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?

  - **Answer:** Predators and diseases

    * **Answer:** As populations go up, pressure from natural enemies could go up *even faster*

  - **Answer:** Insufficient resources

    * **Answer:** Not enough to go around: e.g., oak trees use all the available light

  - **Answer:** Resources are destroyed: e.g., gypsy moths kill all the oak trees

Population regulation

- All the populations we see are *regulated*

  - On average, population growth is higher when the population is lower

  - Maybe with a time delay

- Why is this interesting?

  - Lots of populations don't *look like* they are regulated

Sometimes regulation is apparent

- Some species seem to fill a niche (mangroves)

- or deplete their own food resources (gypsy moths)

Sometimes regulation is not apparent

- Other species seem like they could easily be more common (pine trees)

  - May be controlled by cryptic (hard to see) natural enemies (like disease or parasites
  - May be controlled by 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?

  - **<u>Answer</u>:** Because the long-term average value of r has to be *very* close to 0
  - **<u>Answer</u>:** This is true for *every* population
  - **<u>Answer</u>:** This is unlikely to occur by chance
  - **<u>Answer</u>:** Thus, it must be through direct or indirect responses to the population size
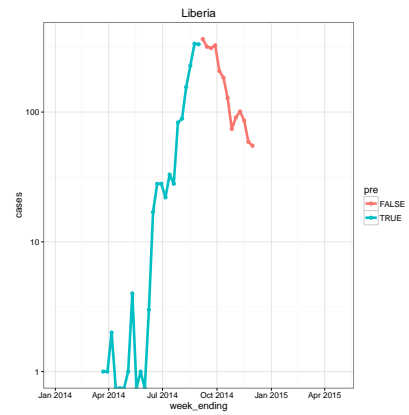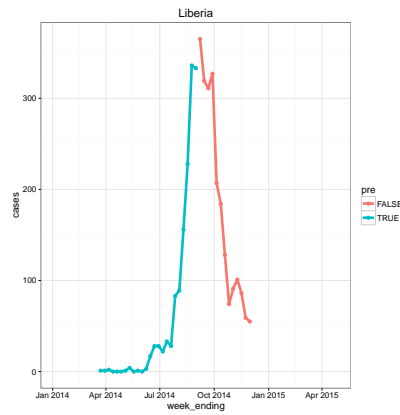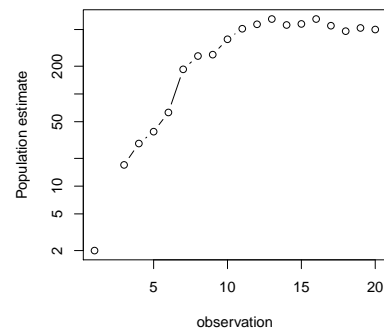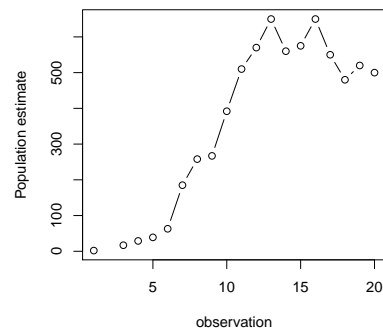
1.1 Population Examples

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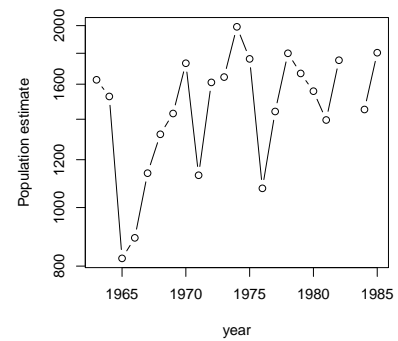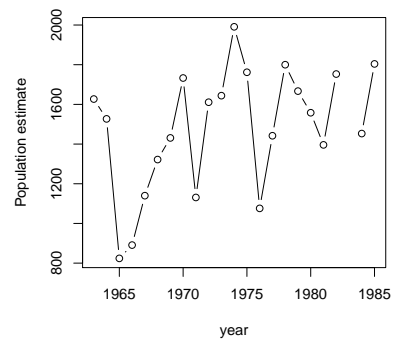
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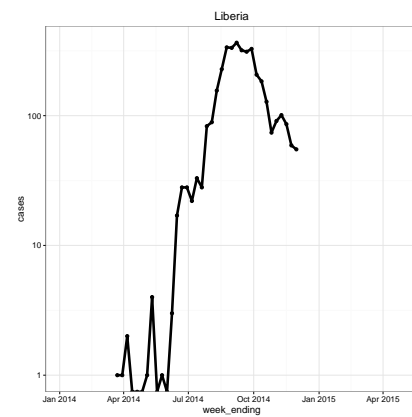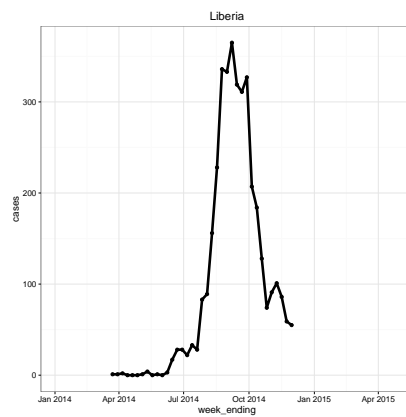
Ebola

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?
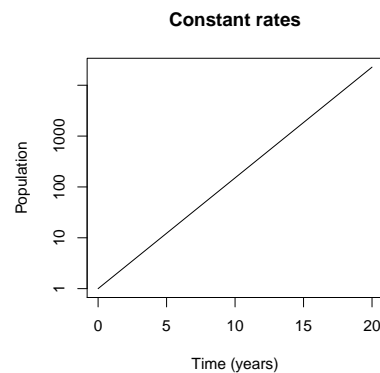
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2   Continuous-time regulation

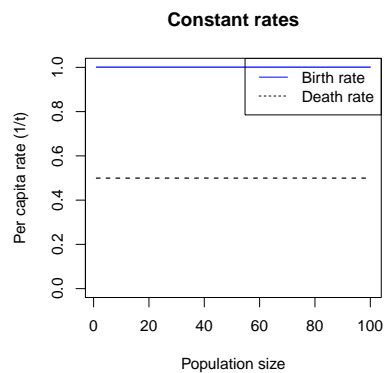## Build on the linear model

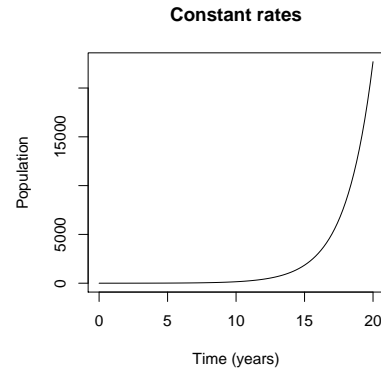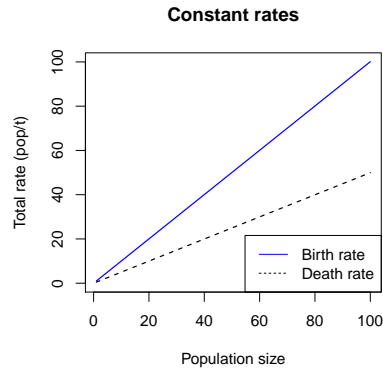- Our linear population model is:

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

- Per-capita rates are constant

- **Population-level rates are linear**

- Behaviour is exponential

Individual perspective

Population perspective

Constant rates

Total rate (pop/t) vs Population size

Birth rate
Death rate

Constant rates

Population vs Time (years)

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

- Reproductive number now also changes with N:

    - **Answer:** $\mathcal{R}(N) = b(N)/d(N)$

- When the population is crowded, individuals are stressed and the reproductive number will typically go down.

Carrying capacity

- If a population has $\mathcal{R}(N) > 1$ when it's not crowded

- The population should increase 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:

    - $b(N) = b_0 \exp(-N/N_b)$
    - $d(N) = d_0 \exp(N/N_d)$ (**fixed a typo here**)

- 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?

    - **Answer:** The same as before: population size (or density)
    - **Answer:** We are still assuming that's all we need to know

Parameters

- What quantities describe the rules for this system?

    - **Answer:** b_0 [1/time]
    - **Answer:** d_0 [1/time]
    - **Answer:** N_b [indiv] (or [indiv/area])
    - **Answer:** N_d [indiv] (or [indiv/area])

Characteristic *scale*

- A characteristic scale for density dependence is analogous to a characteristic time

- For example: $b(N) = b_0 \exp(-N/N_b)$

    - N_b is the characteristic scale of density-dependence in birth rate
    - If $N \ll N_b$, density dependence is linear (and relatively small)
    - If $N \gg N_b$, density dependence is exponential, and very large (virtually no births)
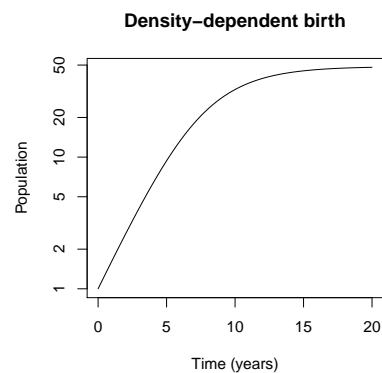
Model

- Dynamics:

    - $$\frac{dN}{dt} = (b_0 \exp(-N/N_b) - d_0 \exp(N/N_d))N \textbf{ (fixed the same typo here)}$$

- Exact solution:

    - Insanely complicated

- Behaviour of the solution:

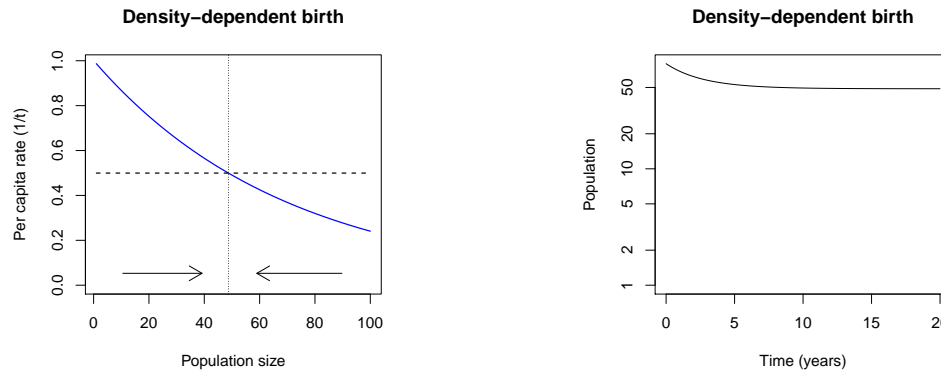   - Pretty easy!

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

Per capita rate (1/t) vs Population size

Density−dependent birth

Population vs Time (years)

High starting population

Density−dependent birth

Per capita rate (1/t) vs Population size

Density−dependent birth

Population vs Time (years)

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

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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
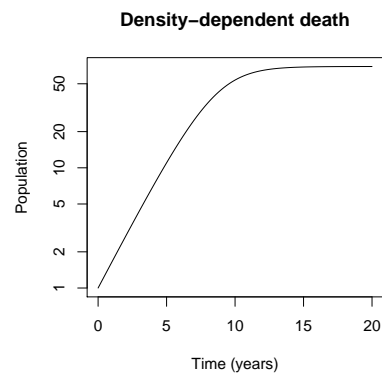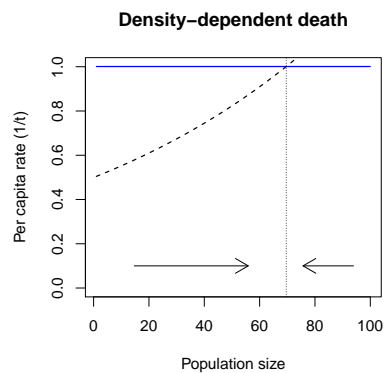
Population perspective picture
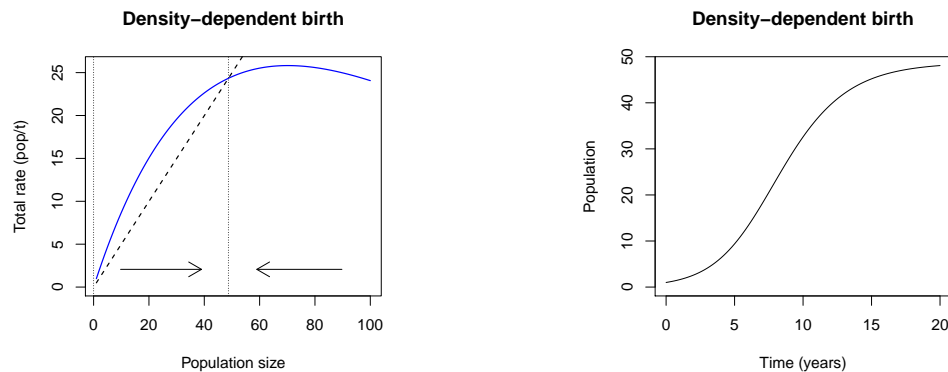
Decreasing birth rate

- 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
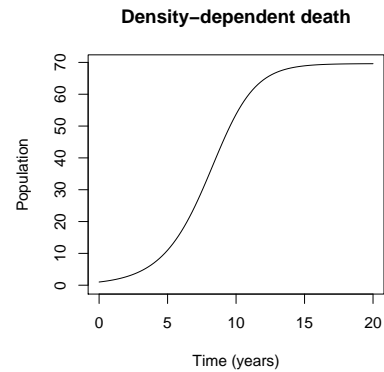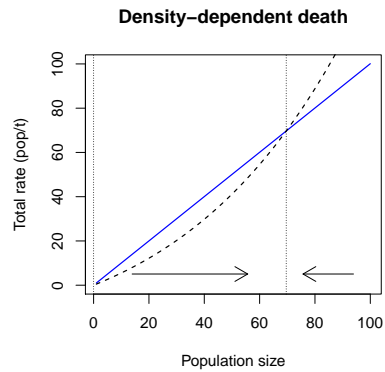
Increasing death rate

- 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
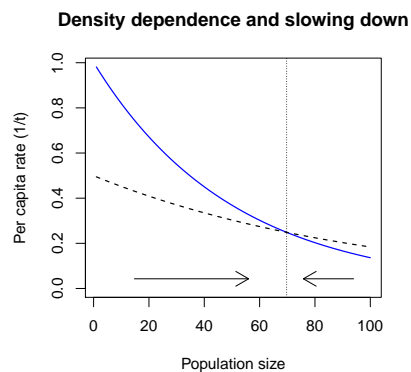
Individual perspective

Population perspective

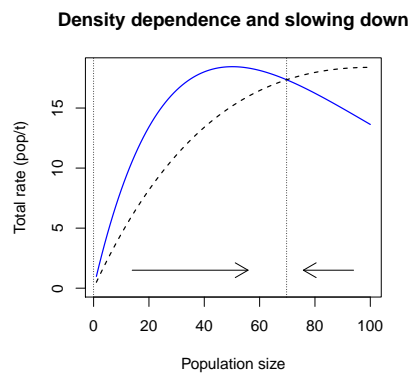**Density−dependent death**

Density−dependent death

Decreasing death rate

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

- How is this consistent with density dependence?

    – **Answer:** Birth rate must decrease even faster

Individual perspective

Density dependence and slowing down

Density dependence and slowing down

Population perspective

Density dependence and slowing down

Total rate (pop/t) vs Population size

Density dependence and slowing down

Population vs Time (years)

Other examples

- There are two other possible scenarios for density dependence

- For fun, you can try to think of what they are

- But all of these examples have similar behaviour

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

Maximum growth rates

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

  - **Answer:** When density is low. This is an assumption.

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

  - **Answer:** Intermediate between low density and the carrying capacity. This is a something we learn from the model

2.3 Equilibria and time scales

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

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

- In this simple model, when does equilibrium occur?

    - **<u>Answer</u>:** $b(N) = d(N)$ (the carrying capacity)
    - **<u>Answer</u>:** $N = 0$ (the population is absent)

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:
        * **<u>Answer</u>:** It should increase $(b > d)$
    - If population is just above the equilibrium:
        * **<u>Answer</u>:** It should decrease $(d > b)$

Basic reproductive number

- The reproductive number of a population not affected by crowding is called the **basic reproductive number**

    - Written $\mathcal{R}_0$ or $\mathcal{R}_{\max}$.

- In this model, when $\mathcal{R}_0 < 1$ the population:

    - **<u>Answer</u>:** Always decreases

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

    - **Answer:** Increases when it is small

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

    - **Answer:** $\mathcal{R}_0 = b(0)/d(0)$
    - **Answer:** $\mathcal{R}_0$, $b(0)$, and $d(0)$ are limits

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

R_0 < 1

R_0 < 1
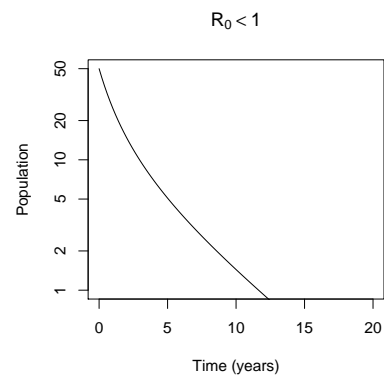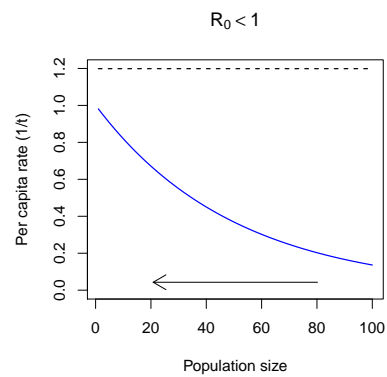
Population perspective

R_0 < 1

R_0 < 1
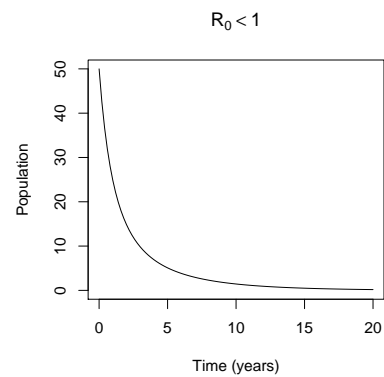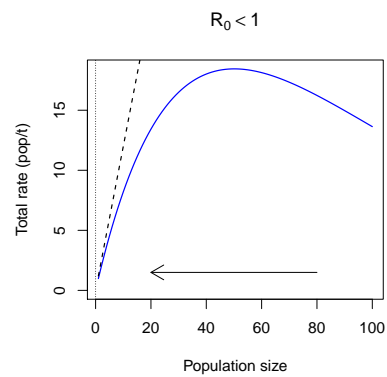
$\mathcal{R}_0$ and thresholds

- 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
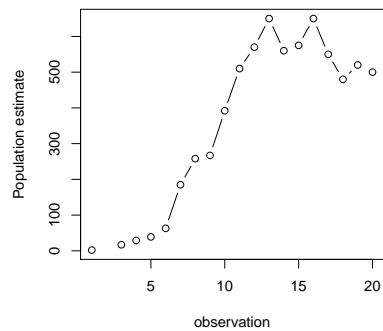
Dynamics of density-dependent populations

- 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

  - **Answer:** If I went from A to B, I can't go from B to A by following the same rules

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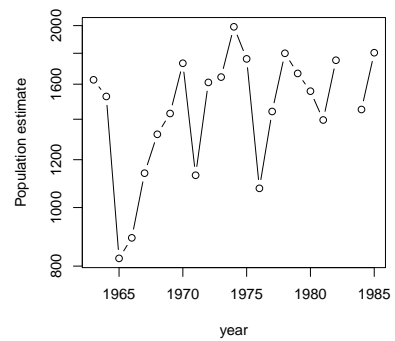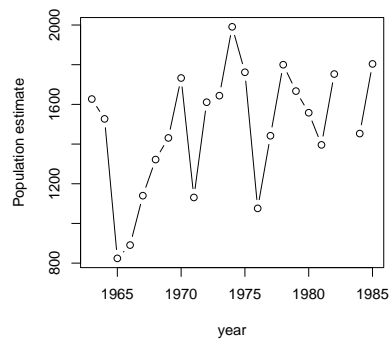
Paramecia
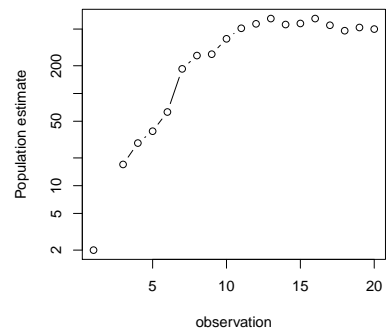
Dynamics of real-world populations

- Initial exponential growth and leveling off frequently observed

- Exponential approach to equilibrium hard to observe

  - Real populations are subject to **stochastic** (random) effects

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– 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).

- **Answer:** Birth rate, or death rate, or both

- **Answer:** *Not* the population multiplier

- **Answer:** Rates might depend on the past, but the births and deaths are happening in the current population

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?

  - **Answer:** It *keeps* growing

  - **Answer:** It needs to *pass* the equilibrium and look back in time before it will stop growing

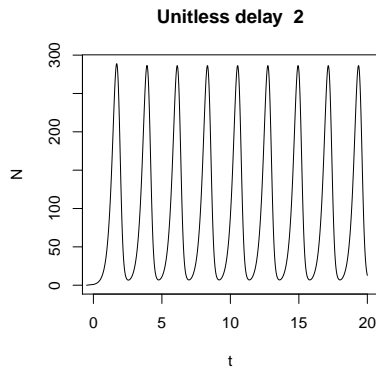- So what happens in the long term?

Time-delayed dynamics

Unitless delay 1

Time-delayed dynamics

Unitless delay 1.5

Time-delayed dynamics

Unitless delay 2
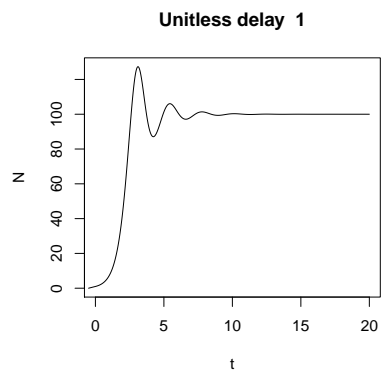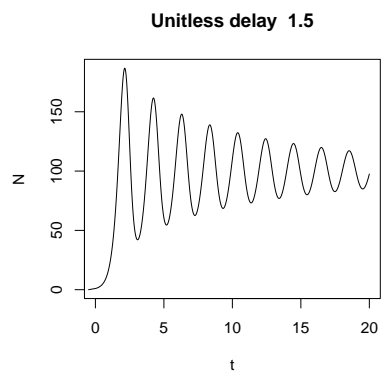
Time-delayed population models

- 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?

  - **Answer:** It must be something else in the model with units of time

  - **Answer:** It should have something to do with behaviour near the equilibrium

  - **Answer:** In fact, we compare the time delay to the characteristic time of approach to the carrying capacity (calculated by ignoring the delays)

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?

  - **Answer:** f_0 [1]
  - **Answer:** p_0 [1]
  - **Answer:** N_f [indiv] (or [indiv/area])
  - **Answer:** N_p [indiv] (or [indiv/area])

What is $\mathcal{R}_0$?

- $\mathcal{R}$ is the fecundity multiplied by the lifespan

  - **Answer:** Lifespan $= 1/\mu = 1/(1-p)$
  - **Answer:** $\mathcal{R} = f/(1-p)$

- $\mathcal{R}_0$ is $\mathcal{R}$ in the limit where density is low

  - **Answer:** $f_0/(1-p_0)$

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
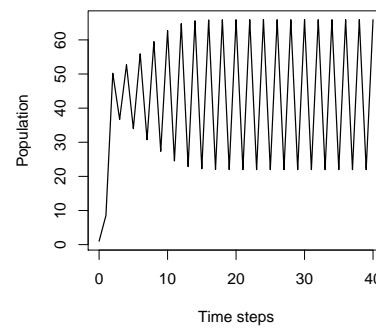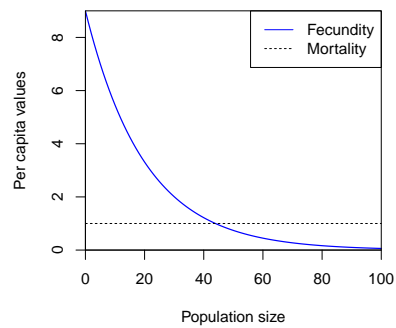
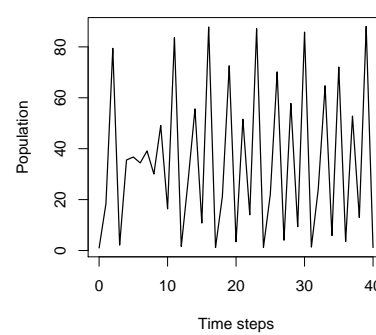- We can even do it in the spreadsheet if we have time
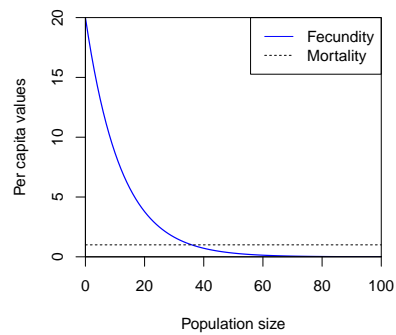
We expect simple dynamics
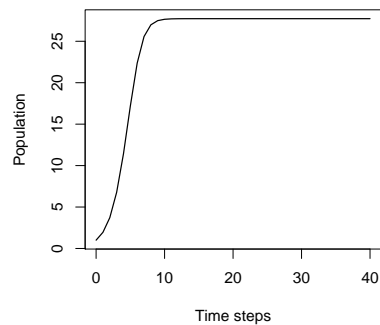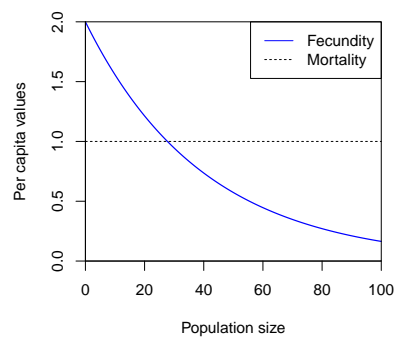
Damped oscillations
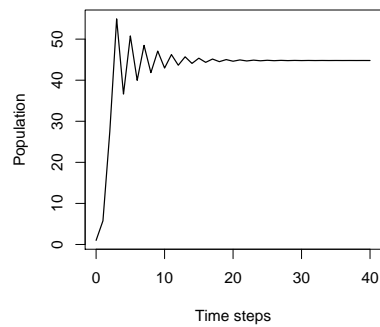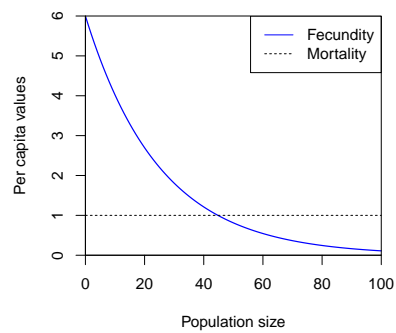
Persistent oscillations

## 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

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Complex behaviour in our simulations

- In our simple models, as N_T increases, what happens to λ?

    – **Answer:** We assume it goes down

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

    – **Answer:** $N_{T+1} = \lambda(N)N_T$

    – **Answer:** It's not obvious! λ goes down, but N goes up.

    – **Answer:** In this model, N_{T+1} always goes down eventually, but other models may differ
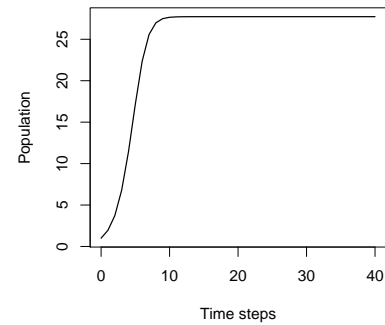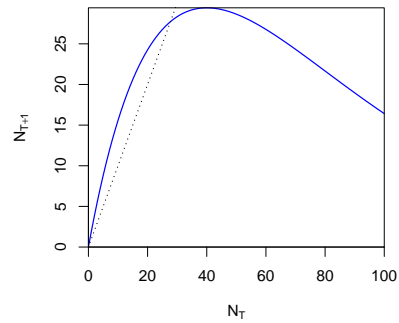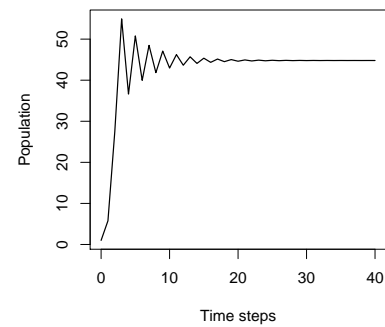
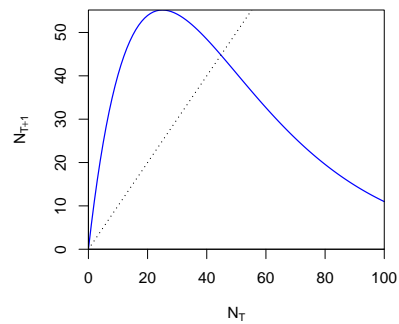## Response to population increase
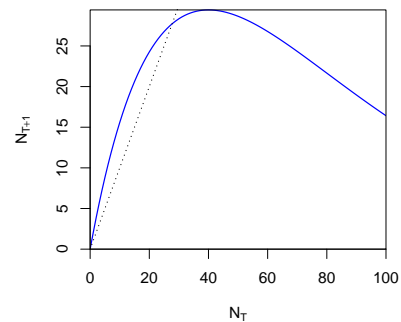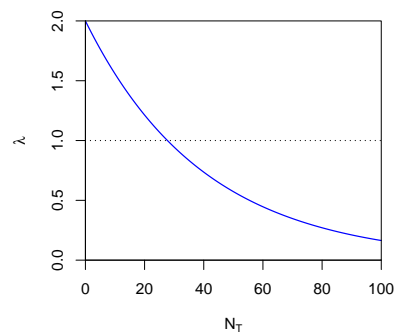
Turnover

- 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

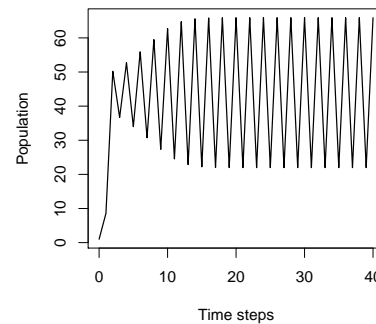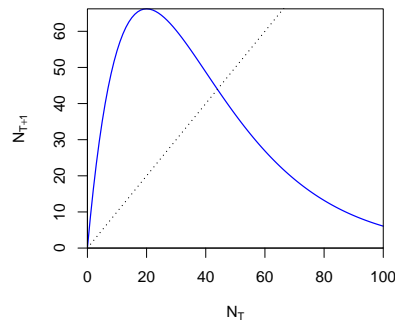   – A small population this year leads to a large population next year

Simple dynamics

Damped oscillations

Persistent oscillations

Complex behaviour in our conceptual model

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

  - **Answer:** If resources are *depleted*
  - **Answer:** If there is a *delayed* effect of individuals' not having enough resources

- When should the mapping *not* turn over?

  - **Answer:** When competition does not lead to depletion
  - **Answer:** When effects of competition are immediate
 - **Answer:** When dominant individuals are not affected by crowding

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 success-
  fully control key resources and do well no matter how large the popu-
  lation is

  - Contest competition doesn't usually lead to turning over, even
    with delay

- How does contest competition square with regulation?

  - **<u>Answer</u>:** Regulation means that λ has to go down with N_T –
  - **<u>Answer</u>:** Regulation means that λ has to go down with N_T;
  - N_{T+1} does not have to.

Contest regulation
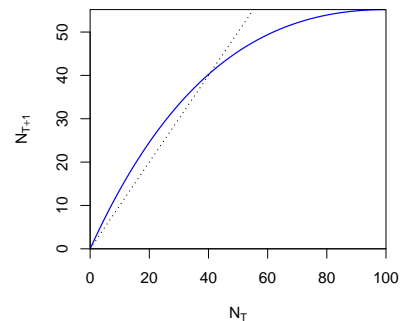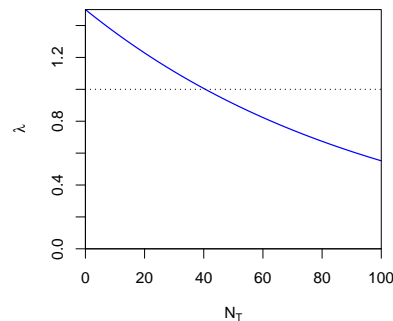
Songbirds

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

  - **<u>Answer</u>:** The ones limited by food are more likely to have scram-
    ble competition and turnover

Plants

- Some plant populations are limited by water, and some by light

- Which is more likely to work out as a scramble?

    - **Answer:** Light is very likely to work out as a "contest" – the taller individuals will win and do OK
    - **Answer:** Water works as a scramble in some environments, and a contest in others

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

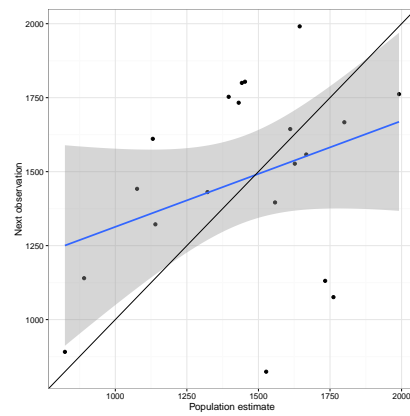## Complex behaviour in real populations

- 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
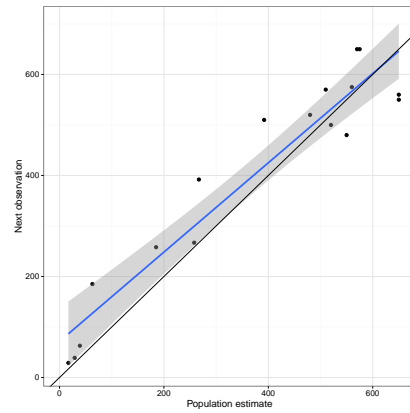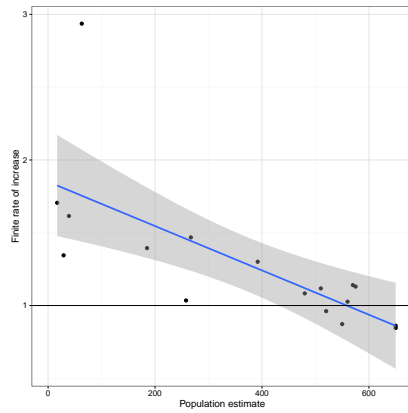
Elk
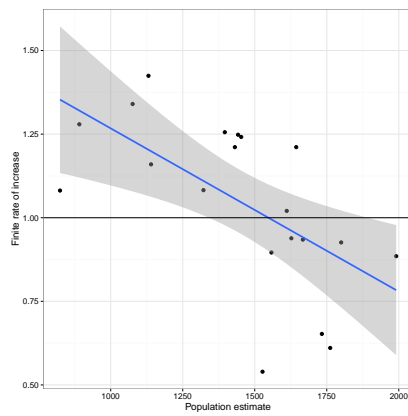
Real populations

- 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?

    - **Answer**:

- What about two butterflies?

    - **Answer**:

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?

    - **Answer**: Individuals may have trouble finding mates
    - **Answer**: Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
    - **Answer**: Individuals in larger populations may hunt co-operatively
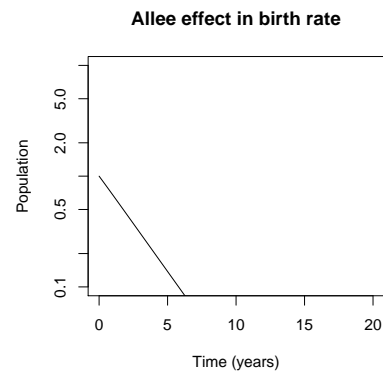   - **Answer**: Genetic effects (inbreeding, loss of valuable variation)

Types of Allee effect
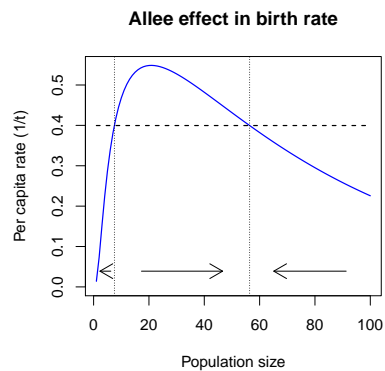
- Allee effects can affect the birth rate

  - **Answer:** if it goes *down* at low density

- ... or the death rate

  - **Answer:** if it goes *up* at low density

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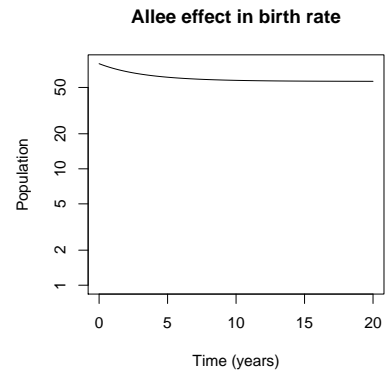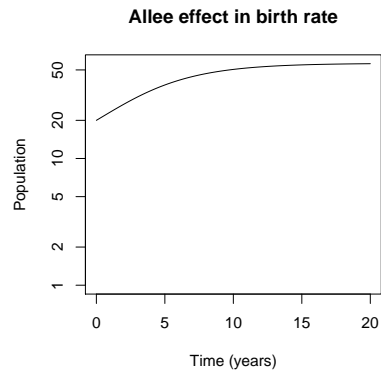
- What will this model do, if the initial population is:

  - low, medium or high?

Individual perspective

Allee effect in birth rate

Allee effect in birth rate

Individual perspective

Allee effect in birth rate

Allee effect in birth rate

Population perspective

Allee effect in birth rate

Allee effect in birth rate

Population perspective

Allee effect in birth rate
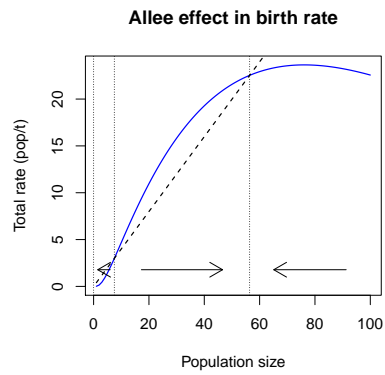
Allee effect in birth rate
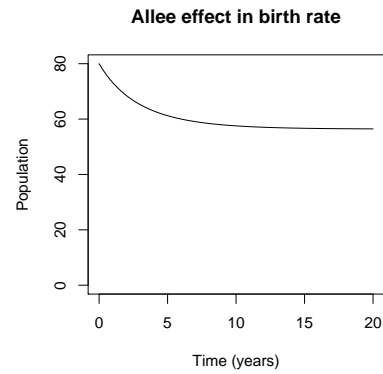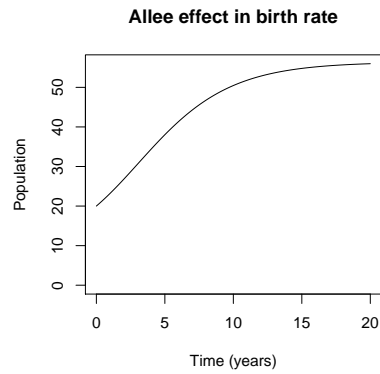
Allee effect in death rate

- 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

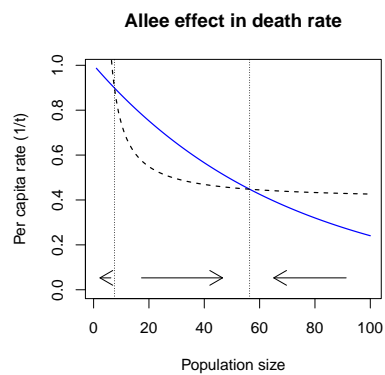**Allee effect in death rate**

Allee effect in death rate

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

  - **<u>Answer:</u>** If $\mathcal{R}_0 < 1$ population can't invade, but if $\mathcal{R}_{\max} > 1$ it can still 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
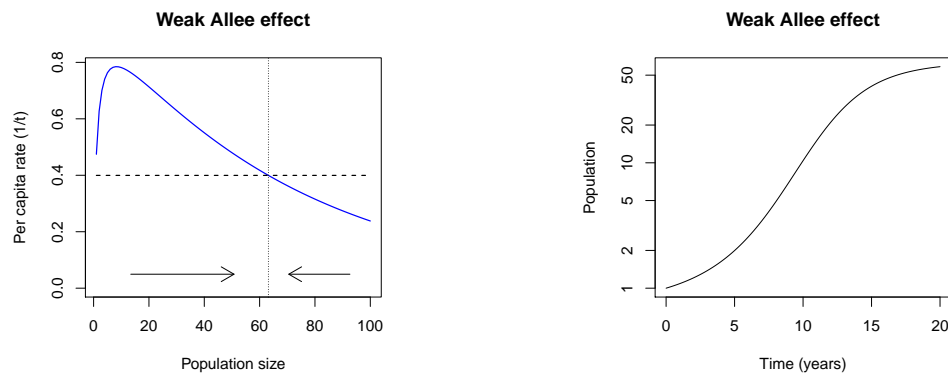
Weak Allee effect

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?

    - **Answer:** Maybe it's a weak effect
    - **Answer:** Maybe conditions have changed (it used to be a weak effect, or no effect)
    - **Answer:** Maybe a large initial group established by chance

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?

  - **Answer:** $\lambda = 1.5$ (remember not to multiply by the sex ratio twice!)
  - **Answer:** Almost anything can 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

  - **Answer:** Population could be lucky or unlucky

- What if $\lambda < 1$?

  - **Answer:** The population would go extinct eventually, even if it's lucky

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

  - **Answer:** A bad year is bad for everyone

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

  - **Answer:** Large populations can average out over *time*
  - **Answer:** If the "mean" value of R_0 is greater than 1, large population should survive the ups and downs

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