

# UNIT 3 Non-linear population models

# Outline

## Introduction

### Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

# Introduction

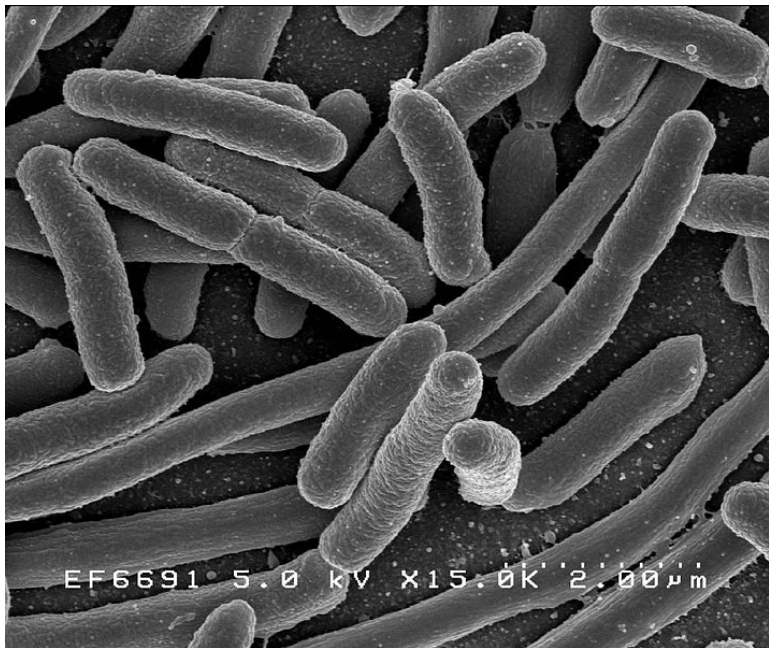
- ▶ In **linear** population models, per capita rates are independent of population size
- ▶ In **non-linear** models, not so much
- ▶ Why might per capita birth and death rates change with population size?
- ▶ What does this imply about population **dynamics**?

# The first law of population dynamics

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

# The second law of population dynamics

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



# The third law of population dynamics

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

# Long-term growth rates

- ▶ Populations maintain long-term growth rates very close to  $r = 0$
- ▶ This is not possible just by chance, or averaging:
  - ▶ Population size must affect its own growth rate
  - ▶ Directly or indirectly
  - ▶ Long term or short term



# Changing growth rates

- ▶ What is an example of a density-dependent mechanism that affects growth rate?
  - ▶ \* Predators
    - ▶ \* But! Unless the amount of predators increases as well, they might do *worse* at controlling the population
  - ▶ \* Diseases
    - ▶ \* We have the same concern as above. But diseases are *very* likely to increase in large populations.
  - ▶ \* Insufficient resources
    - ▶ \* Limitation: e.g., oak trees use all the available light
    - ▶ \* Destruction: gypsy moths kill all the oak trees
  - ▶ \* Not everything that harms the species is density dependent!

# 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?
  - ▶ \* Because the long-term average value of  $r$  has to be very close to 0
  - ▶ \* This is true for every population
  - ▶ \* This is unlikely to occur by chance
  - ▶ \* Thus, it must be through direct or indirect responses to the population size

# Outline

## Introduction

### Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

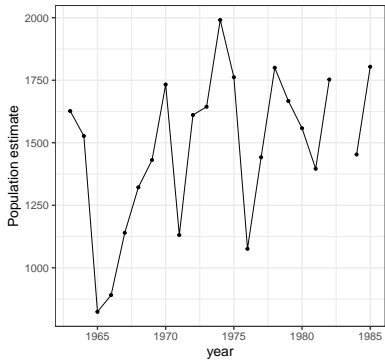
Allee effects

Stochastic effects

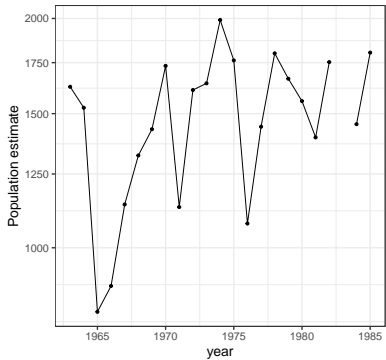
(preview)

## Elk

Elks in Grand Teton

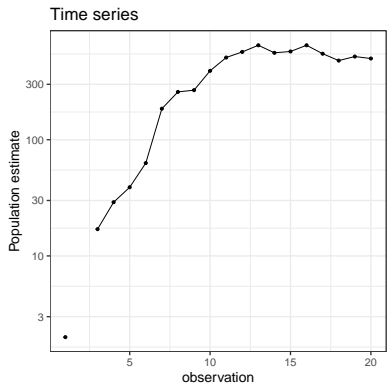
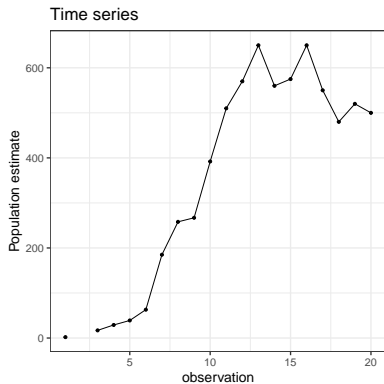


Elks in Grand Teton



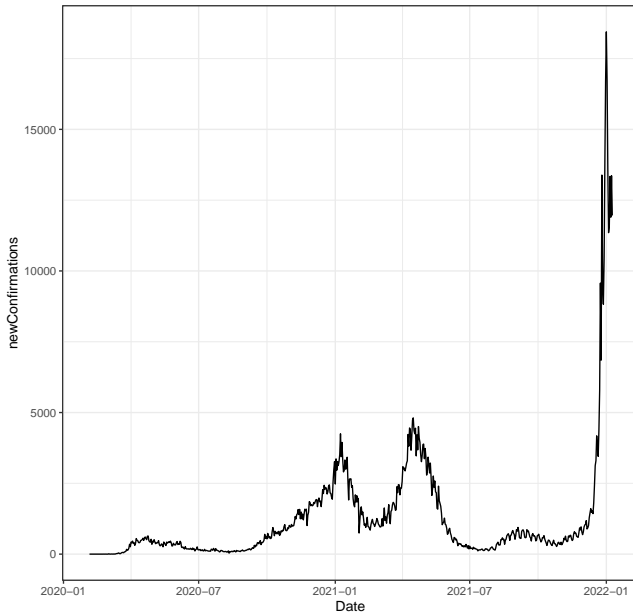


# Paramecia (preview)



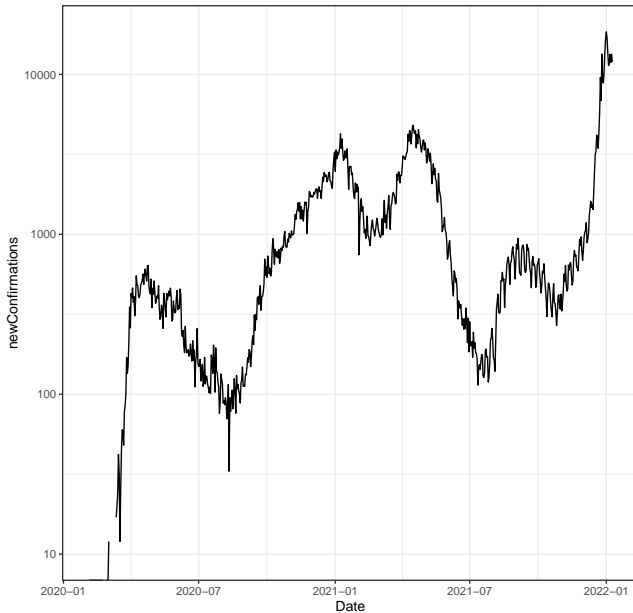
# Coronavirus (preview)

ON coronavirus

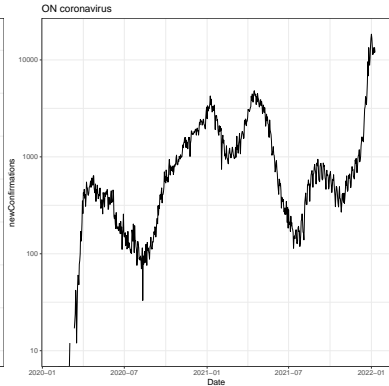
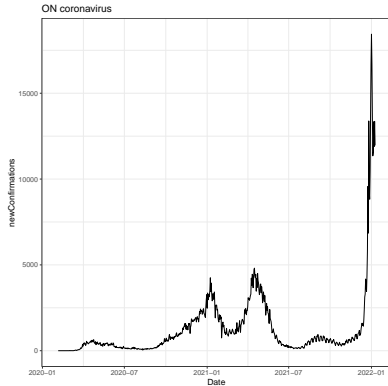


# Coronavirus (preview)

ON coronavirus



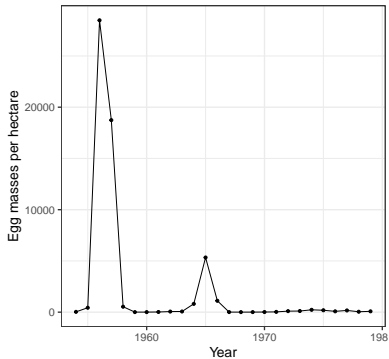
# Coronavirus (preview)



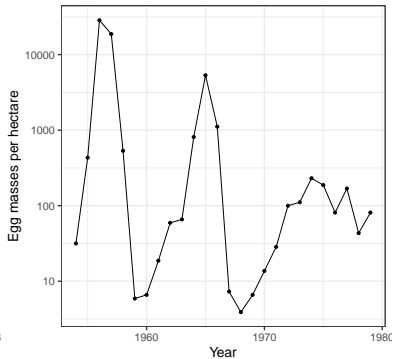
Add This picture may be updated automatically

# Gypsy moths (preview)

Gypsy moth eggs



Gypsy moth eggs



# 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?

# Outline

## Introduction

Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

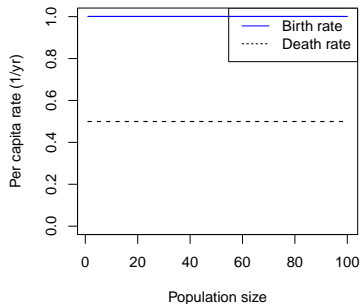
# Build on the linear model

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

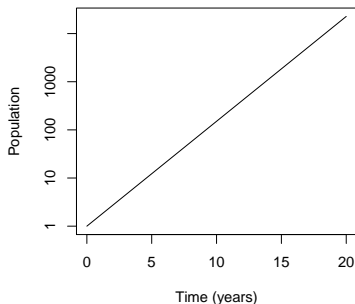


# Individual perspective

Constant rates



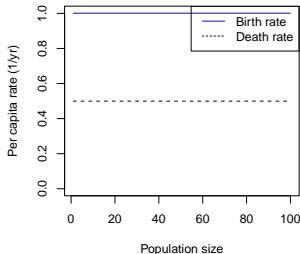
Constant rates



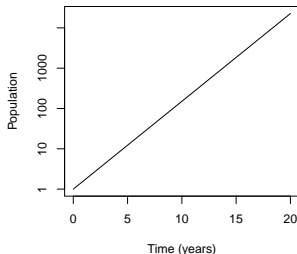
## Individual perspective

- ▶ 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

Constant rates

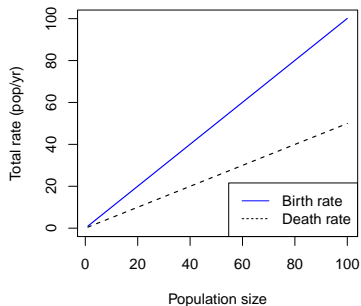


Constant rates

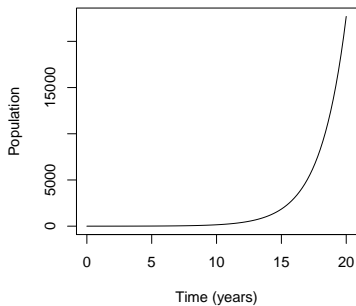


# Population perspective

**Constant rates**

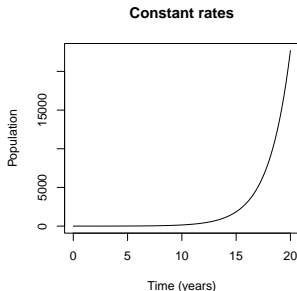
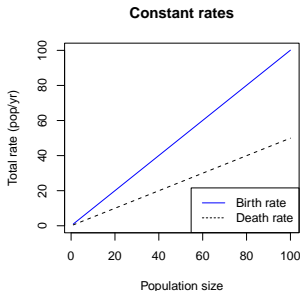


**Constant rates**



# 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

# 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  $N$ :
  - ▶ \*  $\mathcal{R}(N) = b(N)/d(N)$
- ▶ When the population is crowded, individuals are stressed and the reproductive number will typically go down.



# Carrying capacity

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

# Logistic model

- ▶ A popular model of density-dependent growth is the logistic model
- ▶ Per capita instantaneous growth rate  $r$  is a function of  $N$ 
  - ▶  $r(N) = r_{\max}(1 - N/K)$
  - ▶ Consistent with various assumptions about  $b(N)$  and  $d(N)$
- ▶ Population increases to  $K$  and 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 smooth and keeps track of birth and death rates separately
  - ▶ Birth rate goes down with characteristic scale  $N_b$
  - ▶ Death rate goes up with characteristic scale  $N_d$

# Exponential-rates vs. logistic

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

# Outline

## Introduction

Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

# 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?
  - ▶ \* The same as before: population size (or density)
  - ▶ \* We are still assuming that's all we need to know
    - ▶ \* In other words, that all individuals are the same.



# Parameters

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

# Characteristic *scale*

- ▶ A characteristic scale for density dependence is analogous to a characteristic time
  - ▶ It is a *parameter* with the same units as a state variable, and sets a standard by which we measure that variable
  - ▶ Nothing (with units) is big or small until it's compared to something with the same units
- ▶ 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:

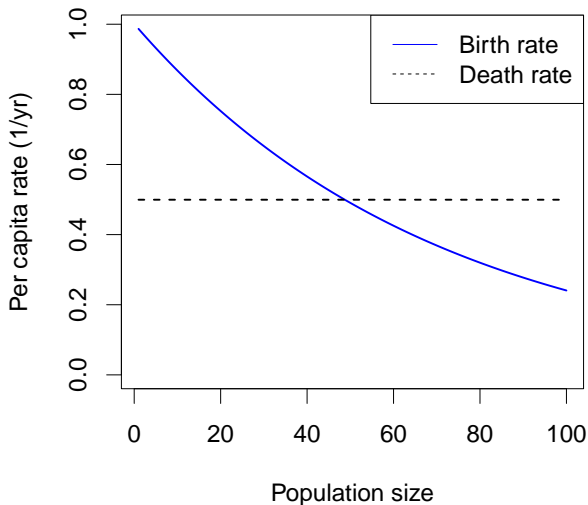
- ▶ Pretty easy!

# Dynamics

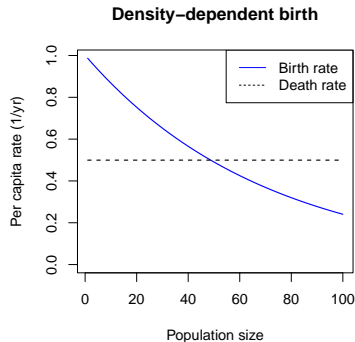
- ▶ What sort of **dynamics** do we expect from our conceptual model?
  - ▶ I.e., how will it change through time?
- ▶ What will the population do if it starts
  - ▶ near zero?
  - ▶ near the equilibrium?
  - ▶ at a high value?

## *A model (present)*

### Density-dependent birth

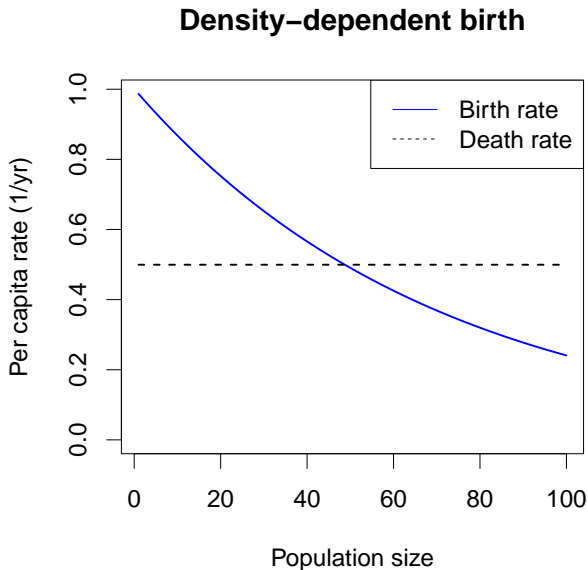


# What is the characteristic scale?



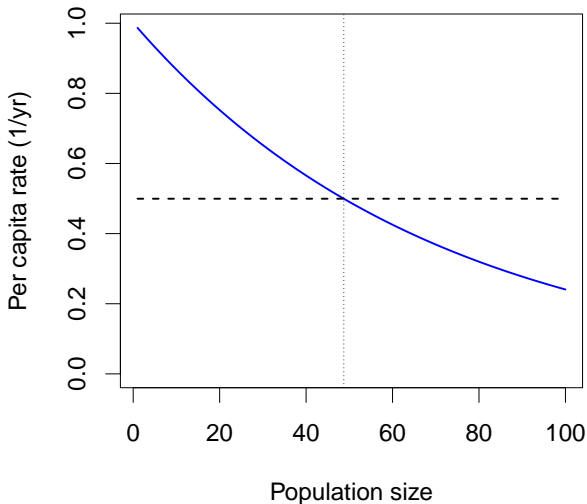
- ▶ No density dependence in death rate
- ▶ Characteristic scale for birth rate is about 70 indiv

*What will this model do? (present)*



*What will this model do? (present)*

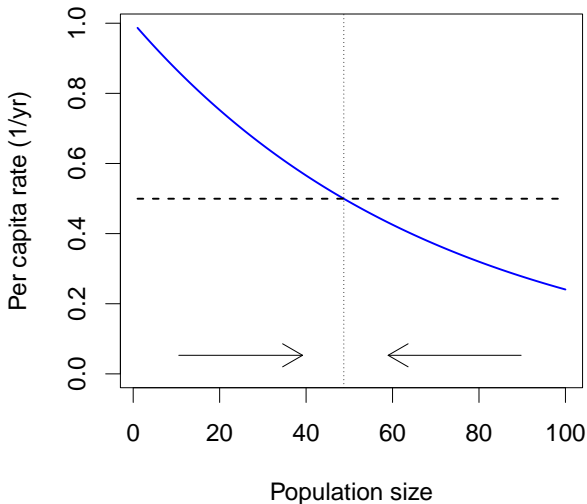
### Density-dependent birth



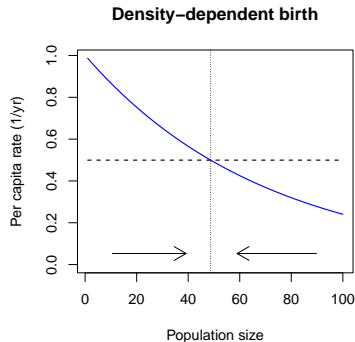


*What will this model do? (present)*

### Density-dependent birth

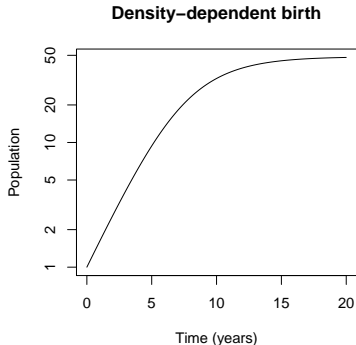
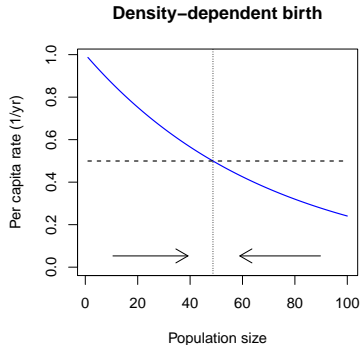


# What will this model do?

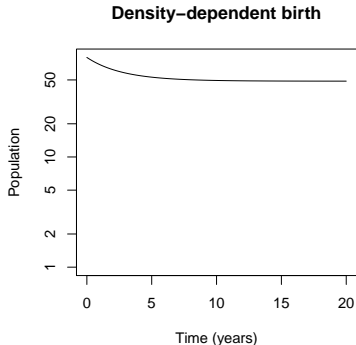
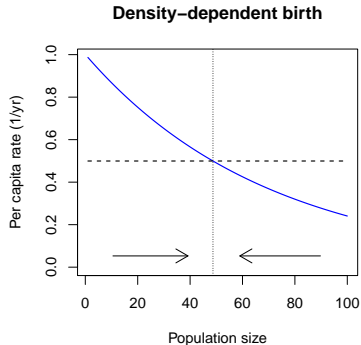


- ▶ Increase when population is below equilibrium
- ▶ Decrease when population is above equilibrium
- ▶ Converge

## Low starting population example (present)

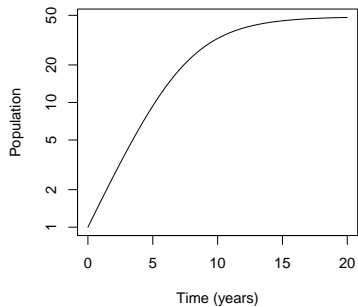


## High starting population example (present)

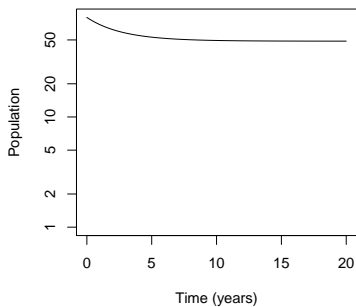


# Examples

**Density-dependent birth**



**Density-dependent birth**



# Outline

## Introduction

Population Examples

## Continuous-time regulation

A simple, continuous-time model

**Simulating model behaviour**

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

# Simulations

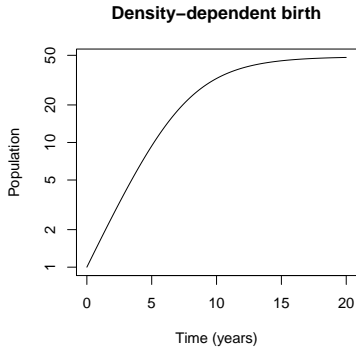
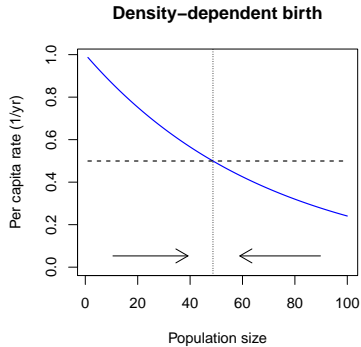
- ▶ We will simulate the behaviour of populations in continuous time using the program R
- ▶ This program generates the pictures in this section by implementing our model of how the population changes instantaneously

# 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



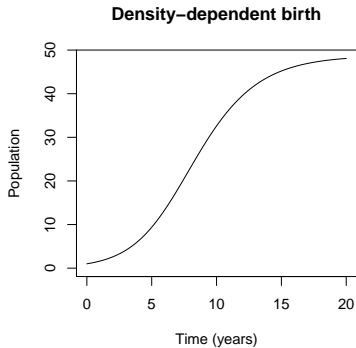
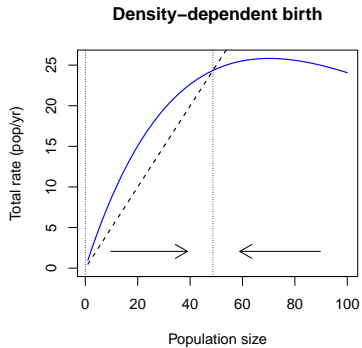
## What will this model do? (repeat)



# Population-scale pictures

- ▶ We can view graphs of our population assumptions on the population scale
  - ▶ total birth and death rates
    - ▶ units [indiv/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



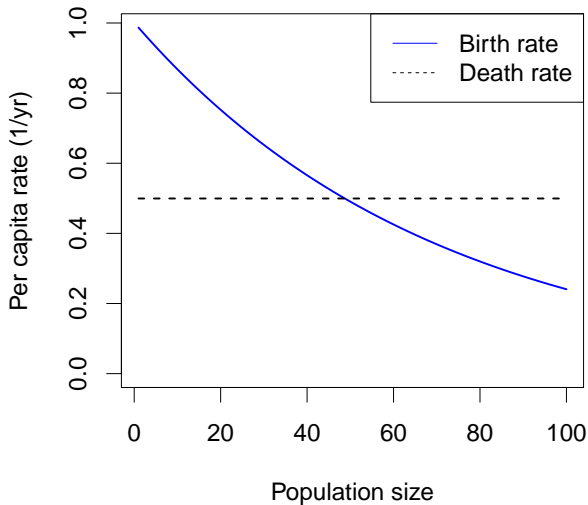
# Decreasing birth rate

- ▶ 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



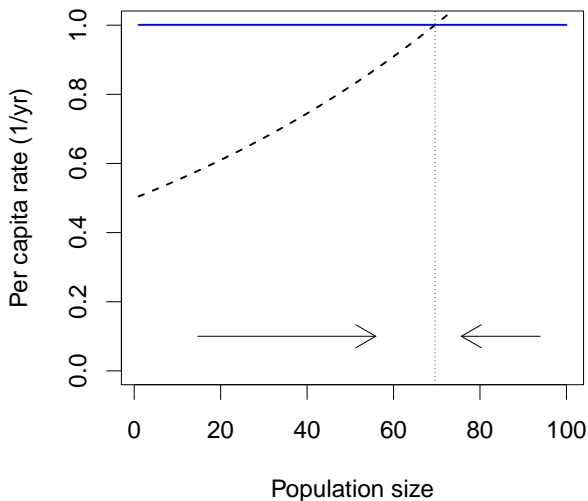
## *Decreasing birth rates (repeat)*

### Density-dependent birth



## *Increasing death rates (present)*

### Density-dependent death



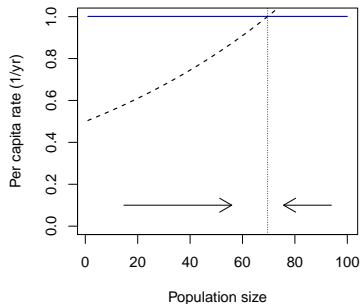
# Increasing death rate

- ▶ 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

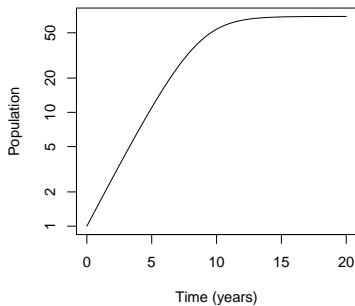


# Individual perspective

Density-dependent death



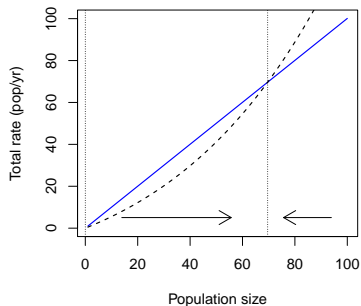
Density-dependent death



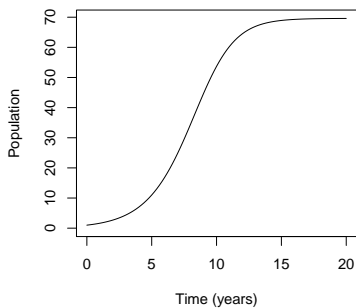


# Population perspective

**Density-dependent death**

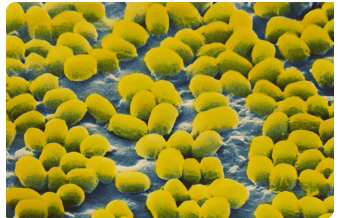


**Density-dependent death**



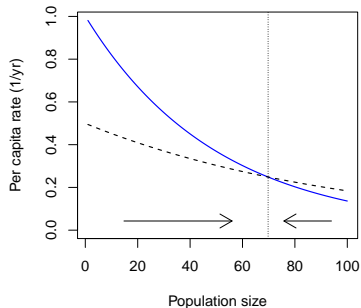
# Decreasing death rate

- ▶ 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?
  - ▶ \* Birth rate must decrease even faster

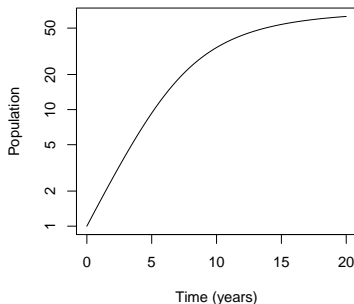


# Individual perspective

Density dependence and slowing down

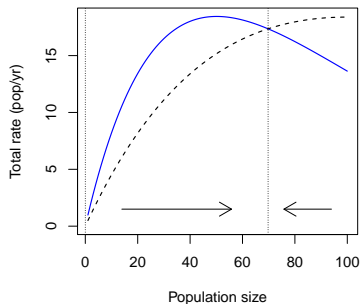


Density dependence and slowing down

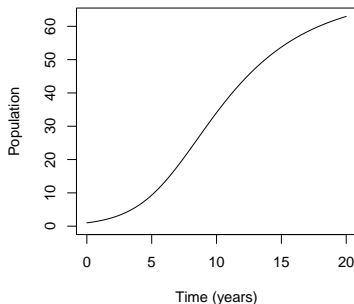


# Population perspective

Density dependence and slowing down



Density dependence and slowing down



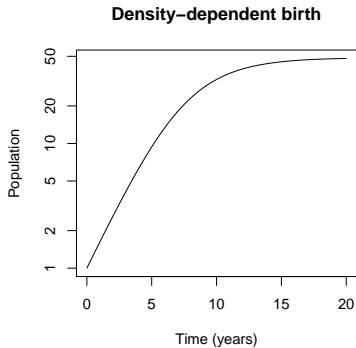
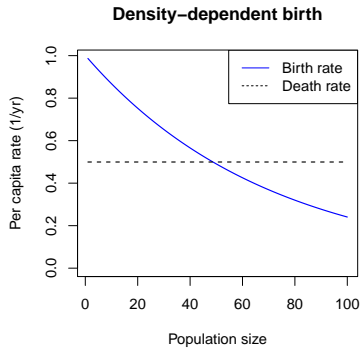
# Other examples

- ▶ 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

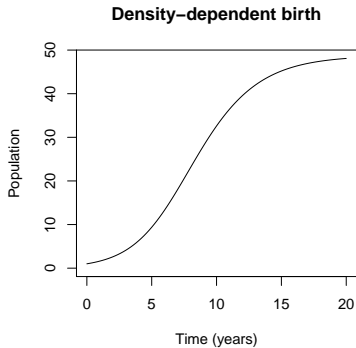
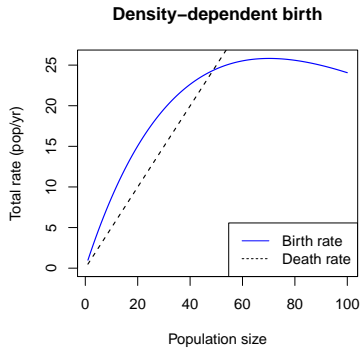
## Maximum growth rates (preview)

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

## Individual perspective (repeat)



## Population perspective (repeat)

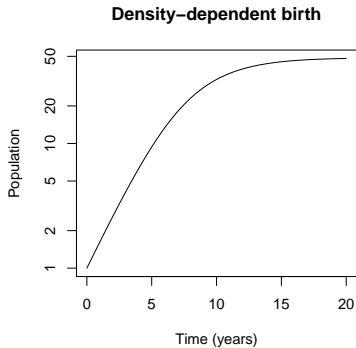
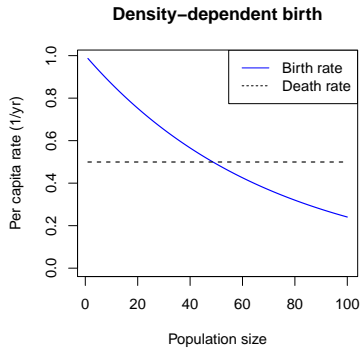




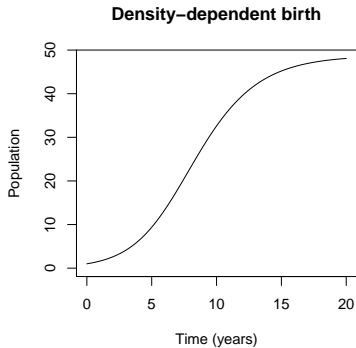
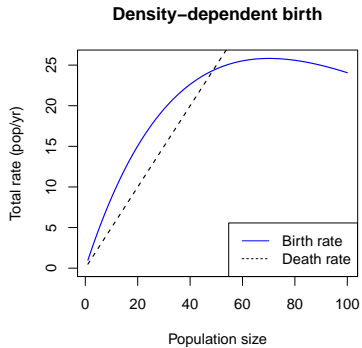
# Maximum growth rates

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

## Individual perspective (repeat)



## Population perspective (repeat)



# Outline

## Introduction

Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

**Equilibria**

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

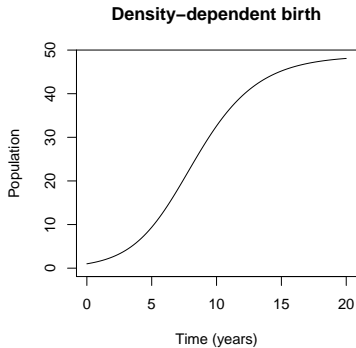
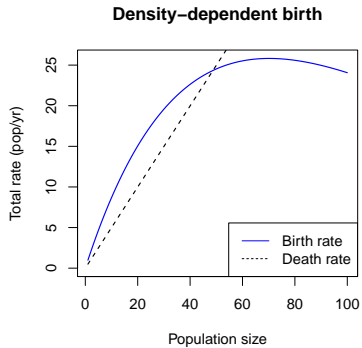
# Equilibria

- ▶ 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?
  - ▶ \*  $(b(N) - d(N))N = 0$
  - ▶ \*  $b(N) = d(N)$  (the carrying capacity)
  - ▶ \*  $N = 0$  (the population is absent)

# Stable and unstable equilibria

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

## Population perspective (repeat)



# What kind of equilibrium?

- ▶ How can we tell an equilibrium is stable?
  - ▶ If population is just below the equilibrium:
    - ▶ \* It should increase ( $b > d$ )
  - ▶ If population is just above the equilibrium:
    - ▶ \* 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:
  - ▶ \* Always decreases
- ▶ When  $\mathcal{R}_0 > 1$  the population:
  - ▶ \* Increases when it is small
  - ▶ \* Eventually  $\mathcal{R}$  will decrease

- ▶ What is  $\mathcal{R}_0$  in our current model?
  - ▶ \*  $\mathcal{R}_0 = b(0)/d(0)$
- ▶ How do we interpret  $b(0)$  and  $d(0)$ ?
  - ▶ \* Nothing actually grows or dies when  $N = 0$
  - ▶ \* We think of  $b(0)$ , and  $d(0)$  (and  $\mathcal{R}_0$ ) as limits
    - ▶ \* What are the values when density is very low?

# Invasion

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

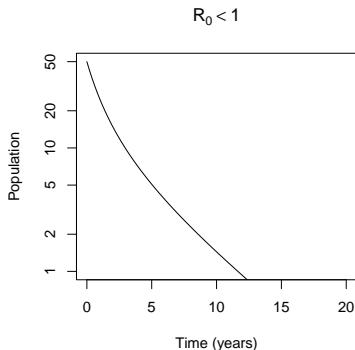
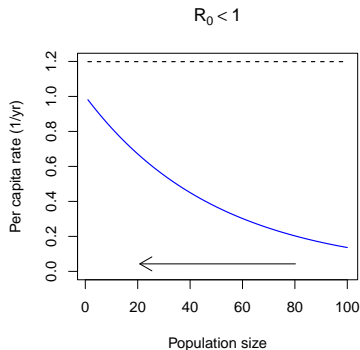
# Invasion examples

- ▶ What are some examples of biological invasions?
  - ▶ \* NOANS
  - ▶ \* NOANS
  - ▶ \* NOANS
  - ▶ \* NOANS

# Different behaviours

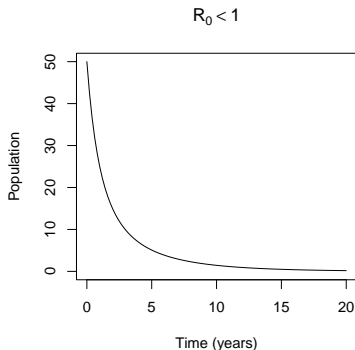
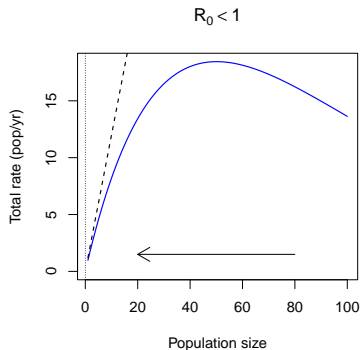
- ▶ When  $\mathcal{R}_0 > 1$ , the population invades
  - ▶ Zero equilibrium is unstable, carrying capacity equilibrium is stable
- ▶ When  $\mathcal{R}_0 < 1$ , the population fails to invade
  - ▶ Zero equilibrium is stable, carrying capacity equilibrium does not exist

# Individual perspective



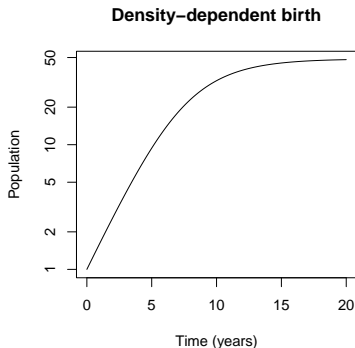
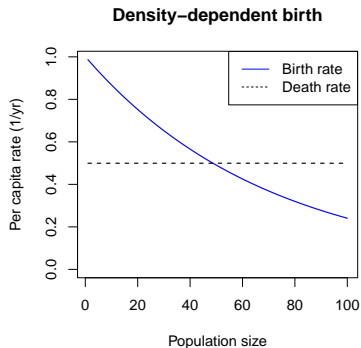
- ▶ When  $R_0 < 1$  population always decreases

# Population perspective



- ▶ When  $R_0 < 1$  population always decreases

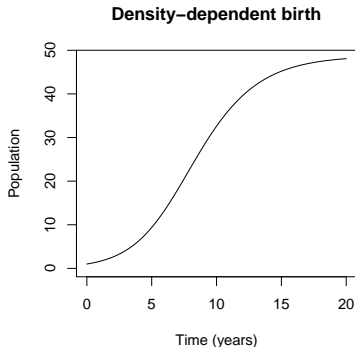
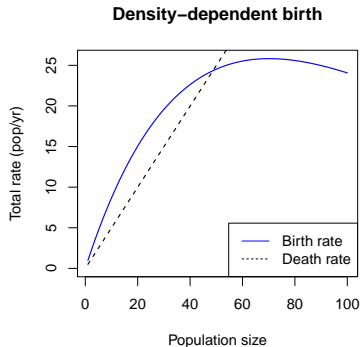
## Individual perspective (repeat)



- When  $\mathcal{R}_0 > 1$  population increases when it is small



## Population perspective (repeat)



- ▶ When  $\mathcal{R}_0 > 1$  population increases when it is small

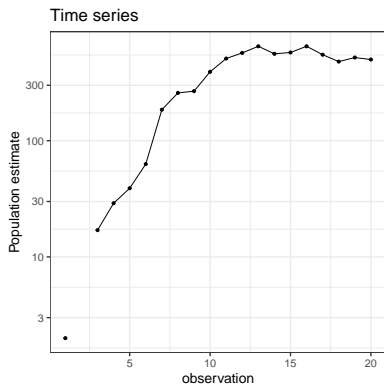
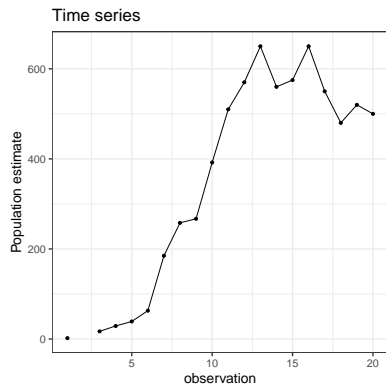
## $\mathcal{R}_0$ and thresholds

- ▶ 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

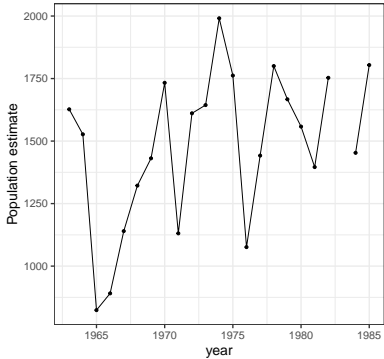
# Smooth dynamics

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

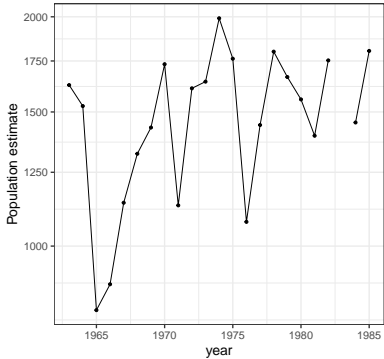
# Paramecia



Elks in Grand Teton



Elks in Grand Teton



# 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

# Summary

- ▶ 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

# Outline

## Introduction

- Population Examples

## Continuous-time regulation

- A simple, continuous-time model

- Simulating model behaviour

- Equilibria

## Discrete-time regulation

- A simple, discrete-time model

- Simulating this system

- Interpreting complex behaviour

## Small populations

- Allee effects

- Stochastic effects



# Outline

## Introduction

- Population Examples

## Continuous-time regulation

- A simple, continuous-time model
- Simulating model behaviour
- Equilibria

## Discrete-time regulation

- A simple, discrete-time model
- Simulating this system
- Interpreting complex behaviour

## Small populations

- Allee effects
- Stochastic effects

# 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:
  - ▶  $N_{T+1} = (p(N_T) + f(N_T))N_T \equiv \lambda(N_T)N_T$
- ▶ This means:
  - ▶ \*  $p$  and  $f$  can change when  $N$  changes

# Assumptions

- ▶ The population is censused at regular time intervals  $\Delta t$
- ▶ All individuals are the same at the time of census
- ▶ Population changes deterministically

# Specific assumptions

- ▶ For our examples, we will assume:
  - ▶  $f(N) = f_0 \exp(-N/N_f)$
  - ▶  $p(N) = p_0 \exp(-N/N_p)$
- ▶ This is the simplest model that is smooth and keeps track of birth and death rates separately
  - ▶ Fecundity goes down with characteristic scale  $N_f$
  - ▶ Survival goes down with characteristic scale  $N_p$

# 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?
  - ▶ \*  $f_0$  [1]
  - ▶ \*  $p_0$  [1]
  - ▶ \*  $N_f$  [indiv] (or [indiv/area])
  - ▶ \*  $N_p$  [indiv] (or [indiv/area])

# What is $\mathcal{R}_0$ ?

- ▶  $\mathcal{R}$  is the fecundity multiplied by the lifespan
  - ▶ \*  $\text{Lifespan} = 1/\mu = 1/(1 - p)$
  - ▶ \*  $\mathcal{R} = f/(1 - p)$
- ▶  $\mathcal{R}_0$  is  $\mathcal{R}$  in the limit where density is low
  - ▶ \*  $f_0/(1 - p_0)$

# 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  $\rightarrow$  low  $\rightarrow$  high  $\rightarrow$  low)
  - ▶ All kinds of other stuff



# Outline

## Introduction

- Population Examples

## Continuous-time regulation

- A simple, continuous-time model

- Simulating model behaviour

- Equilibria

## Discrete-time regulation

- A simple, discrete-time model

- Simulating this system**

- Interpreting complex behaviour

## Small populations

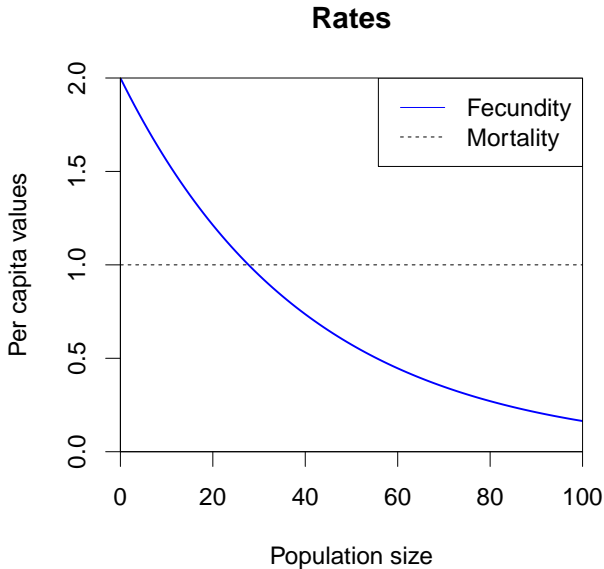
- Allee effects

- Stochastic effects

# Simulating this system

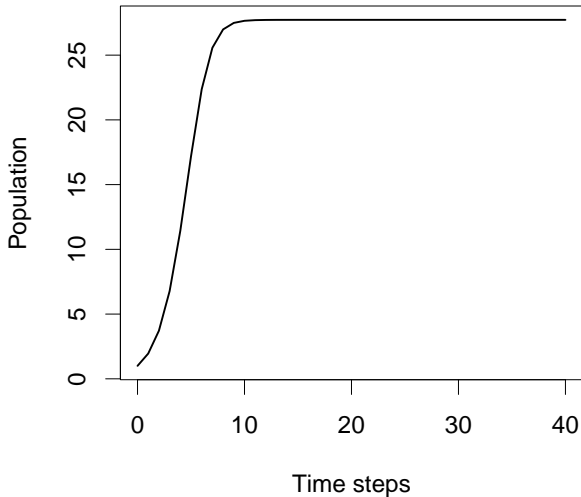
- ▶ This system can be simulated very easily by following the rule for  $N_{T+1}$  as a function of  $N_T$
- ▶ We can even do it in the spreadsheet if we have time

## *What dynamics do we expect? (preview)*

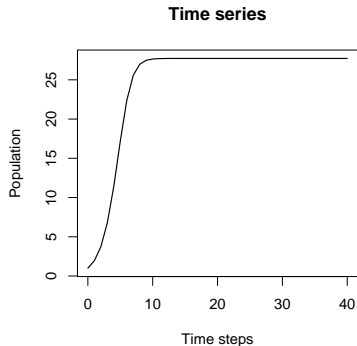
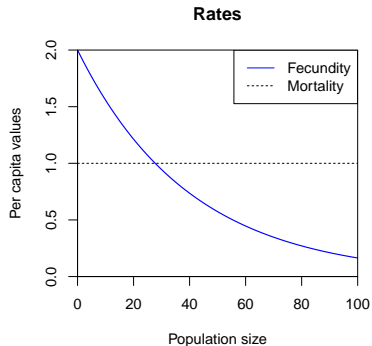


## *What dynamics do we expect? (preview)*

**Time series**

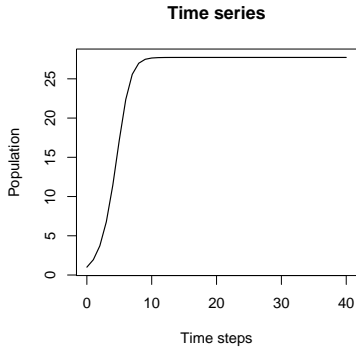
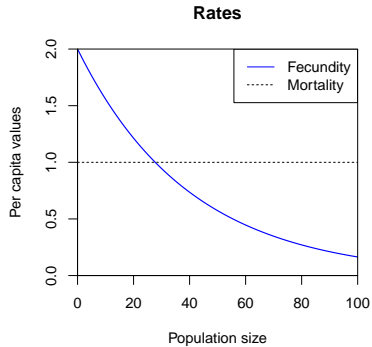


# We expect simple dynamics

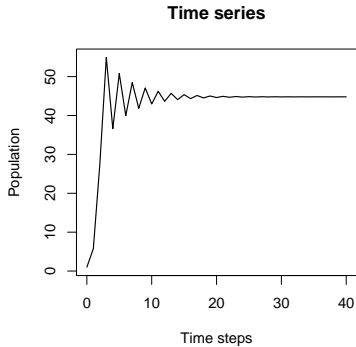
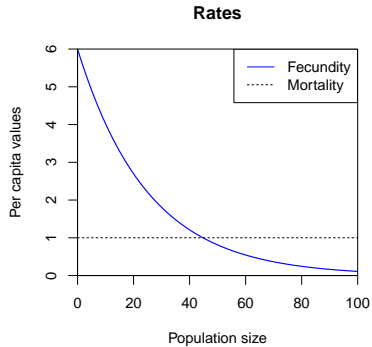


*What dynamics do we get? (present)*

## Simple dynamics (repeat)

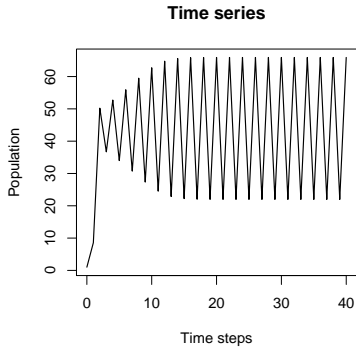
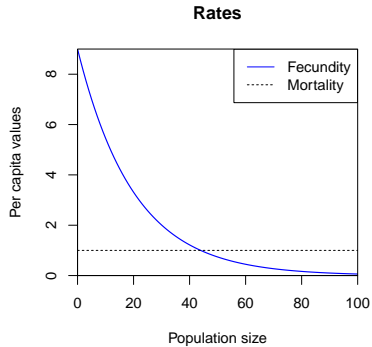


# Damped oscillations

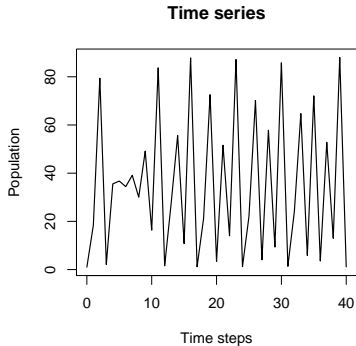
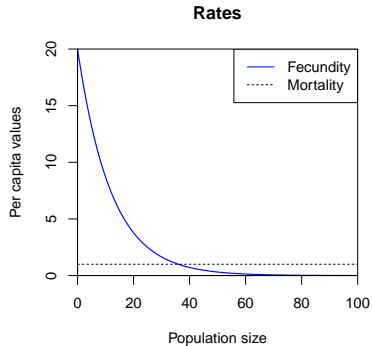




# Persistent oscillations



# Lots of other behaviours



# Outline

## Introduction

- Population Examples

## Continuous-time regulation

- A simple, continuous-time model

- Simulating model behaviour

- Equilibria

## Discrete-time regulation

- A simple, discrete-time model

- Simulating this system

- Interpreting complex behaviour

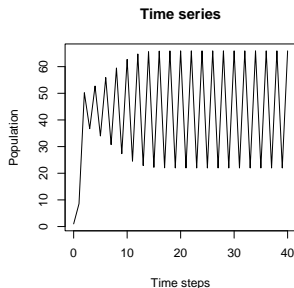
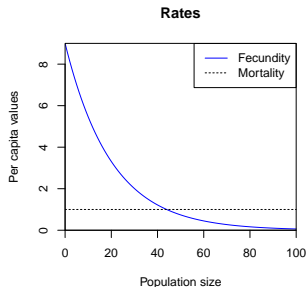
## Small populations

- Allee effects

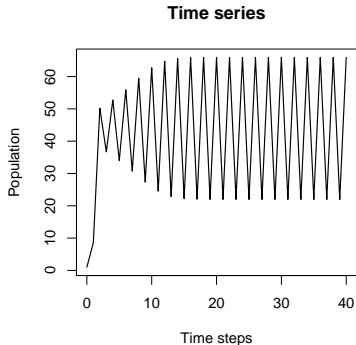
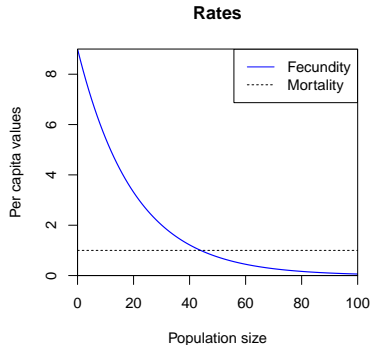
- Stochastic effects

# Interpreting complex behaviour

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



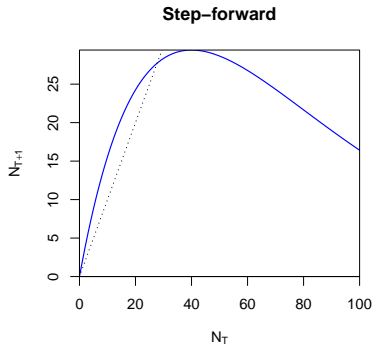
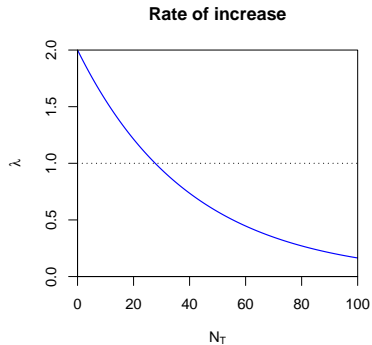
## Interpreting complex behaviour (repeat)



# Complex behaviour in our simulations

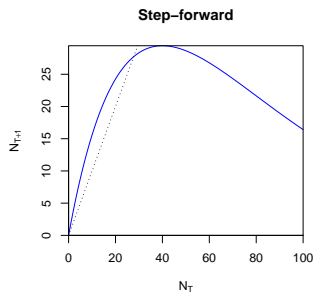
- ▶ In our simple models, as  $N_T$  increases, what happens to  $\lambda$ ?
  - ▶ \* We assume it goes down
- ▶ In our simple models, as  $N_T$  increases, what happens to next year's population?
  - ▶ \*  $N_{T+1} = \lambda(N)N_T$
  - ▶ \* It's not obvious!  $\lambda$  goes down, but  $N$  goes up.
  - ▶ \* In this model,  $N_{T+1}$  always goes down eventually, but other models may differ

# Response to population increase



# Turnover

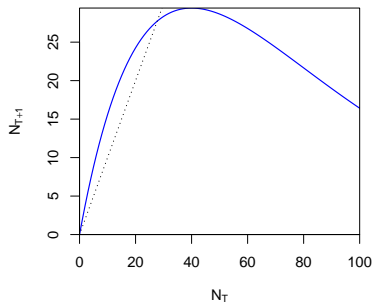
- ▶ When  $N_T$  is small,  $N_{T+1}$  increases with  $N$ .
- ▶ Complex behaviour arises when the relationship between  $N_T$  and  $N_{T+1}$  **turns over** below the equilibrium value
  - ▶ A small population this year leads to a large population next year



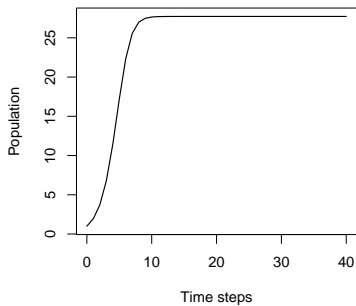


# Simple dynamics

**Step-forward**

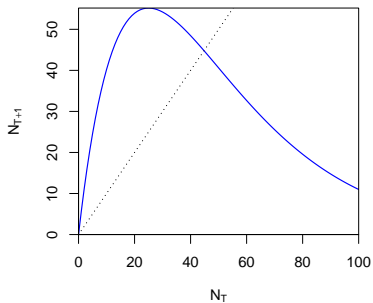


**Time series**

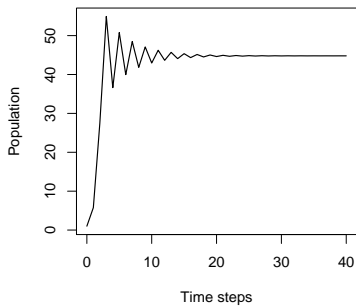


# Damped oscillations

**Step-forward**

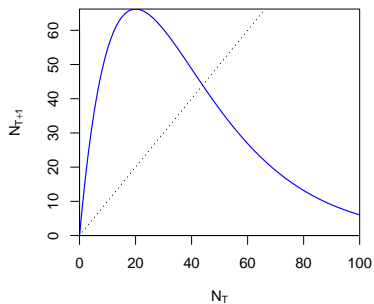


**Time series**

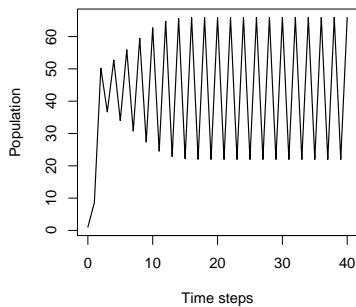


# Persistent oscillations

**Step-forward**



**Time series**



# Complex behaviour in our conceptual model

- ▶ Biologically, when might we expect  $N_{T+1}$  to “turn over”?
  - ▶ \* If resources are *depleted*
  - ▶ \* If there is a *delayed* effect of individuals' not having enough resources
- ▶ When should the mapping *not* turn over?
  - ▶ \* When competition does not lead to depletion
  - ▶ \* When effects of competition are immediate
  - ▶ \* When dominant individuals are not affected by crowding

# Scramble competition

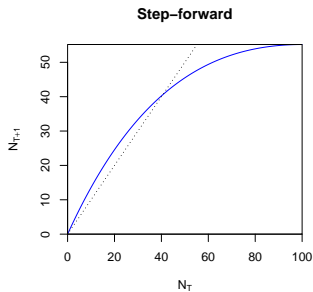
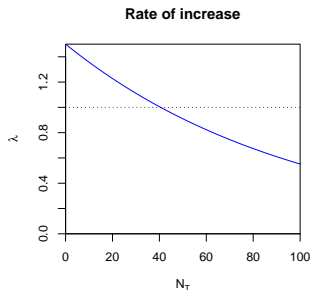
- ▶ **Scramble** competition refers to the case where all individuals in a crowded population are gathering resources at similar rates: as the density goes up there is less resource for everyone, and everyone does less well
  - ▶ If there is any kind of delay, scramble competition can lead to turning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

# Contest competition

- ▶ **Contest** competition refers to a case where some individuals 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?
  - ▶ \* Regulation means that  $\lambda$  has to go down with  $N_T \dots$
  - ▶ \* *not* that  $N_{T+1}$  has to.

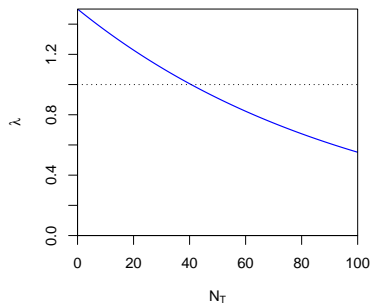
## Contest competition (present)

- ▶ How does contest competition square with regulation?
  - ▶ Regulation means that  $\lambda$  has to go down with  $N_T$  ...
  - ▶ *not* that  $N_{T+1}$  has to.

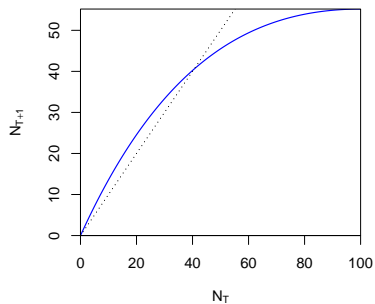


# Contest regulation

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
  - ▶ \* Food can be depleted
    - ▶ \* Making scramble competition and turnover more likely
  - ▶ \* Nest sites can be occupied, but they don't go away
    - ▶ \* More like contest competition, less likely to have turnover



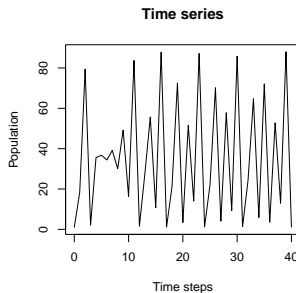
# Plants

- ▶ Some plant populations are limited by water, and some by light
- ▶ Which is more likely to work out as a scramble?
  - ▶ \* Light is very likely to work out as a “contest” – the taller individuals will win and do OK
  - ▶ \* Water works as a scramble in some environments, and a contest in others



# Complex behaviour from a simple model

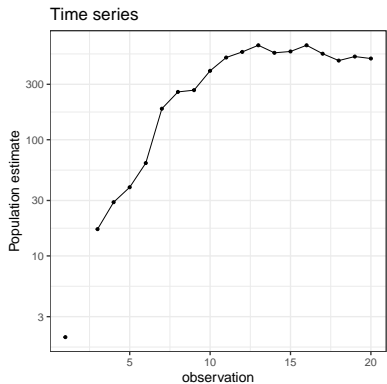
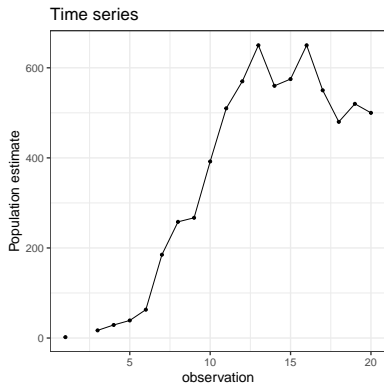
- ▶ It's interesting that we can get complicated behaviour from such a dead-simple model
- ▶ Complex dynamics may have simple causes
- ▶ People always tend to look for specific reasons, but sometimes the changes we observe are just natural dynamics



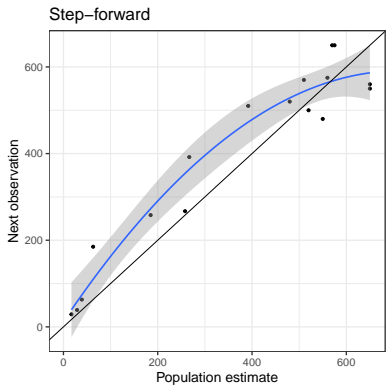
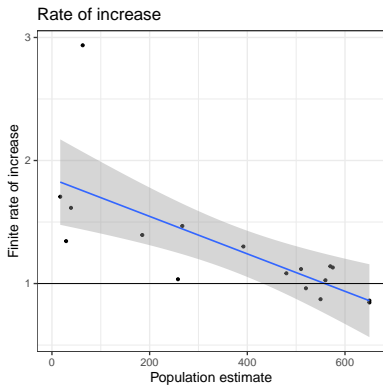
# Complex behaviour in real populations

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

## *Paramecia (repeat)*

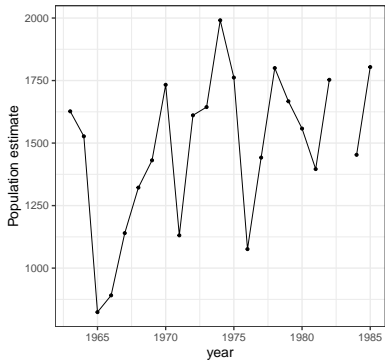


# Paramecia

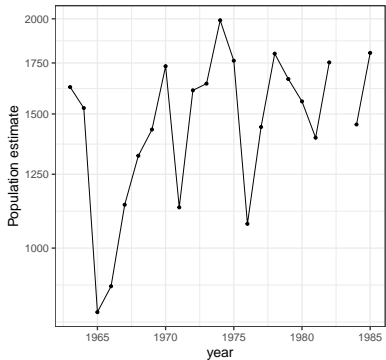


## Elk (repeat)

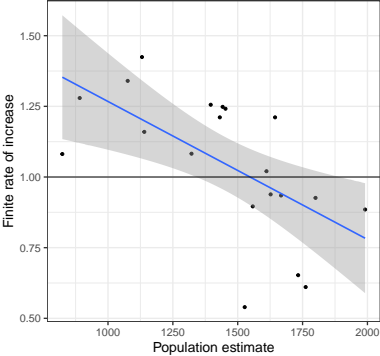
Elks in Grand Teton



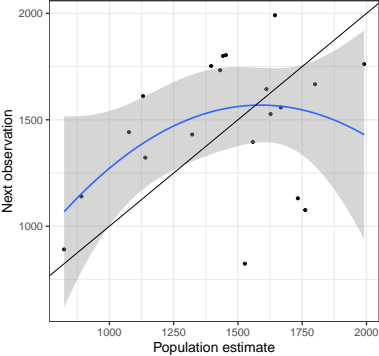
Elks in Grand Teton



Rate of increase



Step-forward





# 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
- ▶ Time-delayed population models are cool!
  - ▶ But not covered in class this year

# Outline

## Introduction

- Population Examples

## Continuous-time regulation

- A simple, continuous-time model
- Simulating model behaviour
- Equilibria

## Discrete-time regulation

- A simple, discrete-time model
- Simulating this system
- Interpreting complex behaviour

## Small populations

- Allee effects
- Stochastic effects

# Example

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



# 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

# Outline

## Introduction

Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

# 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

# *What causes Allee effects?*

- ▶ Why might growth rates be low when populations are small?
  - ▶ \* Individuals may have trouble finding mates
  - ▶ \* Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
  - ▶ \* Individuals in larger populations may hunt co-operatively
  - ▶ \* Genetic effects (inbreeding, loss of valuable variation)

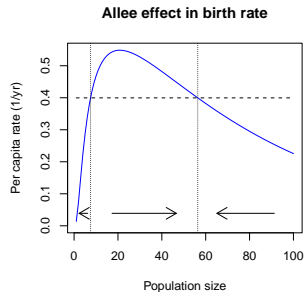
# Types of Allee effect

- ▶ Allee effects can affect the (per capita) birth rate
  - ▶ \* if the rate is *smaller* when density is low
- ▶ ... or the (per capita) death rate
  - ▶ \* if the rate is *larger* when density is low



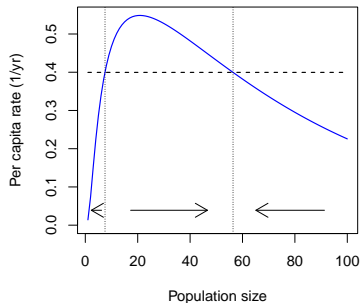
# Allee effect models

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

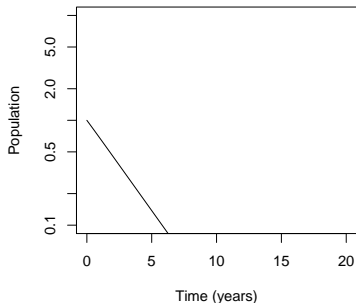


# Individual perspective

**Allee effect in birth rate**

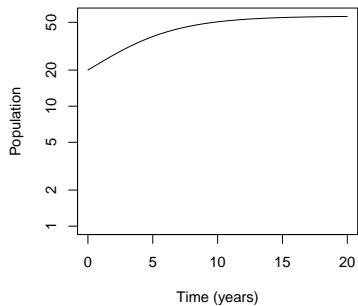


**Allee effect in birth rate**

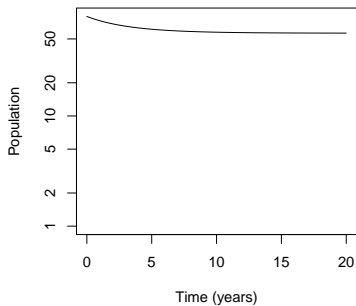


# Individual perspective

**Allee effect in birth rate**

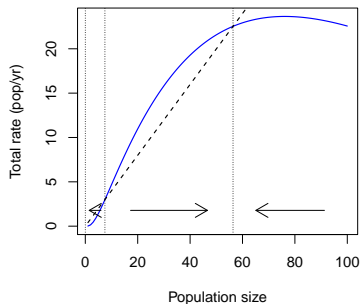


**Allee effect in birth rate**

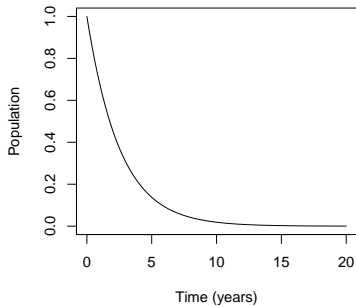


# Population perspective

**Allee effect in birth rate**

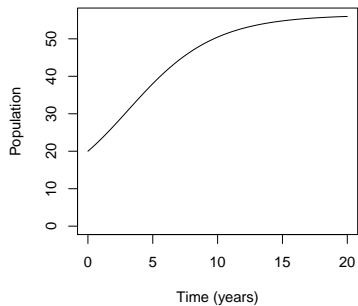


**Allee effect in birth rate**

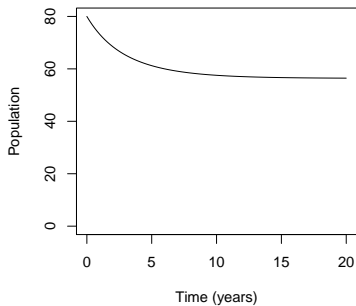


# Population perspective

**Allee effect in birth rate**

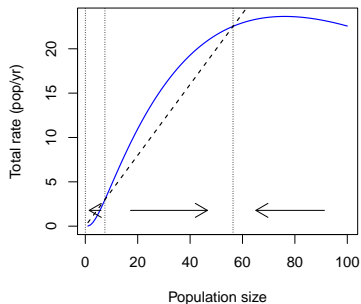


**Allee effect in birth rate**

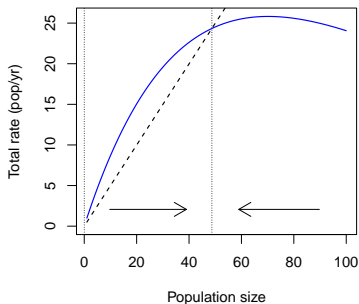


## Population comparison (repeat)

**Allee effect in birth rate**

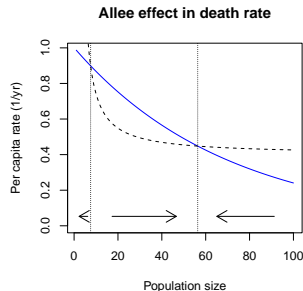


**Density-dependent birth**



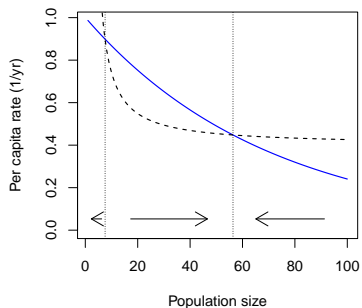
# Allee effect in death rate

- ▶ 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?

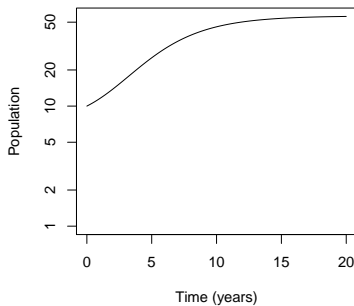


# Individual perspective

Allee effect in death rate



Allee effect in death rate





# More reproductive numbers

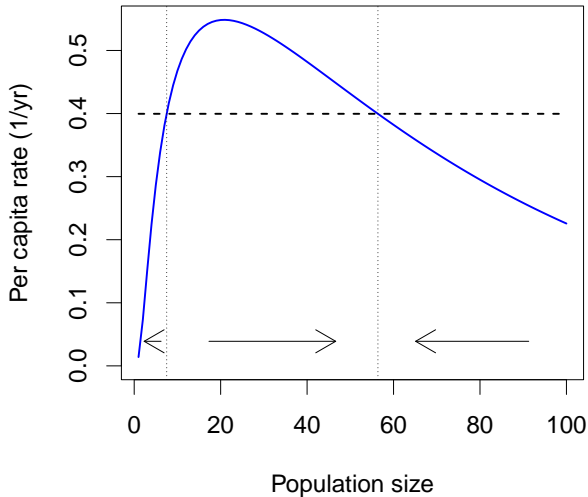
- ▶ The reproductive number  $\mathcal{R}$  means the average lifetime number of offspring per individual
  - ▶ Should be unitless, so we consider offspring at the same stage as the individual.
- ▶ We can apply  $\mathcal{R}$  in general for any set of conditions, or we can distinguish:
  - ▶ the **basic reproductive number**  $\mathcal{R}_0$ :  $\mathcal{R}$  in the limit when the population is small, and
  - ▶ the **maximal reproductive number**  $\mathcal{R}_{\max}$ :  $\mathcal{R}$  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
  - ▶ \* If  $\mathcal{R}_0 < 1$  population can't invade, but if  $\mathcal{R}_{\max} > 1$  it can still persist

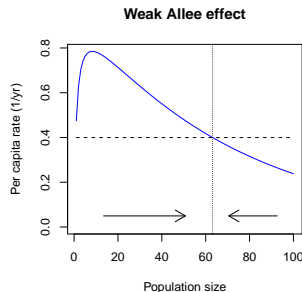
$\mathcal{R}_0$  and  $\mathcal{R}_{max}$  (repeat)

### Allee effect in birth rate



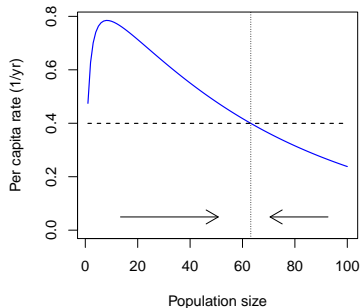
# Weak Allee effects

- ▶ If birth rates go down or death rates go up at low density, we consider this an Allee effect
- ▶ If  $\mathcal{R}_0 < 1$  we say it's a **strong** Allee effect
  - ▶ \* Population can't invade
- ▶ If  $\mathcal{R}_0 > 1$  we say it's a **weak** Allee effect

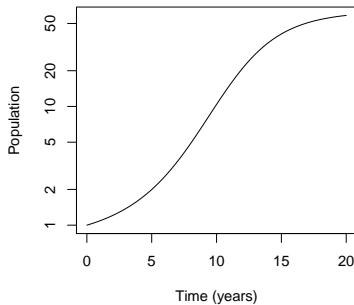


# Individual perspective

**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?
  - ▶ \* Maybe it's a weak effect
  - ▶ \* Maybe conditions have changed (it used to be a weak effect, or no effect)
  - ▶ \* Maybe a large initial group established by chance
  - ▶ \* Maybe the population arrived recently (and won't necessarily stick around)

# Outline

## Introduction

Population Examples

## Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria

## Discrete-time regulation

A simple, discrete-time model

Simulating this system

Interpreting complex behaviour

## Small populations

Allee effects

Stochastic effects

# 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?
  - ▶ \*  $\lambda = 1.5$
  - ▶ \* Almost anything can happen
  - ▶ *Try this calculation with units*

# 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
  - ▶ \* Population could be lucky or unlucky
- ▶ What if  $\lambda < 1$ ?
  - ▶ \* The population would go extinct eventually, even if it's lucky

# Demographic stochasticity

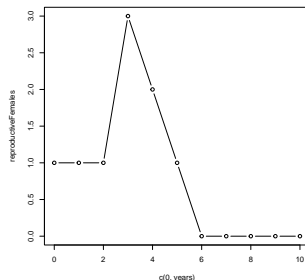
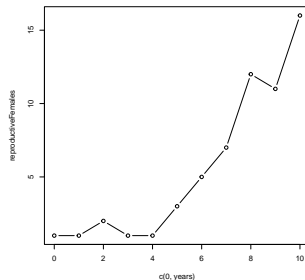
- ▶ **Demographic** stochasticity is stochasticity that operates at the level of individuals
  - ▶ Individuals don't increase gradually, they die or give birth
  - ▶ Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 ...
- ▶ Even if we control conditions perfectly, we can't exactly predict 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
  - ▶ \* A bad year is bad for everyone
- ▶ But small populations are the ones in danger of going extinct
  - ▶ \* Large populations can average out over *time*
  - ▶ \* 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
- ▶ Adds realism
  - ▶ But harder 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