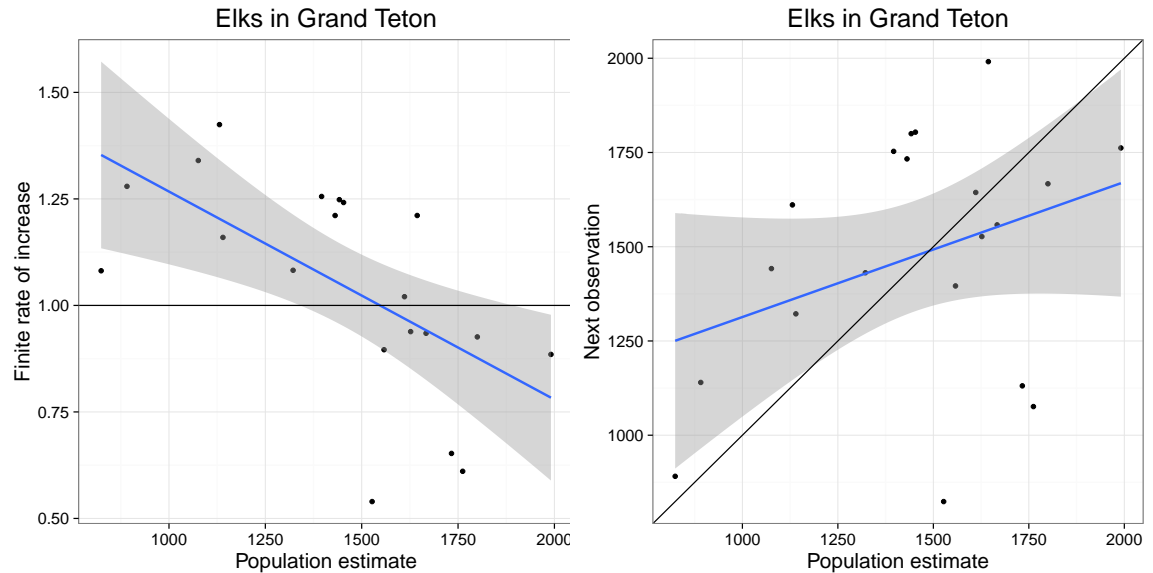
Complex behaviour in real populations

- 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
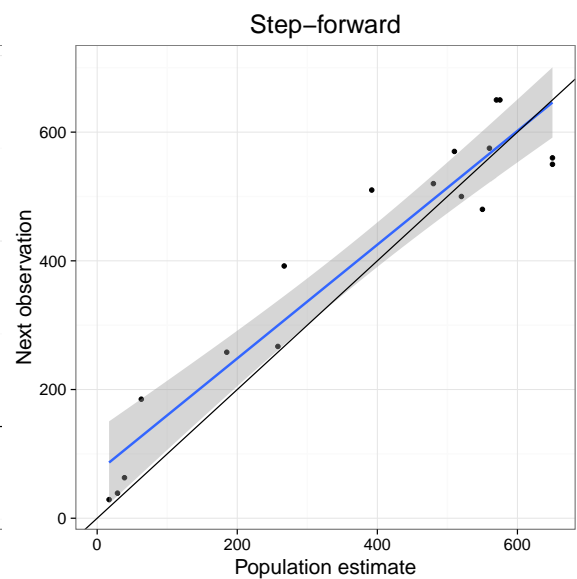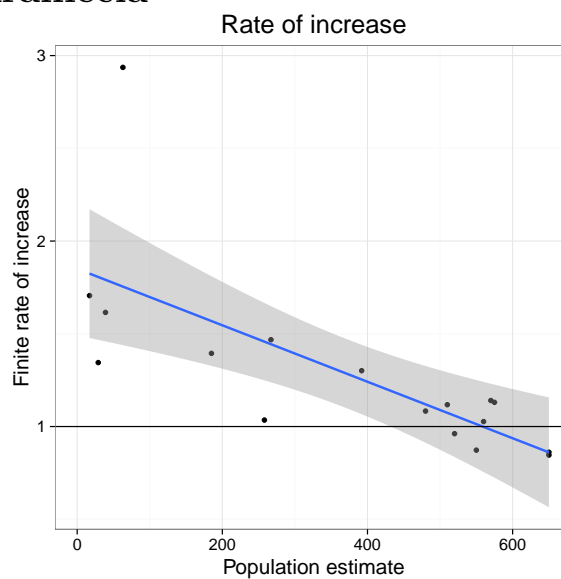
Elk

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

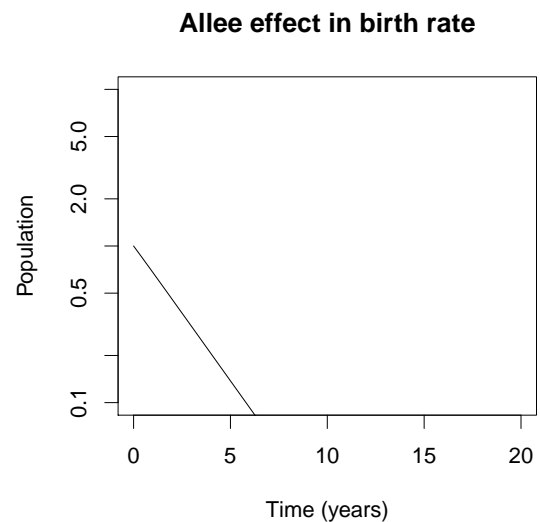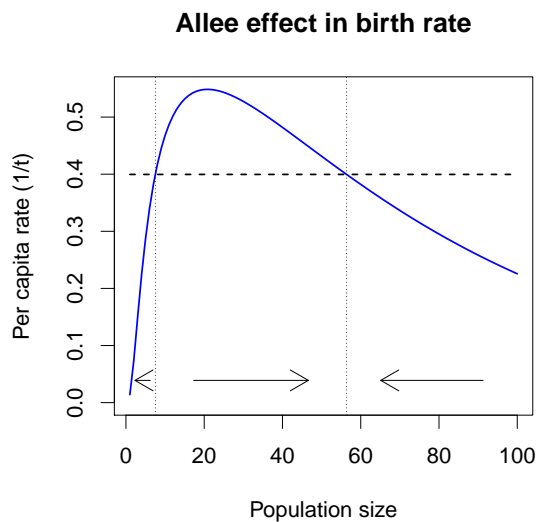- Allee effects can affect the birth rate

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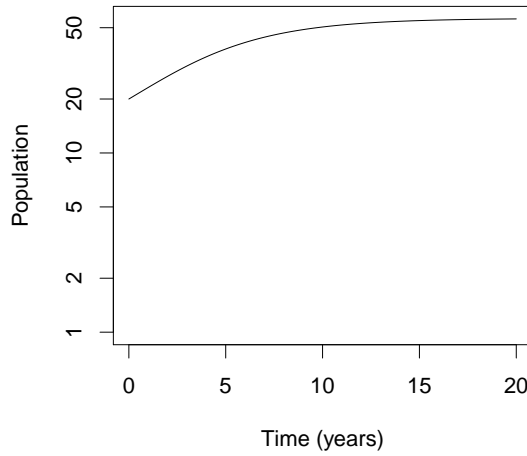- ... or the death rate

  –

Allee effect models

- What will this model do, if the initial population is:

  – low, medium or high?
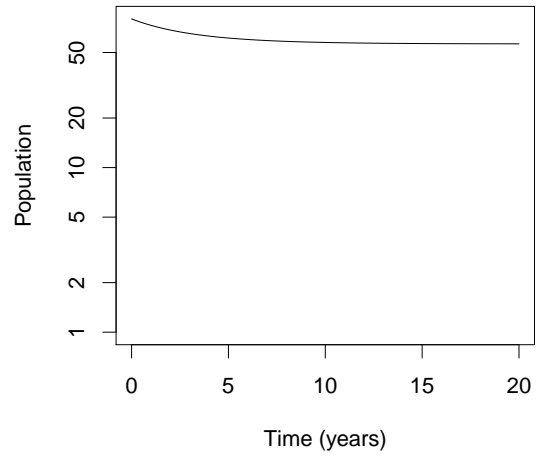
Individual perspective

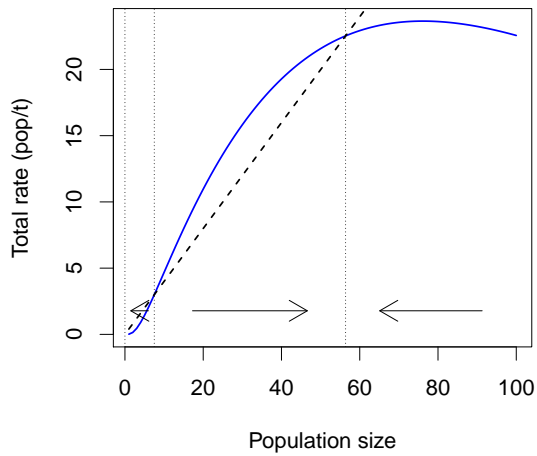## Individual perspective

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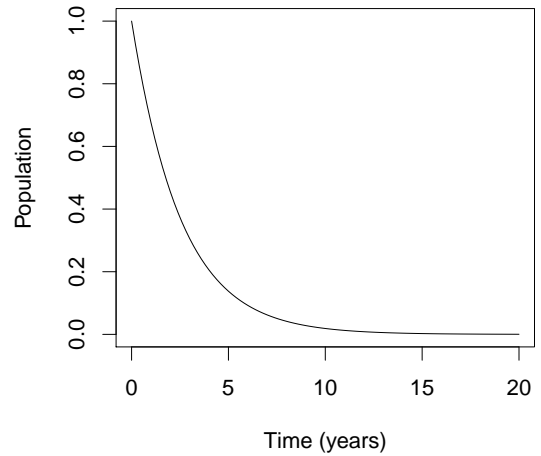## Allee effect in birth rate

Allee effect in birth rate

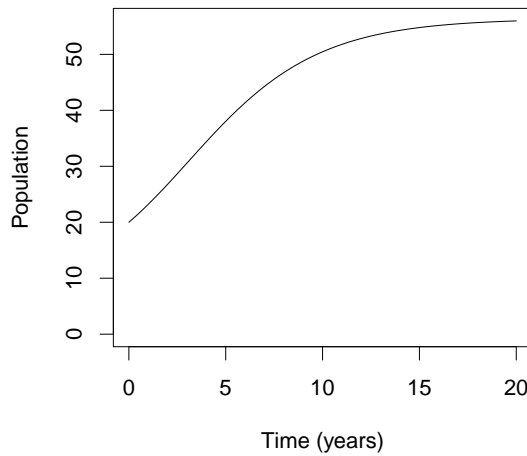

Population perspective

Allee effect in birth rate

Allee effect in birth rate

Population perspective

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Allee effect in birth rate

(left plot: Population vs Time (years))

Allee effect in birth rate

(right plot: Population vs Time (years))
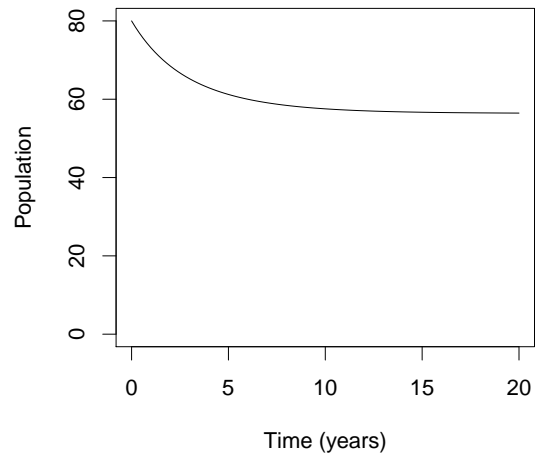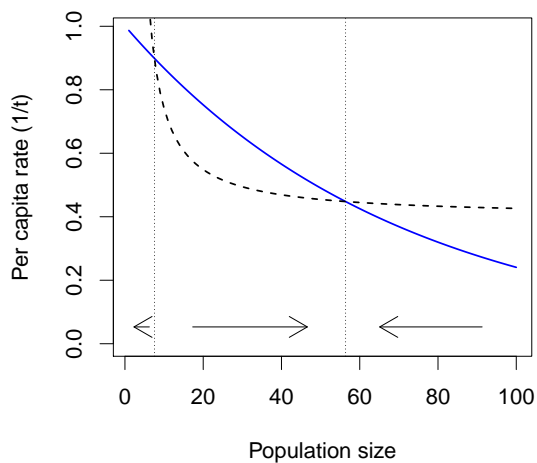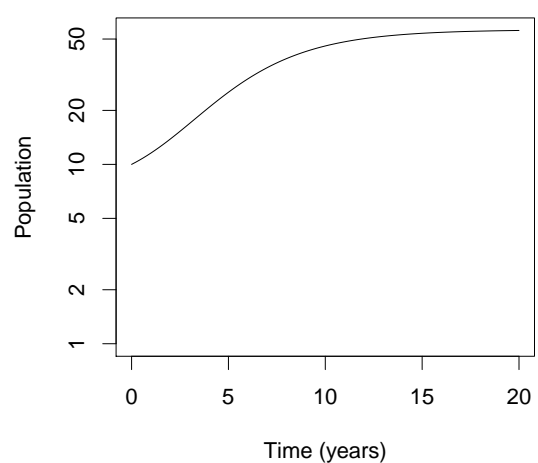
Allee effect in death rate

- 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

Allee effect in death rate

(left plot: Per capita rate (1/t) vs Population size)

Allee effect in death rate

(right plot: Population vs Time (years))

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

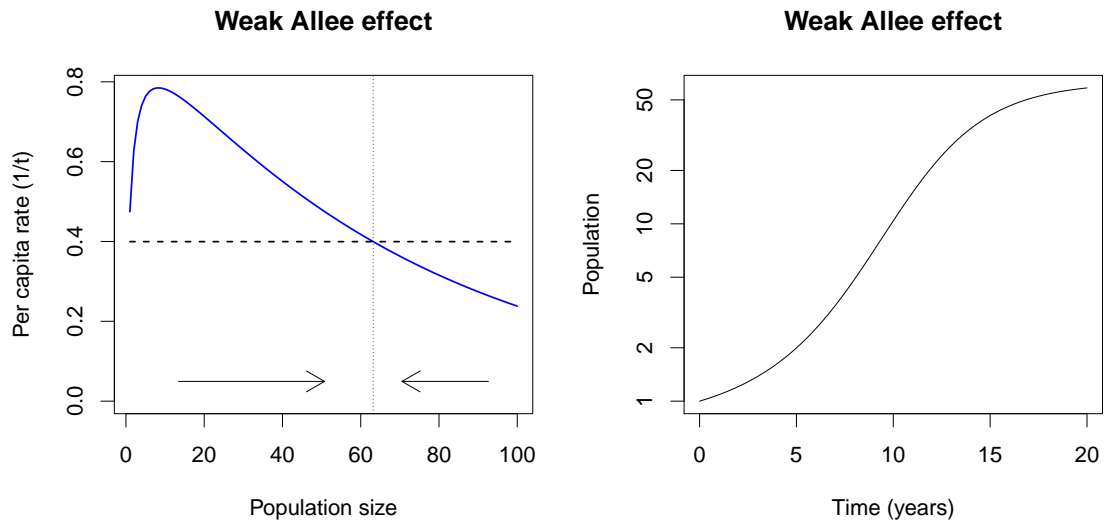- When Allee effects are present, it's no longer true that a species that can't invade can't persist

    -

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

Weak Allee effect

Weak Allee effect

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?

    –

    –

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 $\lambda < 1$?

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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