UNIT 3 Non-linear population models

Outline

Introduction

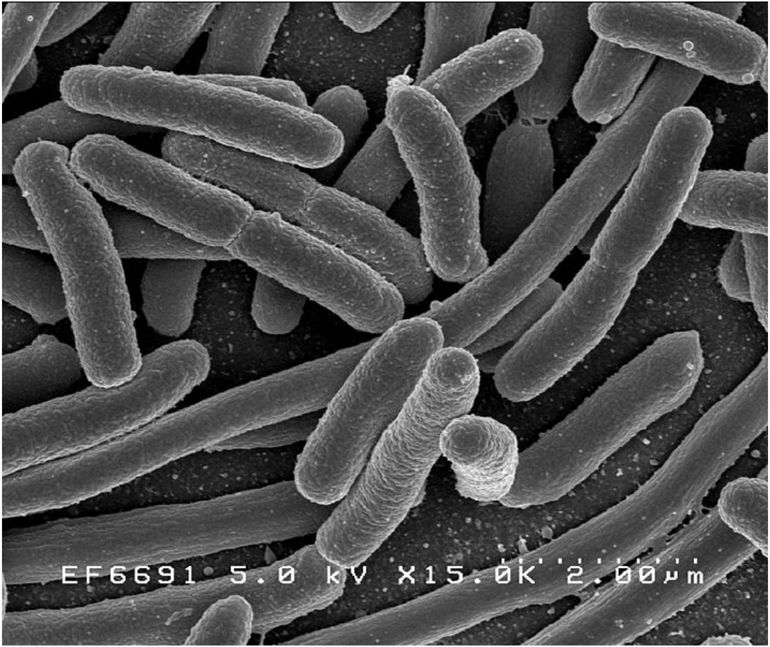
- In **linear** population models, per capita rates are independent of population size
- In **non-linear** models, not so much
- Why might per capita birth and death rates change with population size?
- What does this imply about population **dynamics**?

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
  - Size changes would be too extreme:
  - $> 20000\times$ after 10 characteristic times
- Something is changing the average rate at which populations we observe grow



Remark: Often something to do with crowding

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
    - * Sometimes. Only if predator number can increase fast enough.
  - * Diseases
    - * Usually can increase fast enough
  - * 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!
    - * Seasonal and climatic fluctuations don't *regulate*

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

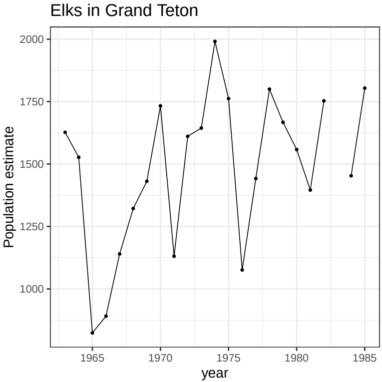
How do we know it's regulation?

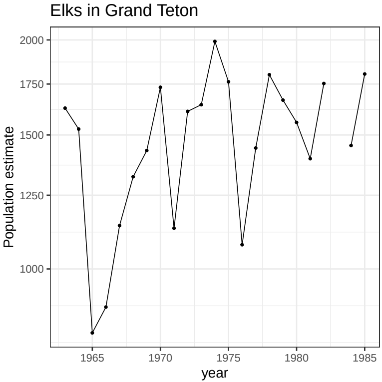
- Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
  - * Because the long-term average value of r has to be *very* close to 0
  - * This is true for *every* population
  - * This is unlikely to occur by chance
  - * Thus, it must be through direct or indirect responses to the population size

Outline

(preview)

Elk


Elks in Grand Teton
Population estimate
2000
1750
1500
1250
1000
1965
1970
1975
1980
1985
year


Elks in Grand Teton
Population estimate
2000
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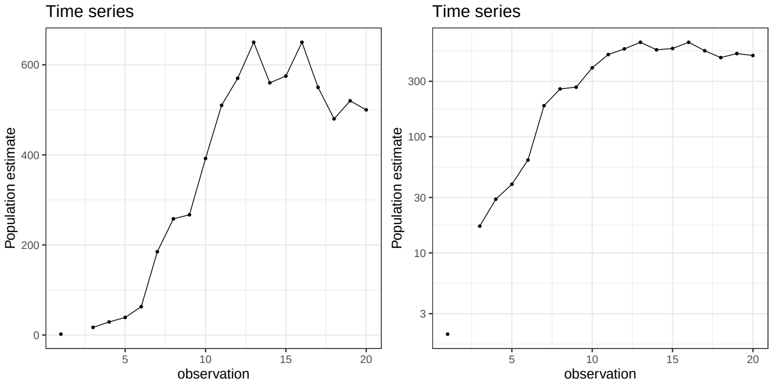
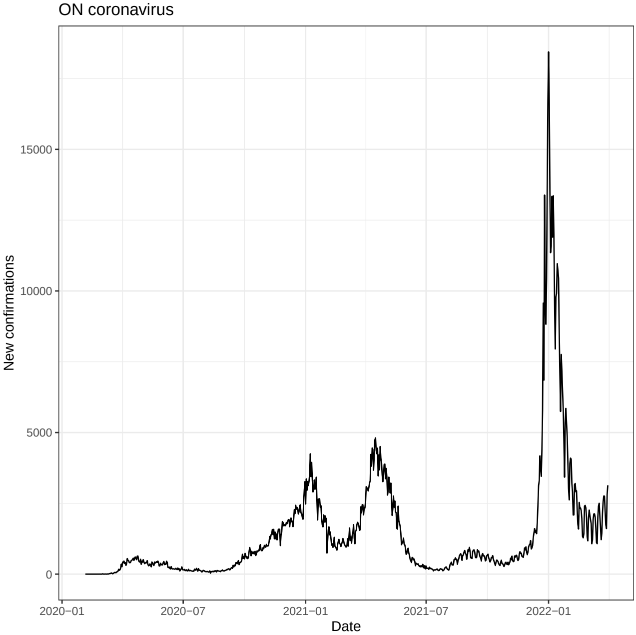
year

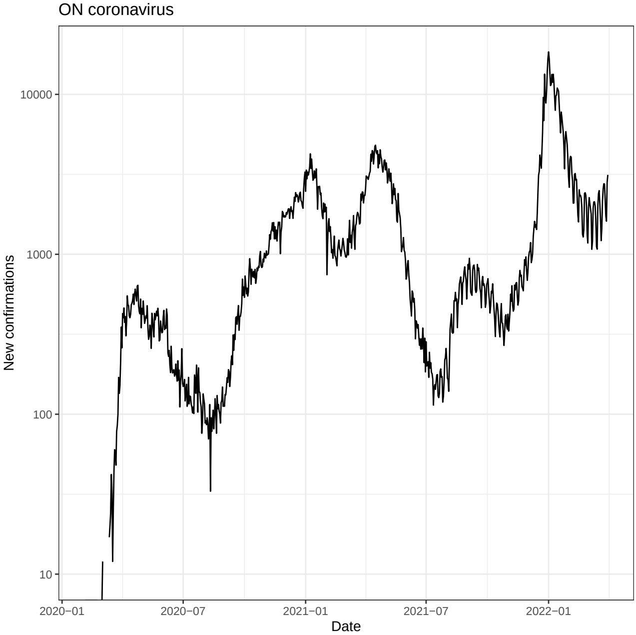
Paramecia (preview)



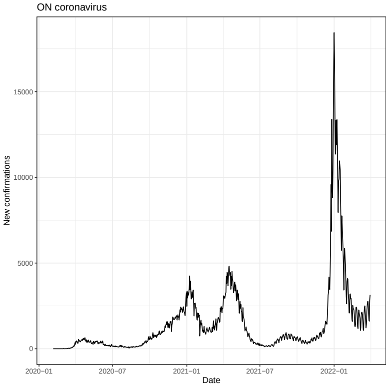
Coronavirus (preview)

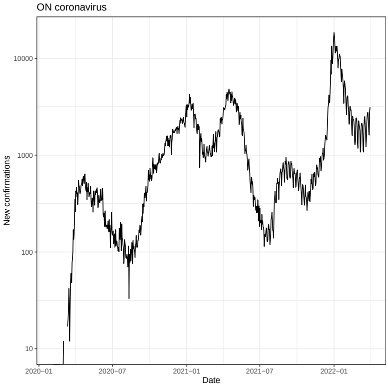


Coronavirus (preview)



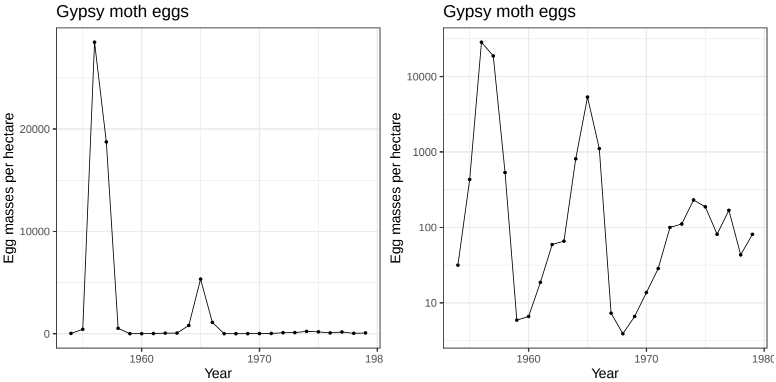
Coronavirus (preview)





Aadd Picked a cutoff date; talk about the testing regime maybe

Gypsy moths (preview)



Gypsy moths

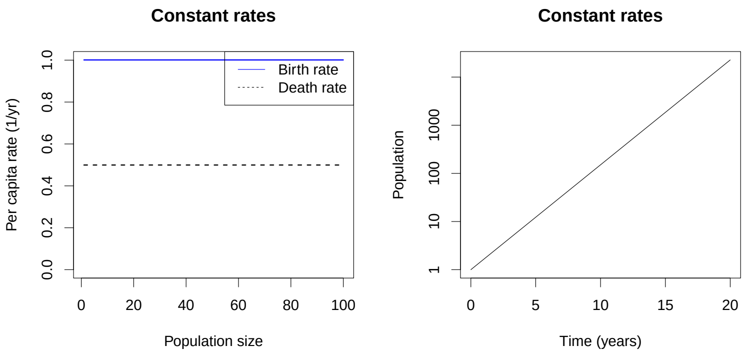
- What are some factors that limit gypsy-moth populations?
- Which are likely to be affected by the moths?
  - Directly or indirectly, in the short or long term?

Outline

Build on the linear model

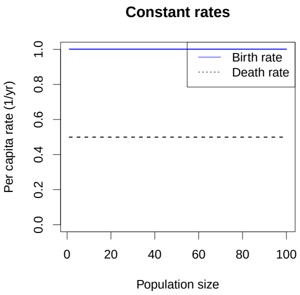
- Our linear population model is:
  - $\frac{dN}{dt} = (b - d)N$
- Per-capita rates are constant
- **Population-level rates are linear**
- Behaviour is exponential

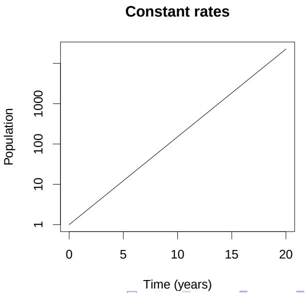
Individual perspective



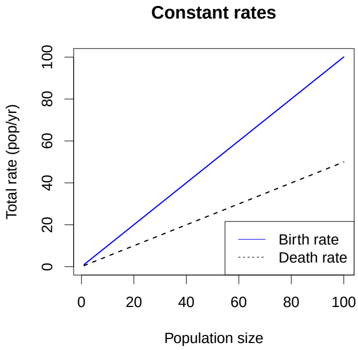
Individual perspective

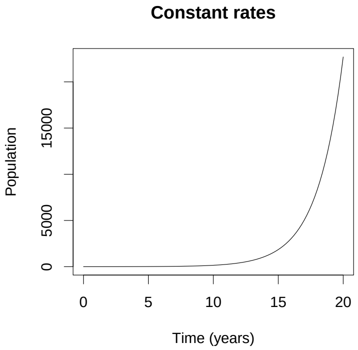
- Per capita rate shows birth and death per individual
- Corresponds to the time plot showing growth on a log scale
  - On the log scale we see *multiplicative* or *proportional* change





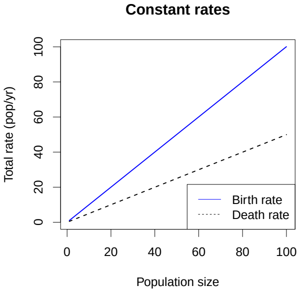
Population perspective

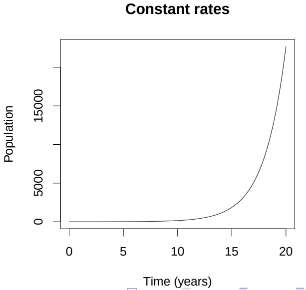




Population perspective

- 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

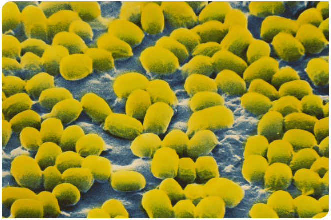
- Population has *per capita* birth rate $b(N)$ and death rate $d(N)$
  - Per-capita rates change with the population size
- Our non-linear model is: $\dfrac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$
  - Defines how fast the population is changing at any instant

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.
  - * birth rates go down, death rates go up, or both

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
  - $r(N) = r_{\text{max}}(1 - N/K)$
  - 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
- We don't call this a linear model
  - * *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
- *Looks* a little more scary than the logistic

Outline

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
  - When $N \ll N_b$, density dependence is linear (and relatively small)
  - When $N \gg N_b$, density dependence is exponential, and has very large effect

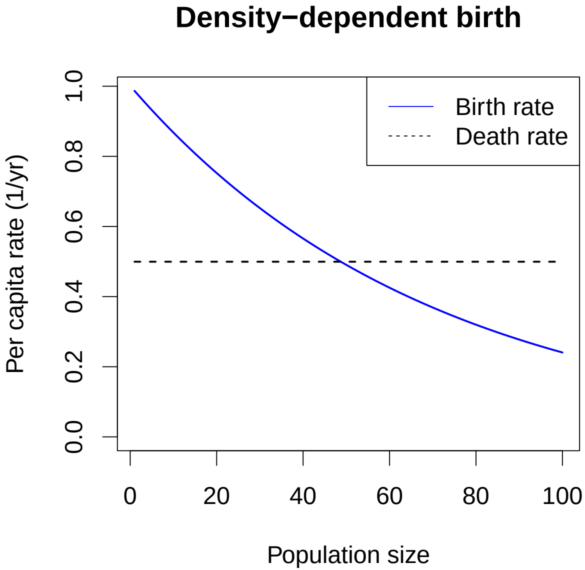
Model

- 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!

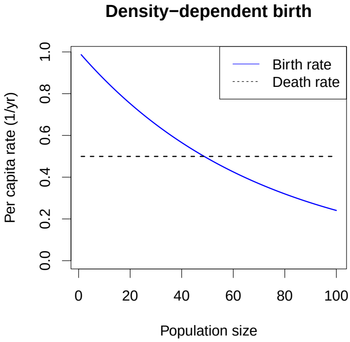
Dynamics

- 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)

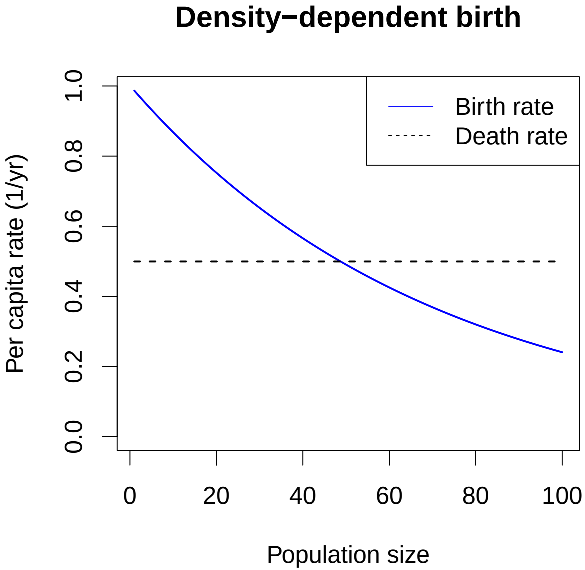


What is the characteristic scale?

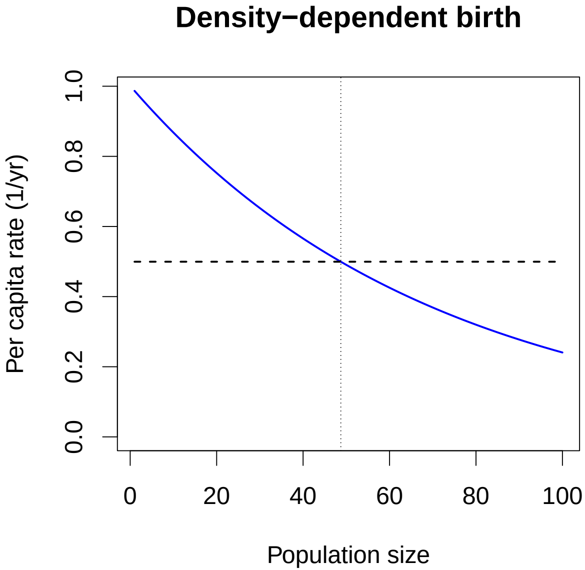


- No density dependence in death rate
- Characteristic scale for birth rate is about 70 indiv

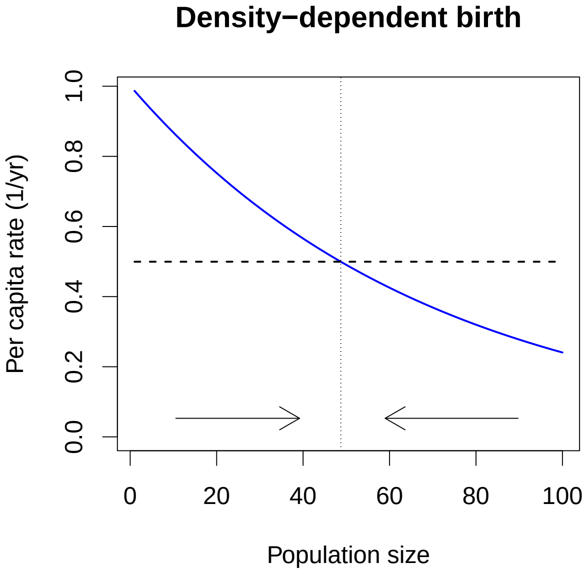
What will this model do? (present)



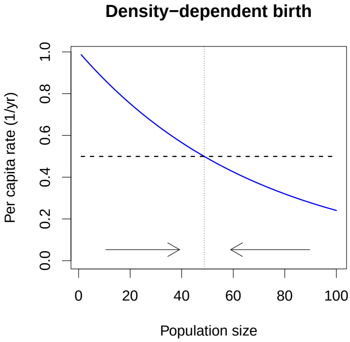
What will this model do? (present)



What will this model do? (present)

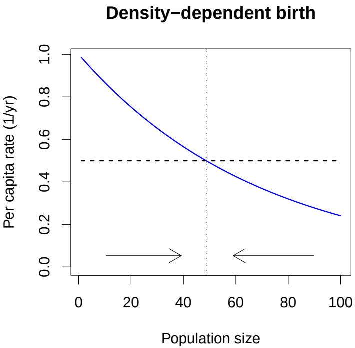


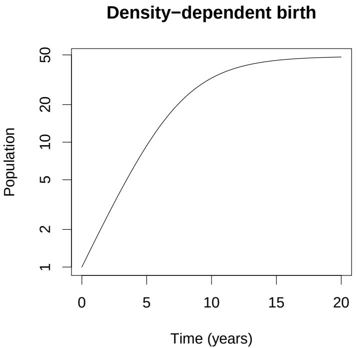
What will this model do?



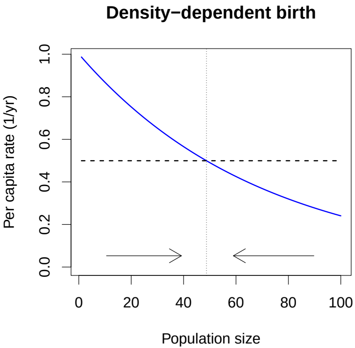
- Increase when population is below equilibrium
- Decrease when population is above equilibrium
- Converge

Low starting population example (present)





High starting population example (present)



Examples

Density−dependent birth
Population
1
2
5
10
20
50
0
5
10
15
20
Time (years)

Density−dependent birth
Population
1
2
5
10
20
50
0
5
10
15
20
Time (years)

Outline

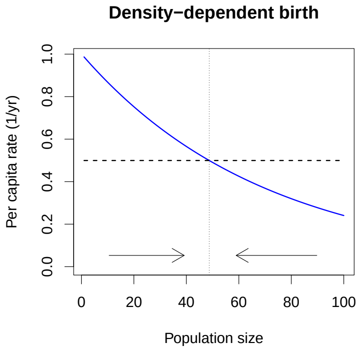
Simulations

- 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

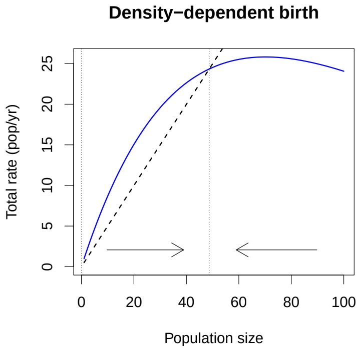
What will this model do? (repeat)



Population-scale pictures

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

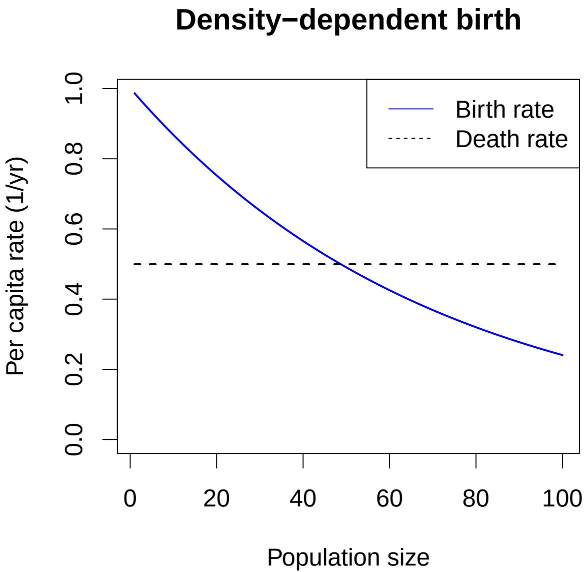
Population perspective picture



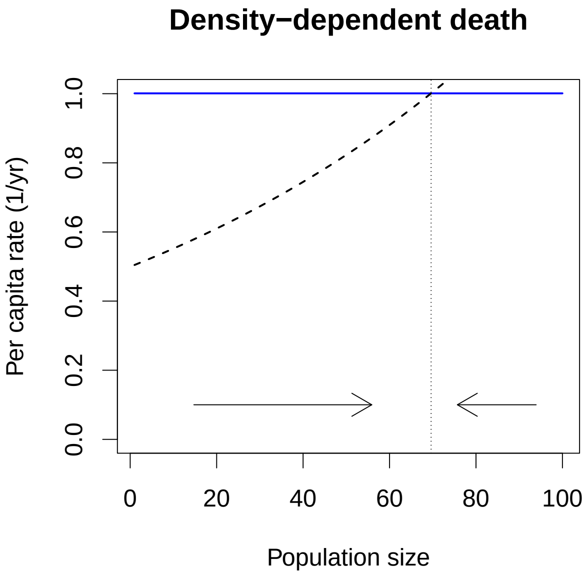
Decreasing birth rate

- 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

Decreasing birth rates (repeat)



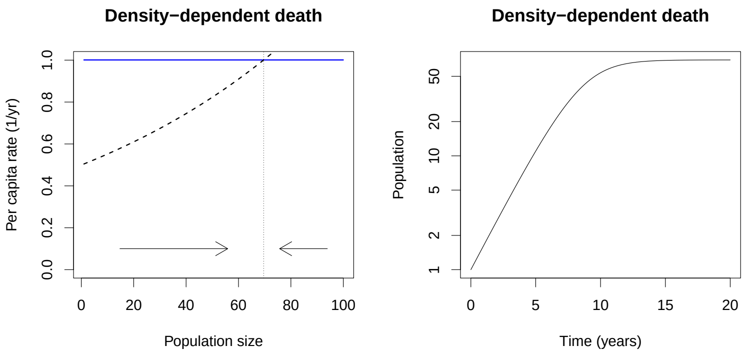
Increasing death rates (present)



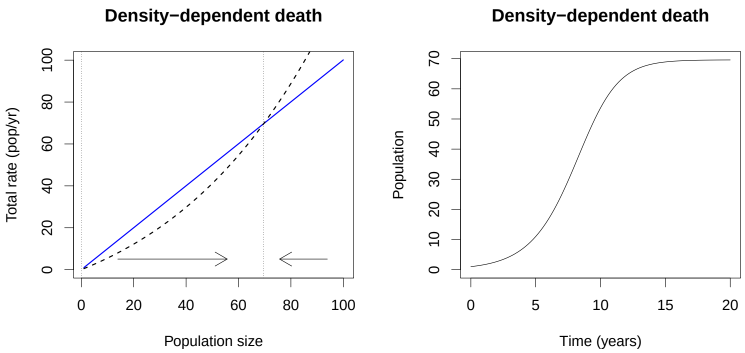
Increasing death rate

- 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 regulated primarily by adult crowding.

Individual perspective



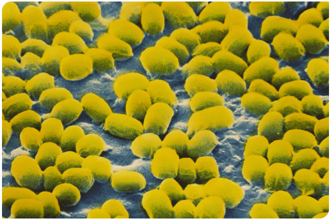
Population perspective



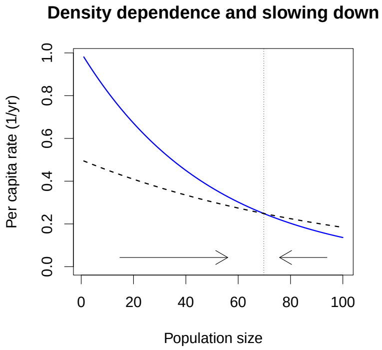
Decreasing death rate

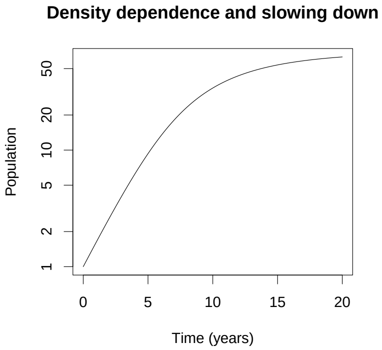
- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate *decreases*

- How is this consistent with density dependence?
    - * Birth rate must decrease even faster

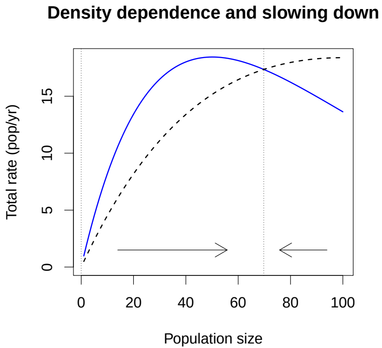


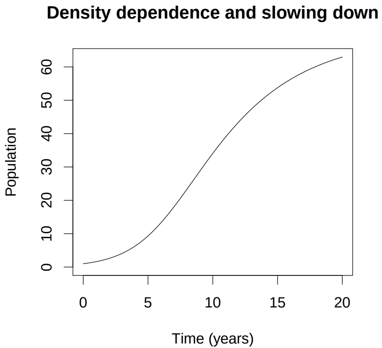
Individual perspective





Population perspective





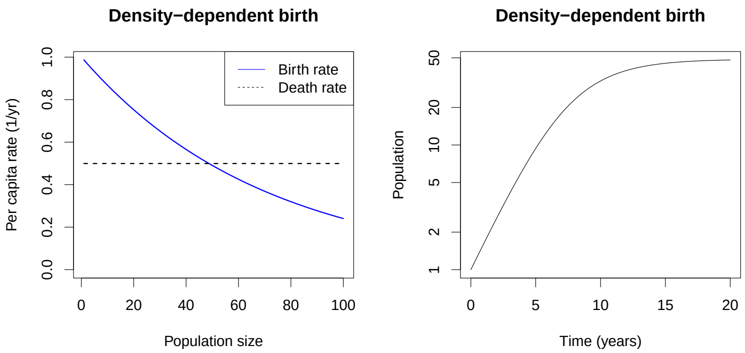
Other examples

- There are two other possible scenarios for density dependence
  - For fun, you can try to think of what they are
- But all of these examples have similar behaviour
  - Increase from low density
  - Decrease from high density
  - Approach carrying capacity

Maximum growth rates (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)

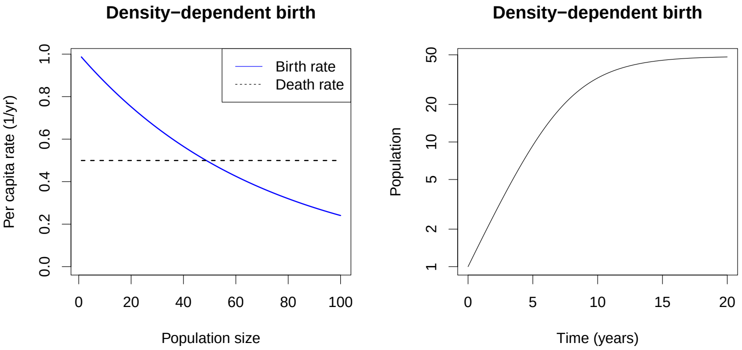


Population perspective (repeat)

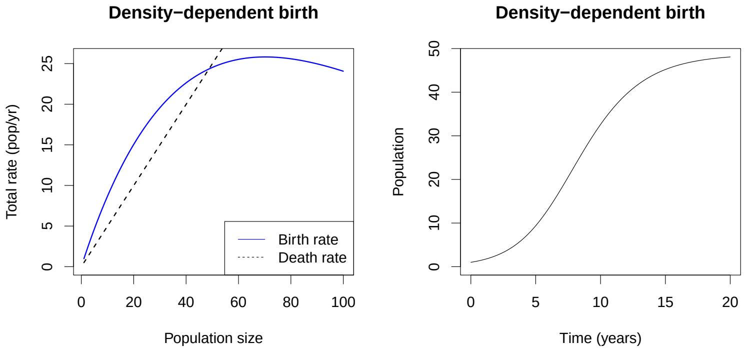
Maximum growth rates

- 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 something we learn from the model

Individual perspective (repeat)



Population perspective (repeat)



Outline

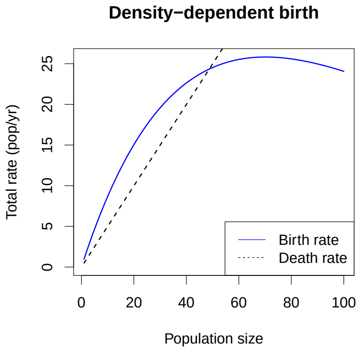
Equilibria

- 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?
  - * $(b(N) - d(N))N = 0$
  - * $b(N) = d(N)$ (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 $\mathcal{R}_{\mathrm{max}}$.
- 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

Basic reproductive number

- 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 $\mathcal{R}_0 > 1$

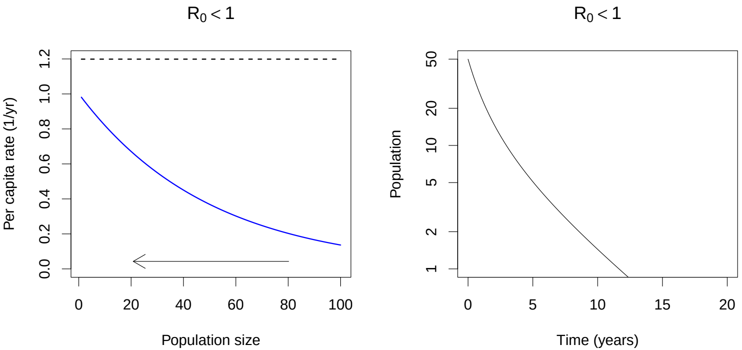
Invasion examples

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

Describing equilibria

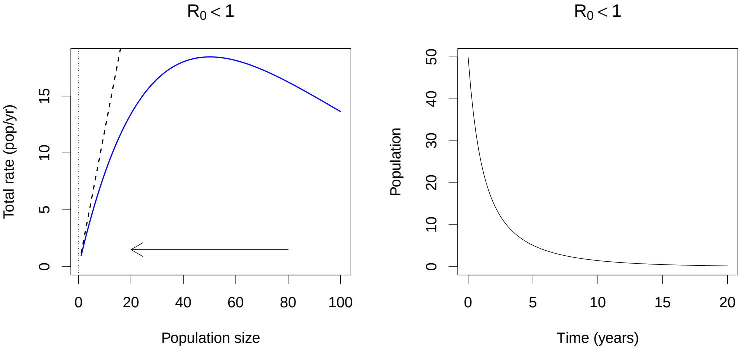
- When $\mathcal{R}_0 > 1$, the population invades
  - * Zero equilibrium is unstable, carrying capacity equilibrium is stable
- When $\mathcal{R}_0 < 1$, the population fails to invade
  - * Zero equilibrium is stable, carrying capacity equilibrium does not exist

Individual perspective



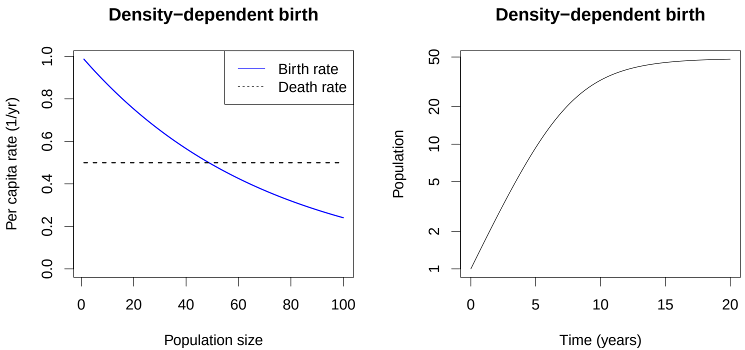
- When $\mathcal{R}_0 < 1$ population always decreases

Population perspective



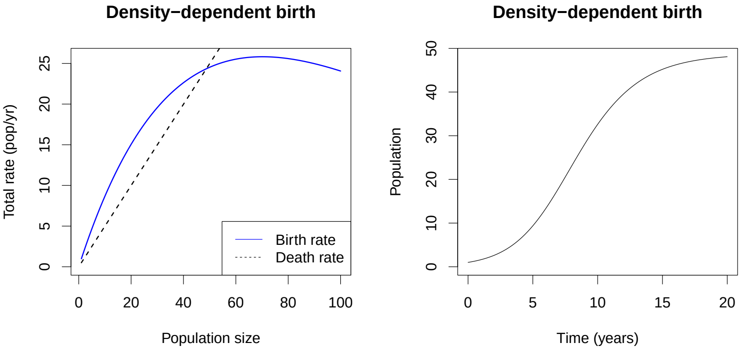
- When $\mathcal{R}_0 < 1$ population always decreases

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

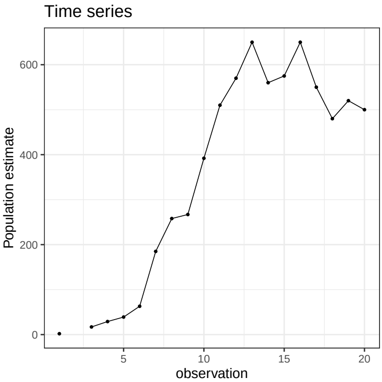
$\mathcal{R}_0$ and thresholds

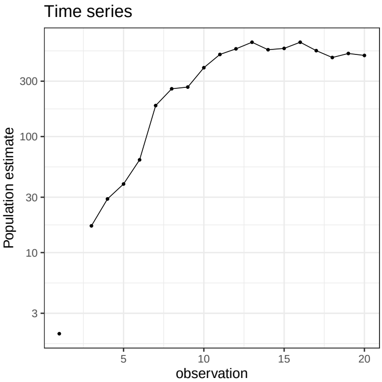
- A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
  - It will suddenly disappear at the population level
  - Even while it can still survive and reproduce at an individual level
- This is why there are no white spruce trees in Cootes Paradise
- And no malaria in the mainland United States

Smooth dynamics

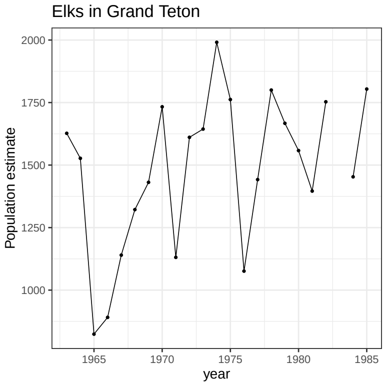
- Populations following this model change *smoothly*
  - Equations tell how the population will change at each instant
- They have no memory
  - Birth rate and death rate are determined by population size alone
- Cycling is impossible
  - * If I went from A to B, I can't go from B to A by following the same rules

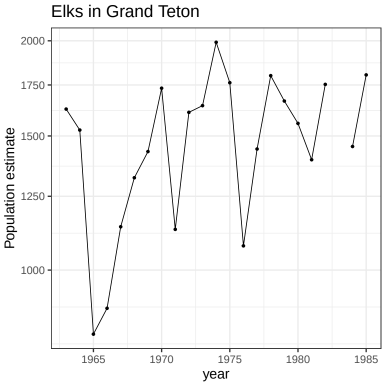
Paramecia (repeat)





Elk (repeat)


Elks in Grand Teton
Population estimate
2000
1750
1500
1250
1000
1965
1970
1975
1980
1985
year


Elks in Grand Teton
Population estimate
2000
1750
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1000
1965
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1975
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1985
year

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

Outline

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 Δt
- All individuals are the same at the time of census
- Population changes deterministically

Specific assumptions

- For our examples, we will assume:
  - $f(N) = f_0 \exp(-N/N_f)$
  - $p(N) = p_0 \exp(-N/N_p)$
- 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
  - * 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

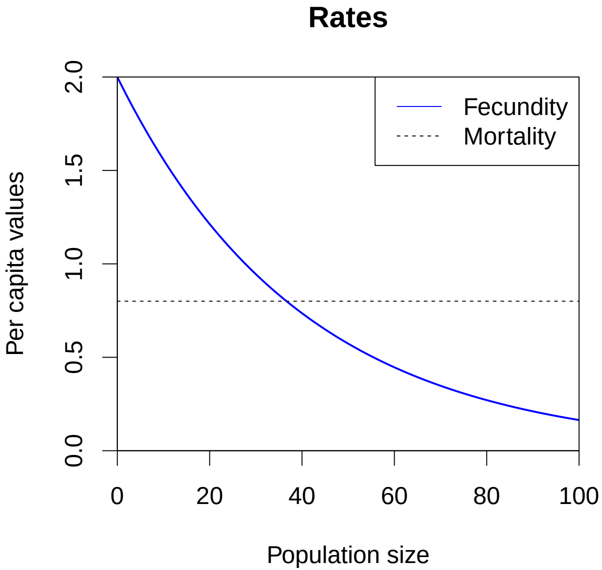
- When $\mathcal{R}_0 < 1$ population always declines
- When $\mathcal{R}_0 > 1$, population can show:
  - Smooth behaviour (like the continuous-time model)
  - Damped oscillations (like delayed models)
  - Two-year cycles (high $\rightarrow$low $\rightarrow$high $\rightarrow$low)
  - All *kinds* of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

Outline

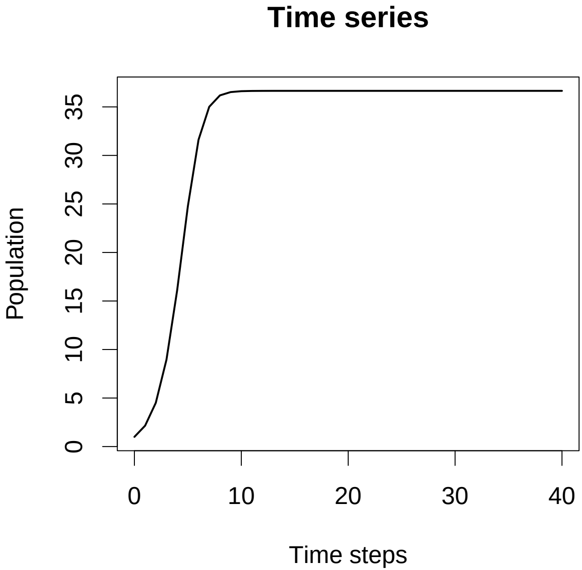
Simulating this system

- 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

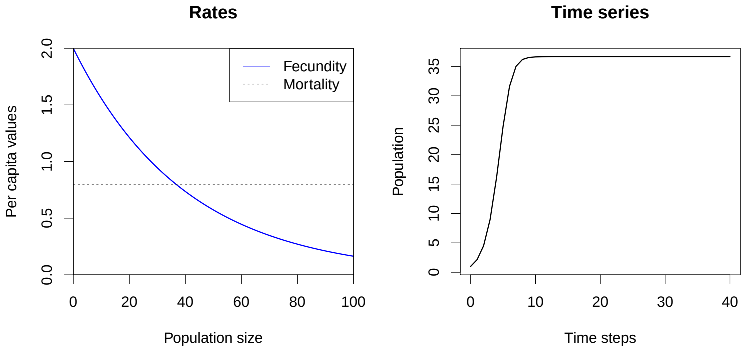
What dynamics do we expect? (preview)



What dynamics do we expect? (preview)

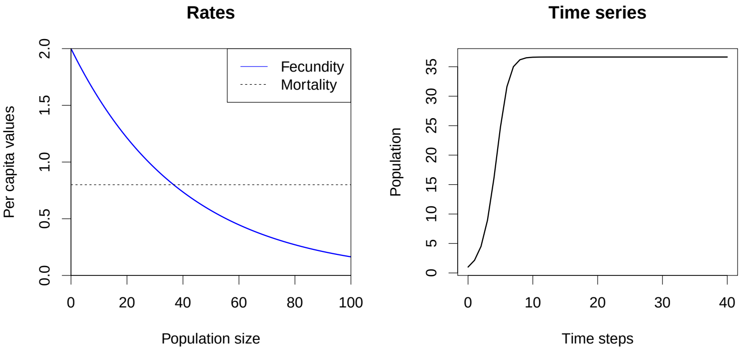


We expect simple dynamics

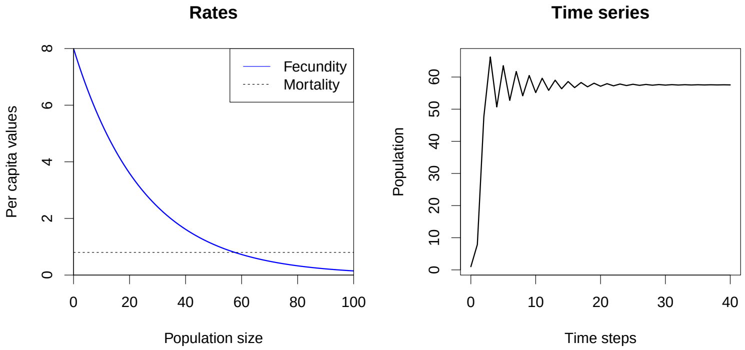


What dynamics do we get? (present)

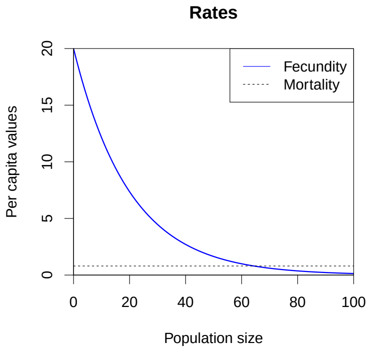
Simple dynamics (repeat)

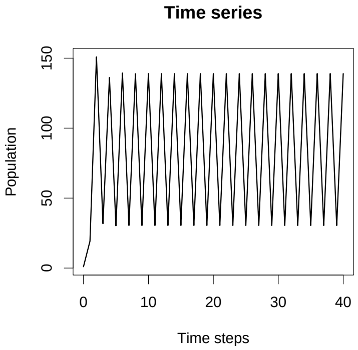


Damped oscillations

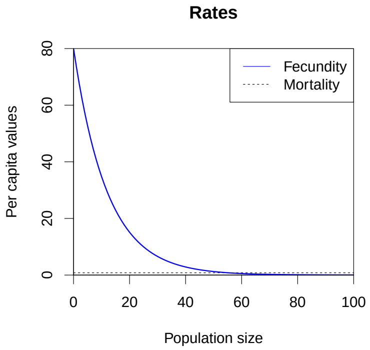


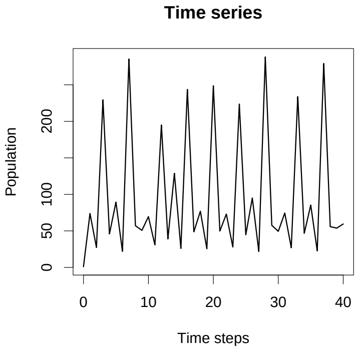
Persistent oscillations





Lots of other behaviours

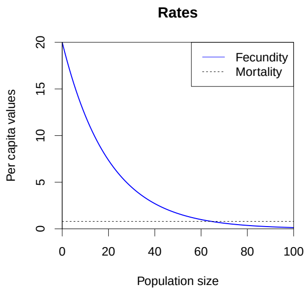


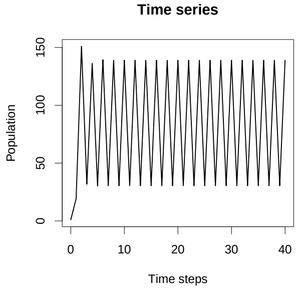


Outline

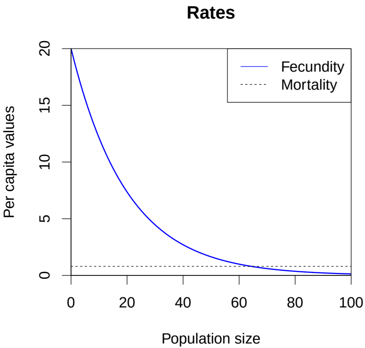
Interpreting complex behaviour

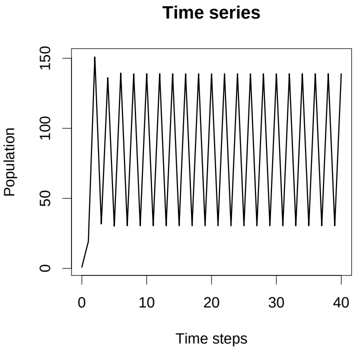
- In a simple cycle:
  - Low populations this year mean high populations next year
  - and vice versa





Interpreting complex behaviour (repeat)

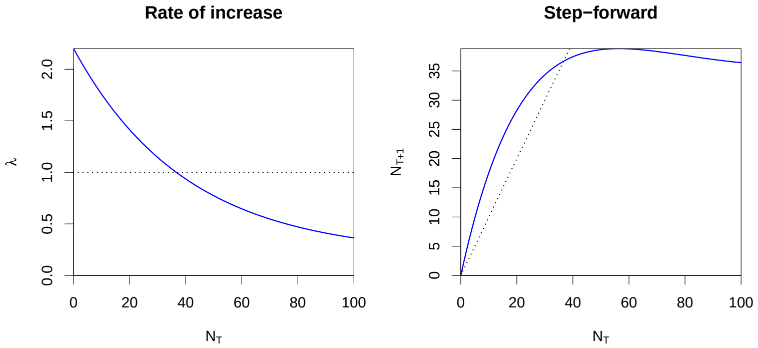




Complex behaviour in our simulations

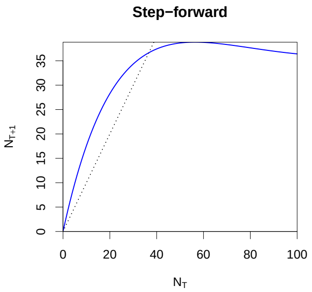
- In our simple models, as N_T increases, what happens to λ?
  - * We assume it goes down
- In our simple models, as N_T increases, what happens to next year's population?
  - * $N_{T+1} = \lambda(N)N_T$
  - * It's not obvious! λ goes down, but N goes up.
  - * In this model, N_{T+1} always goes down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

Response to population increase

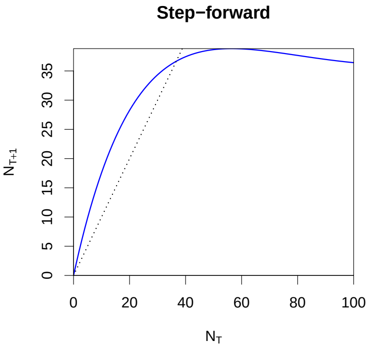


Turnover

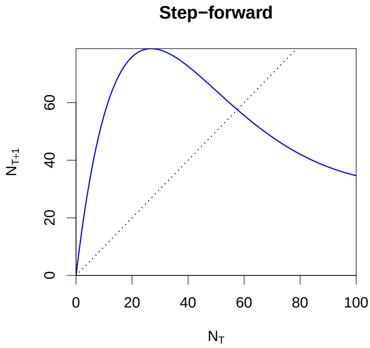
- When N_T is small, N_{T+1} increases with N.
- Complex behaviour arises when the relationship between N_T and N_{T+1} **turns over** below the equilibrium value
  - A small population this year leads to a large population next year

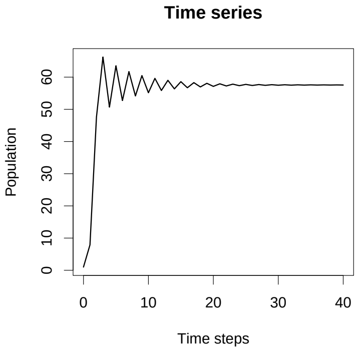


Simple dynamics

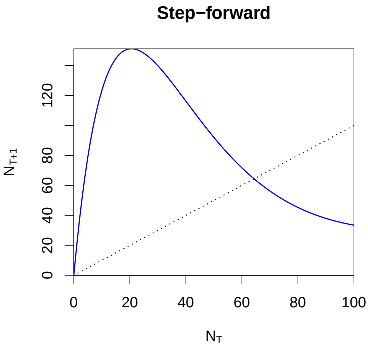


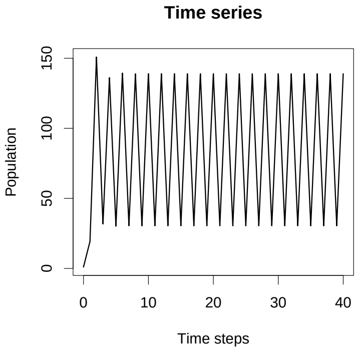
Damped oscillations





Persistent oscillations





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

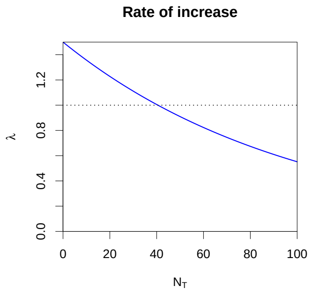
Scramble competition

- **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

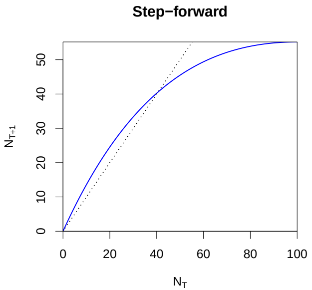
Contest competition

- **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 λ has to go down with N_T ...
  - * *not* that N_{T+1} has to.

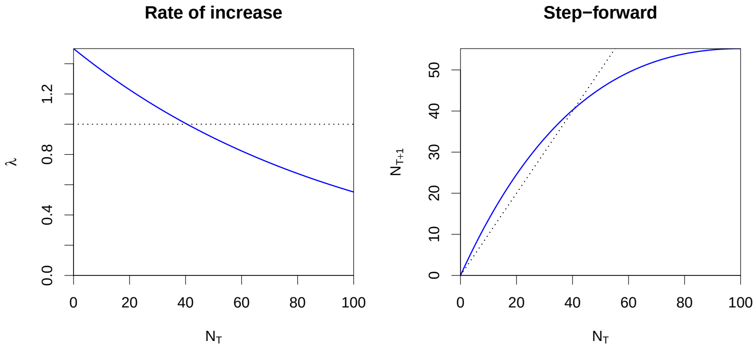
Contest competition (present)



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



Contest regulation



Songbirds

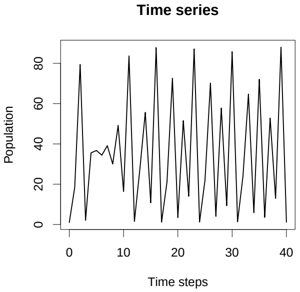
- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
  - * Food can be depleted
    - * Making scramble competition and turnover more likely
  - * Nest sites can be occupied, but they don't go away
    - * 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

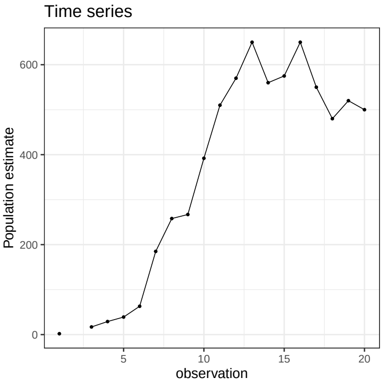
- It's interesting that we can get complicated behaviour from such a dead-simple model
- Complex dynamics may have simple causes
- People always tend to look for specific reasons, but sometimes the changes we observe are just natural dynamics

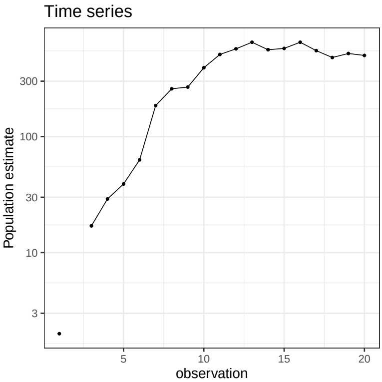


Complex behaviour in real populations

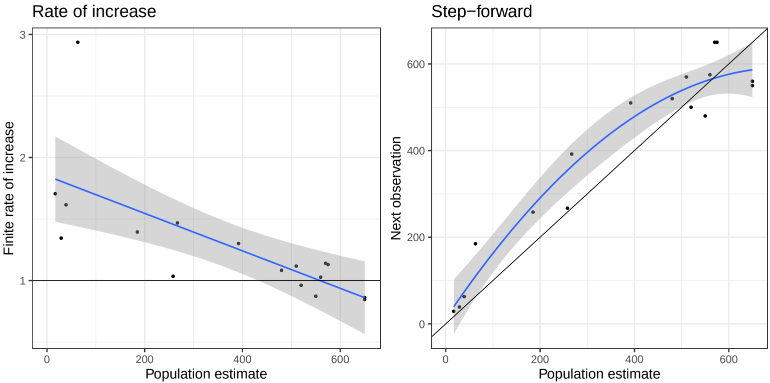
- We can plot λ and N_{T+1} vs. N for real population data
- We expect λ to decrease (on average)
- We're curious about N_{T+1}.

Paramecia (repeat)



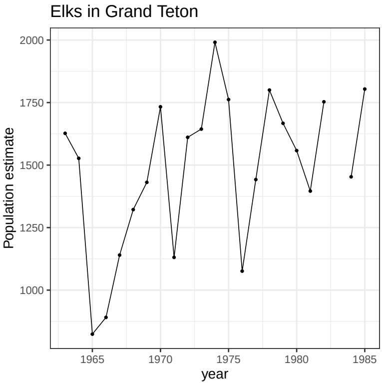


Paramecia



Rate of increase
Finite rate of increase
3
2
1
0
200
400
600
Population estimate
Step−forward
Next observation
600
400
200
0
0
200
400
600
Population estimate

Elk (repeat)


Elks in Grand Teton
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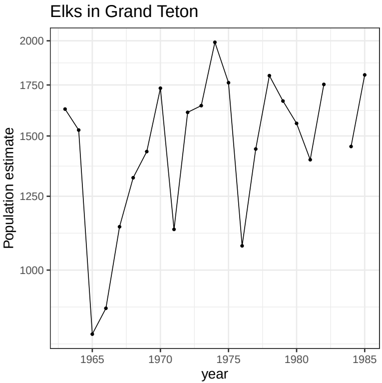
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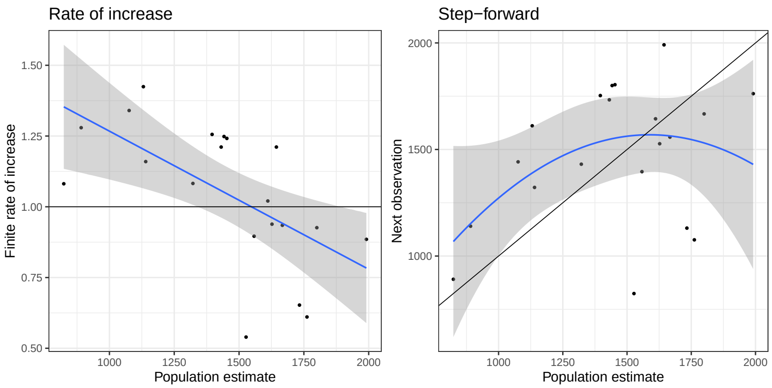
Elk



Rate of increase
Finite rate of increase
1.50
1.25
1.00
0.75
0.50
1000
1250
1500
1750
2000
Population estimate
Step−forward
Next observation
2000
1500
1000
1000
1250
1500
1750
2000
Population estimate

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

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

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?

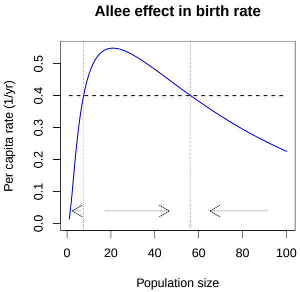
- Why might growth rates be low when populations are small?
  - * Individuals may have trouble finding mates
  - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
  - * Individuals in larger populations may hunt co-operatively
  - * Genetic effects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

Types of Allee effect

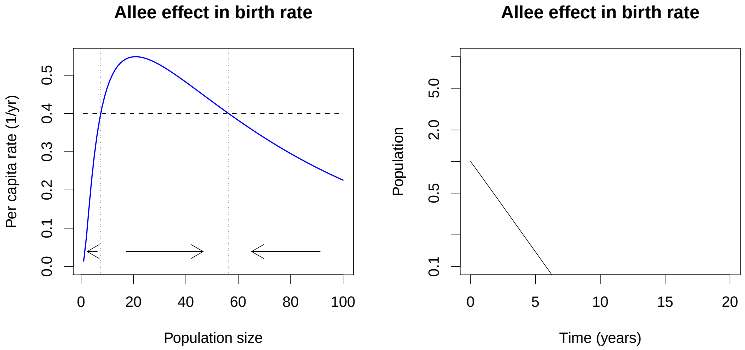
- Allee effects can affect the (per capita) birth rate
  - * if the rate is *smaller* when density is low
- … or the (per capita) death rate
  - * if the rate is *larger* when density is low

Allee effect models

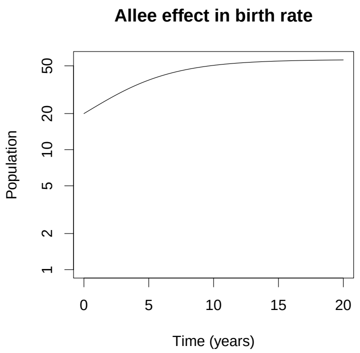
- What will this model do, if the initial population is:
  - low, medium or high?

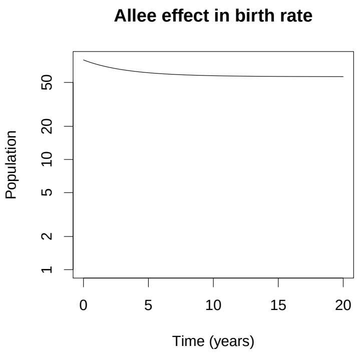


Individual perspective

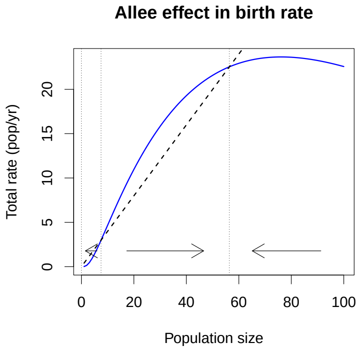


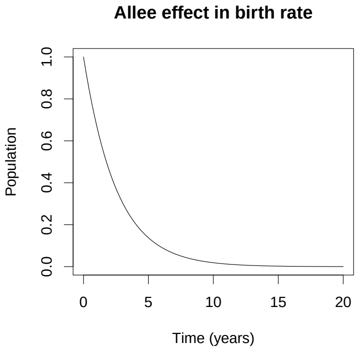
Individual perspective



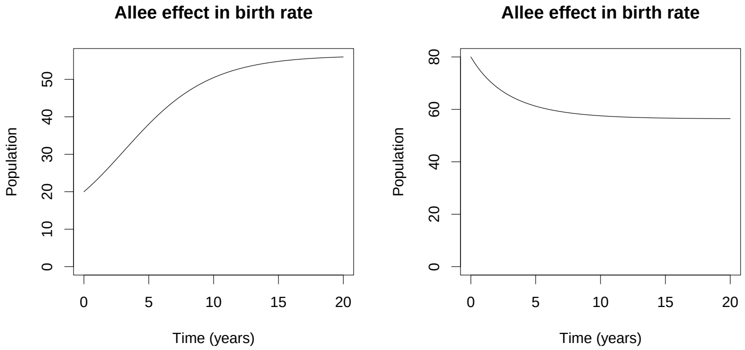


Population perspective

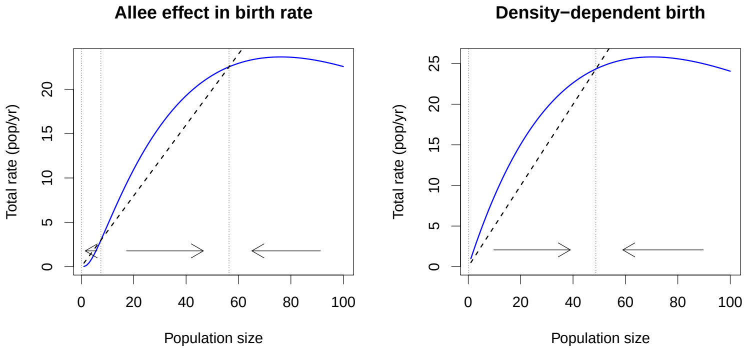




Population perspective

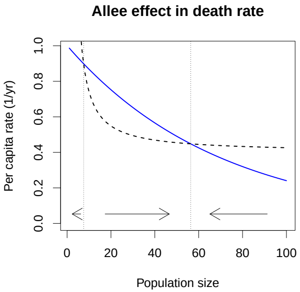


Population comparison (repeat)

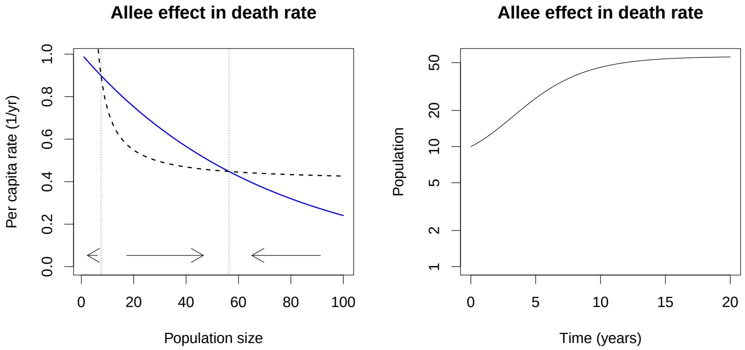


Allee effect in death rate

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



Individual perspective



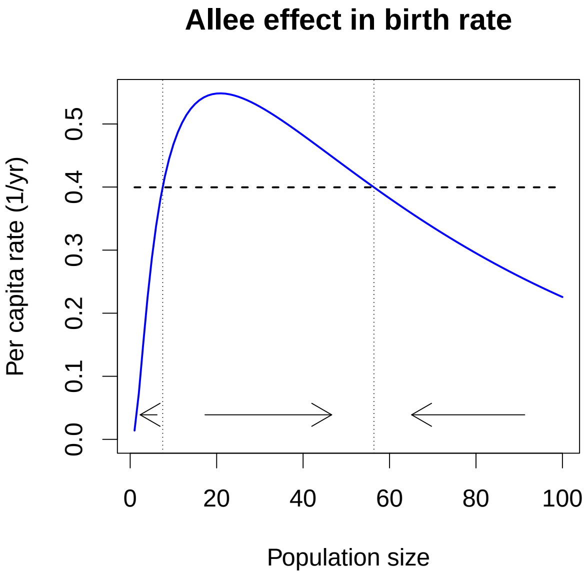
More reproductive numbers

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

Invasion

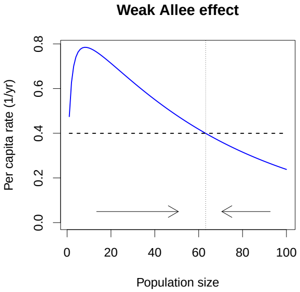
- We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct
  - A population that can't invade can never replace itself on average
- When Allee effects are present, it's no longer true that a species that can't invade can't persist
  - * If $\mathcal{R}_0 < 1$ population can't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

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

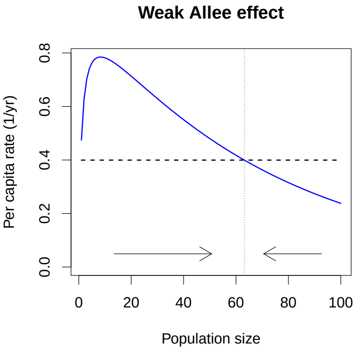


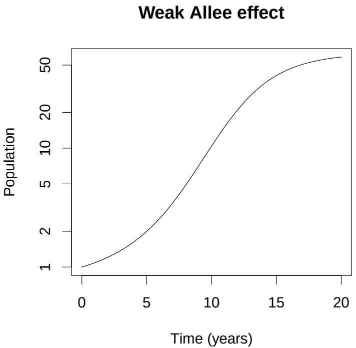
Weak Allee effects

- 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





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

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?
  - * $\lambda = 1.5$
  - * (remember not to multiply by the sex ratio twice!)
  - * 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

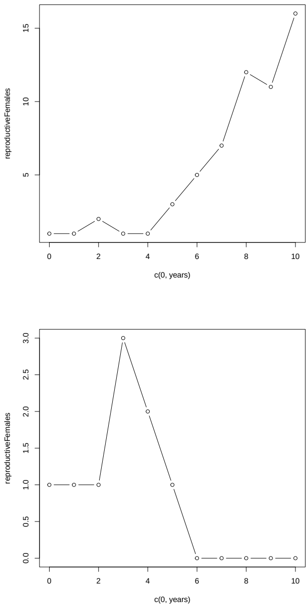
- **Demographic** stochasticity is stochasticity that operates at the level of individuals
  - Individuals don't increase gradually, they die or give birth
  - Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 . . .
- Even if we control conditions perfectly, we can't exactly predict 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