Lecture 16: Population ecology: models without age structure

- Defining populations and individuals
- Taxonomy of simplest possible mathematical models
  - Exponential and geometric population growth models without density dependence
  - Incorporating density dependence; logistic growth model
  - More complex density dependence: time delays, Allee effects

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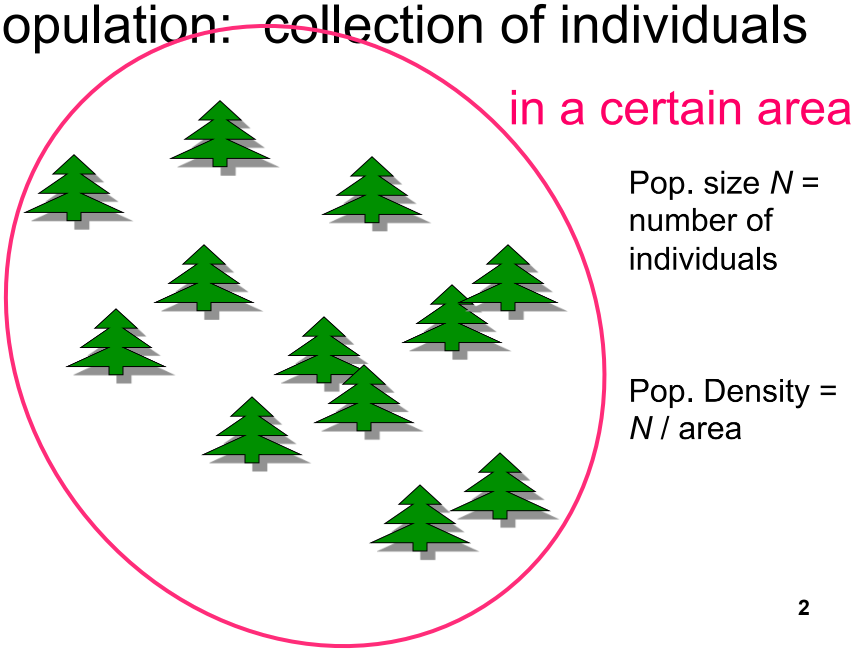
Population: collection of individuals



Pop. size N = number of individuals

Pop. Density = N / area

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Population ecology: what influences *N?*

The goal of most population models

- Predict the trajectory of population growth through time, i.e., N as a function of t
- How many individuals are in the population now? N_t
- (**Time advances one step**) $t \rightarrow t + 1$
- How many individuals are in the population one step later? N_{t+1}

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Simple bookkeeping model: how can N change from N_t to N_{t+1}?

- ***D*** = number who die during one time step
- ***B*** = number born during one time step
- ***E*** = number who emigrate " " "
- ***I*** = number who immigrate " " "
- So, $N_{t+1} = N_t - D + B - E + I$
- Death and emigration are equivalent;
- Birth and immigration are equivalent:
- So, can simplify the model by modeling only death and birth

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Change in population size (N)

How can we calculate how much a population has changed from one time step to another?

change in N = $N_{t+1} - N_t$

But this just tells us the number of individual that were added or lost between time steps – can't make prediction

How can we predict change?

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	Population Size (N)	Change in N
2015	230	
2016	345	115
2017	518	173
2018	777	259

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Predicting growth

How can we predict change?

Look at the **proportion** that it grew by (its **growth rate**)

	Population Size (N)	Change in N	Growth rate
2015	230		
2016	345	115	345/230 = 1.5
2017	518	173	518/345 = 1.5
2018	777	259	777/518 = 1.5

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Growth rate (λ)

The general model is $N_{t+1} = (N_t)\,\lambda$

where λ (lambda) is a multiplicative factor by which the population size changes over one time step ($t + 1$)

But what if we want to figure out other time steps, further in time (e.g., t+2, t+3, etc)?

$$N_{(1)} = (N_0)\,\lambda$$
$$N_{(2)} = [(N_0)\,\lambda\,]\,\lambda = (N_0)\,\lambda^2$$
$$N_{(3)} = (N_0)\,\lambda^3$$

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Geometric growth

$$N_t = N_0\,\lambda^t$$

Population size at time *t*

Initial population size

Growth rate

Time *t*

What is λ?

- =the **per capita** growth rate of a population
- =difference between per capita birth rate and per capita death rate
- =average number of offspring (contribution) left by an individual during one time interval

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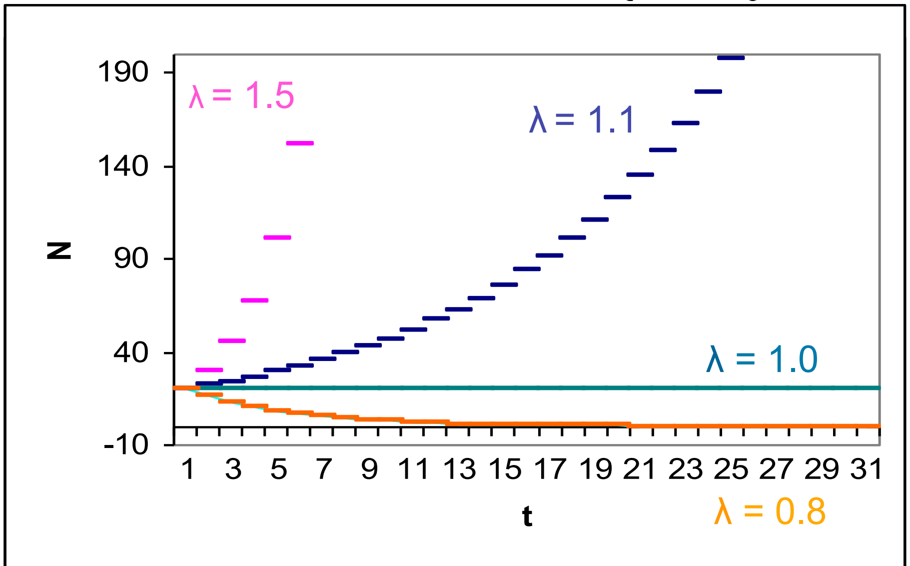
Geometric growth: $N_t = N_0 \lambda^t$



Geometric growth

- One **discrete** reproductive event per unit time
- Growth rate (λ) is fixed (per capita birth and death rates are constant)
- Population growth is unlimited

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Alternative version with continuous time

- Instantaneous, per-capita rates of birth and death fixed (b and d)
- Instantaneous, per-capita rate of population change = $b - d = r$ (a constant)
- Differential equation is $dN/dt = r\,N$

instantaneous rate of change in population size	average contribution of each individual to population growth	population size

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Solving the 2 simplest models of unlimited growth

Discrete-time

- $N_{t+1} = \lambda N_t$
- Solve for N *vs.* t:
- $N_t = N_0 \lambda^t$
- Geometric growth (step function) if $\lambda > 1$

Continuous-time

- $dN/dt = r\,N$
- Solve for N *vs.* t:
- $N_t = N_0 e^{rt}$
- Exponential growth (smooth function) if $r > 0$

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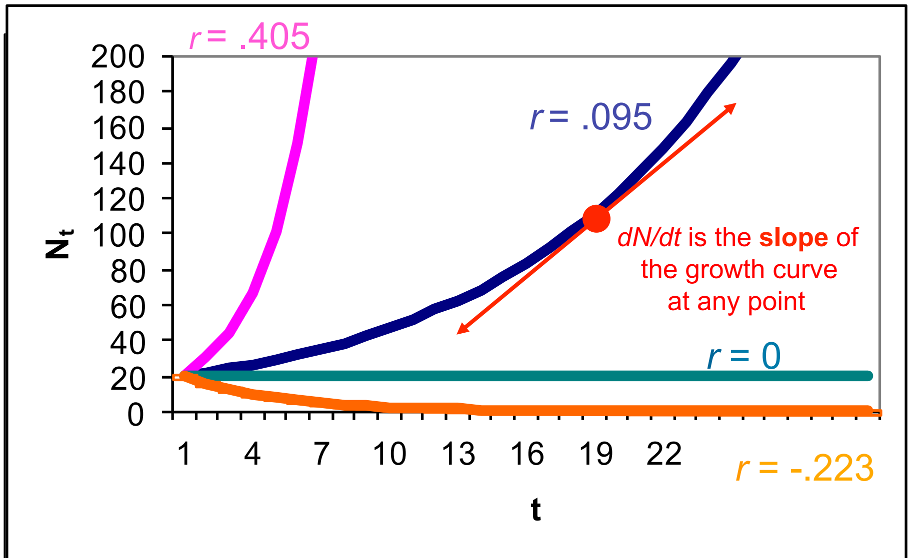
Graphing exponential growth: $N_t = N_0 e^{rt}$



Regardless of which model is adopted, the important consequence is the same

- In both models, the growth rate (λ or r) is a constant that simply reflects biology…
- …but a constant positive growth rate produces a population size that is not constant, but rather exploding in an exponential way.

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So, all species have the potential for positive population growth under good conditions ($\lambda > 1.0$)

All species have the potential for negative population growth under bad conditions ($\lambda < 1.0$)…

…but no species has ever sustained $\lambda > 1.0$ for a long period…and no extant species has maintained $\lambda < 1.0$ for long

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The staggering implications

- Simple exponential growth is a *bad* model of reality over the long term!
- Some factors must tend to keep populations from exploding or going extinct
- Two kinds of factors may be acting
  - Density-dependent regulation (growth depends on N)
  - Density-independent reduction (e.g., weather, predators)

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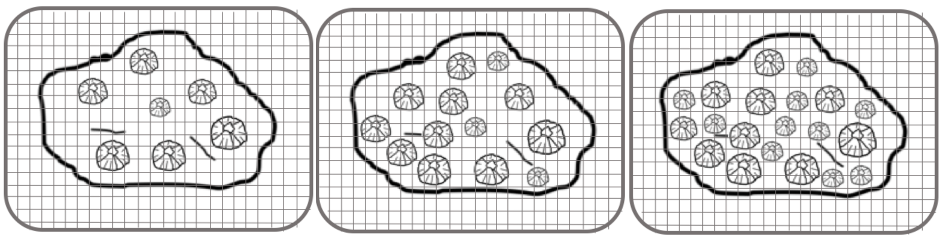
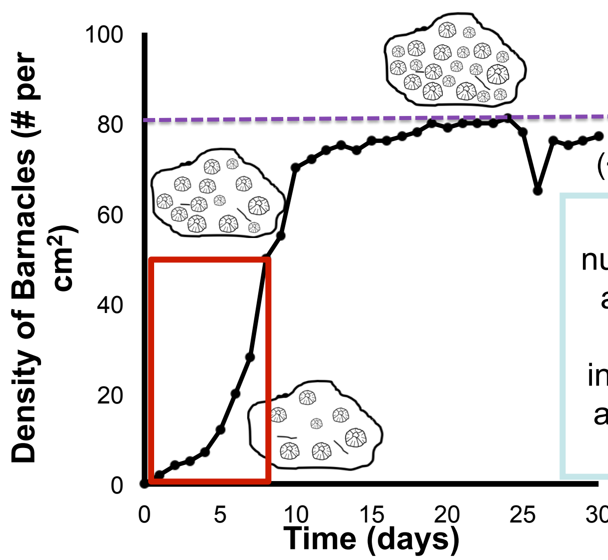
Measuring population growth in nature

- Empty rocks were placed in the intertidal zone.
- Cages were placed on the rocks to prevent predation.
- The population of settling barnacles on these rocks was observed daily for the month of April.



Beginning of April → **End of April**

Trenckmann, E., Smith, M.K., Pelletreau, K.N., Summers, M.M. 2017. An active-learning lesson that targets student understanding of population growth in ecology. *CourseSource*. https://doi.org/10.24918/cs.2017.11 19



Carrying capacity

(~80 barnacles per cm^2

The maximum number of individuals a particular habitat can sustain indefinitely given the amount of available resources.

Connell 1961

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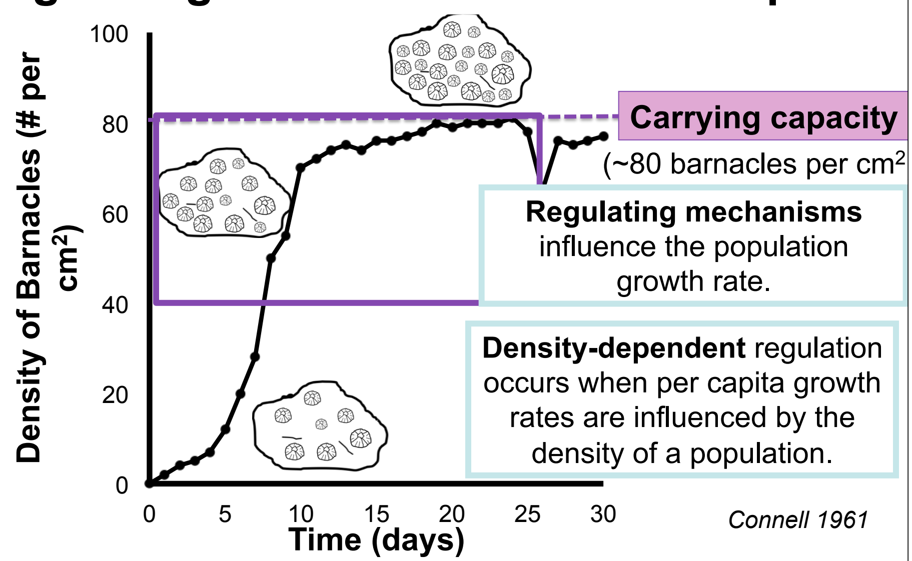
Trenckmann, E., Smith, M.K., Pelletreau, K.N., Summers, M.M. 2017. An active-learning lesson that targets student understanding of population growth in ecology. *CourseSource*. https://doi.org/10.24918/cs.2017.11

What was likely the density-dependent regulating mechanism in this example?



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Classically, d-d growth modeled by the logistic equation (Verhulst 1837)

Exponential growth with a new term added for “brakes”

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

K = carrying capacity

GO! **STOP!**

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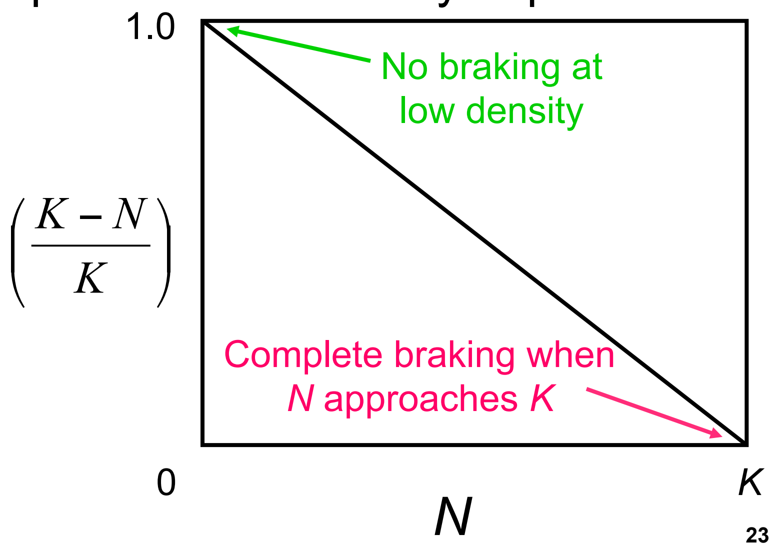
The logistic braking term models the simplest form of density dependence



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Solving logistic for N_t vs. t gives famous "sigmoid growth curve"…

$$N_t = \frac{KN_0 e^{rt}}{K + N_0(e^{rt} - 1)}$$

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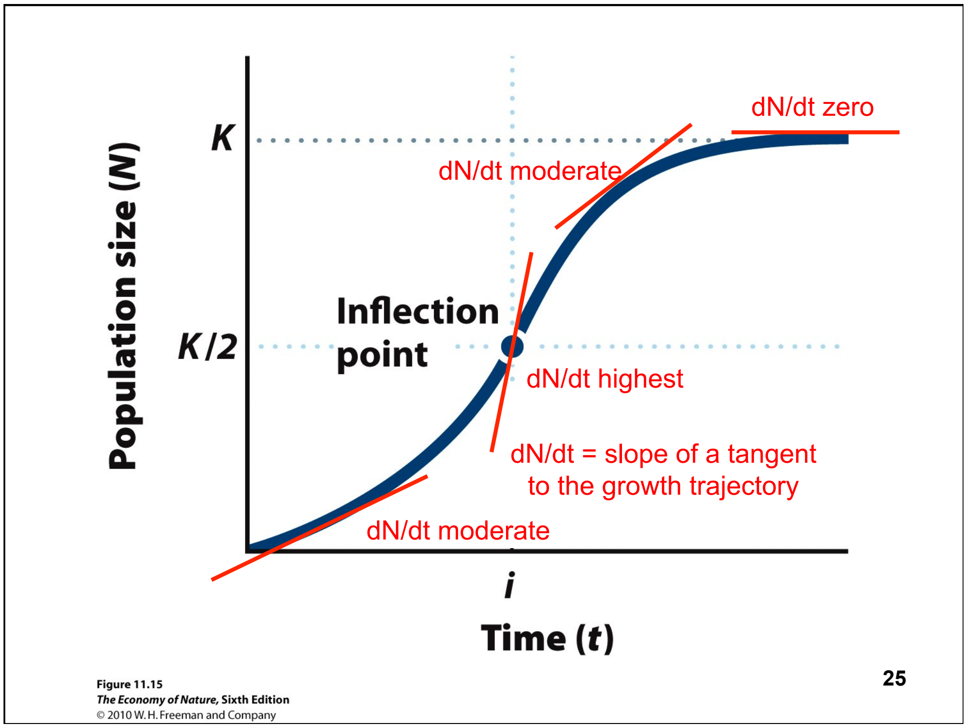

Population size (N)
K
K/2
dN/dt zero
dN/dt moderate
Inflection point
dN/dt highest
dN/dt = slope of a tangent to the growth trajectory
dN/dt moderate
i
Time (t)
Figure 11.15
The Economy of Nature, Sixth Edition
© 2010 W.H. Freeman and Company
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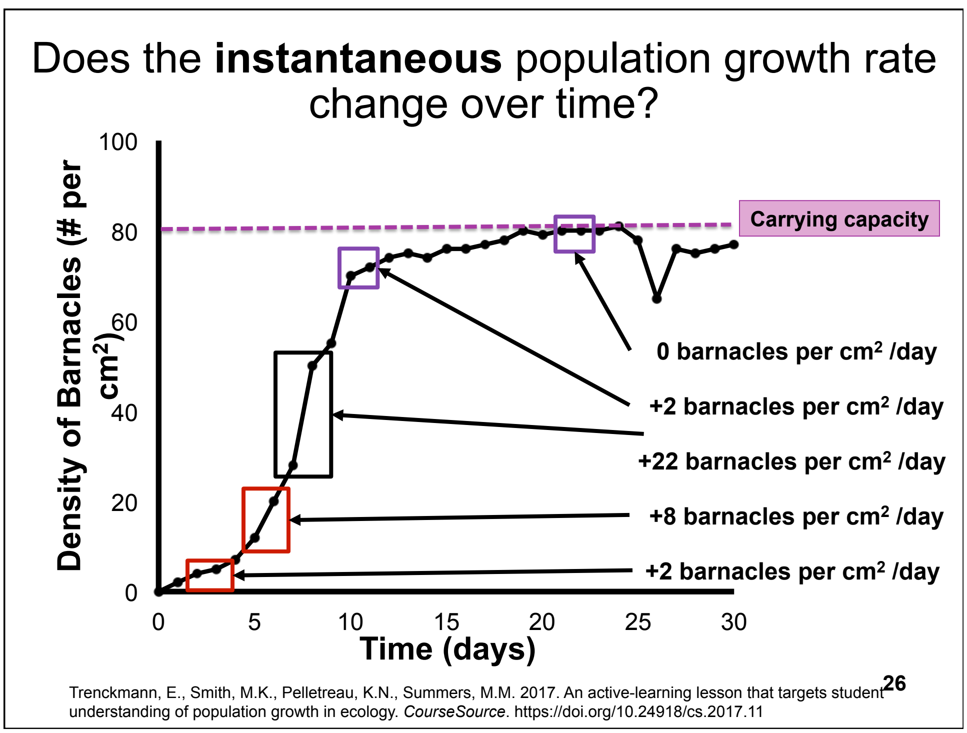

Does the **instantaneous** population growth rate change over time?
Density of Barnacles (# per cm²)
100
80
60
40
20
0
Carrying capacity
0 barnacles per cm² /day
+2 barnacles per cm² /day
+22 barnacles per cm² /day
+8 barnacles per cm² /day
+2 barnacles per cm² /day
0
5
10
15
20
25
30
Time (days)
Trenckmann, E., Smith, M.K., Pelletreau, K.N., Summers, M.M. 2017. An active-learning lesson that targets student understanding of population growth in ecology. *CourseSource*. https://doi.org/10.24918/cs.2017.11
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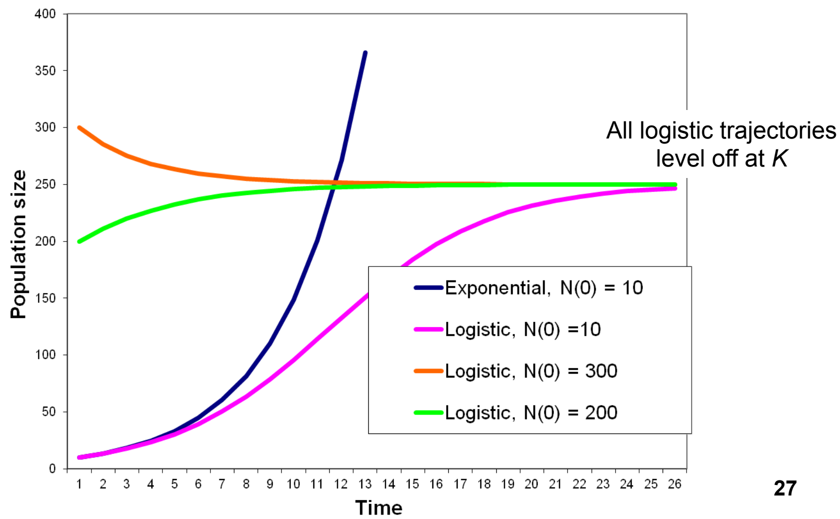
…but logistic trajectories are truly sigmoid only when starting from low numbers:

Exponential (r = 0.3) and logistic (r =0.3, K = 250) growth



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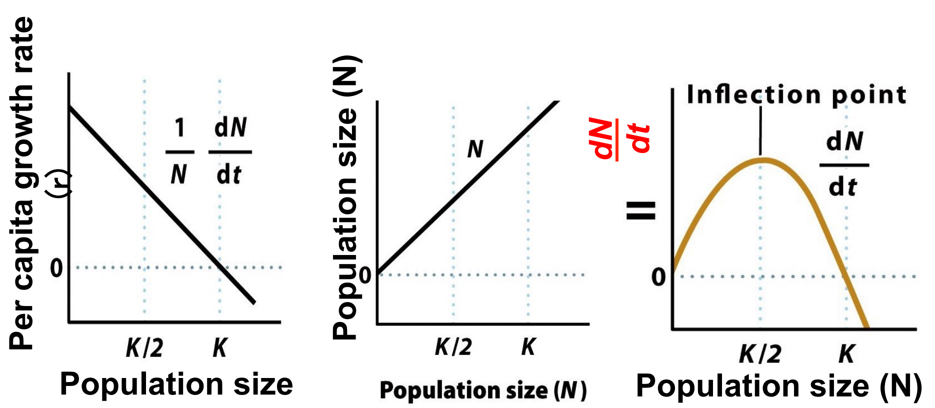

Individual contribution to population size goes down as N approaches K

Population size increases until it reaches K

Highest instantaneous growth rate at K/2 because although individuals are not growing at their fastest there are a lot of them

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Logistic model: good and bad features

- Model of intraspecific competition for resources
- Simple (only one extra parameter beyond exponential)
- Can be expanded to consider multispecies competition

- Too simple: specifies one particular kind of density dependence: perfect compensation
- Always a gradual approach to carrying capacity
- In reality, density-dependence is likely to be non-linear, may see overshoots of *K*

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Possible ways to add more reality and flexibility

- The effect of crowding is probably not a linear function of *N.*
- Could model different braking terms, for example, by using $((K-N)/K)^z$ instead of $((K-N)/K)$

- Add time lags to density dependence (organisms can persist and even reproduce using stored resources).
- Robert May's difference equation model is one way to do this:
- $N_{t+1} = N_t\, e^{(r(1-Nt/K))}$

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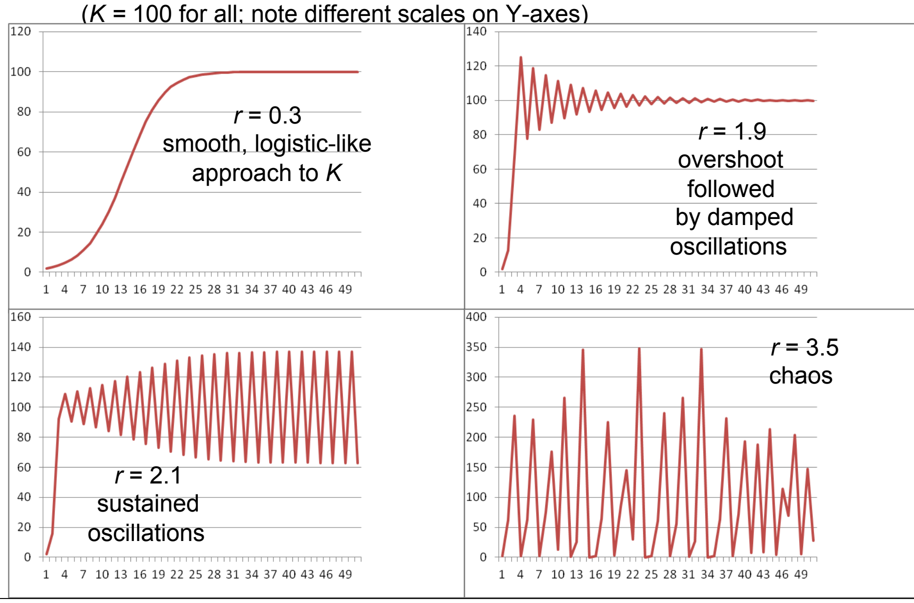
Adding time lags: *N vs. t,* May's difference equation model

$$N_{t+1} = N_t e^{(r(1-Nt/K))}$$

(*K* = 100 for all; note different scales on Y-axes)



In the models above, per-capita growth rate is fastest when population is near zero. But sometimes more density may be beneficial

- *Allee effects are negative effects of low density*, arising from social benefits such as mate finding, group living, group defense
  - Populations may fluctuate between carrying capacity K (upper limit) and another, lower limit
  - Dropping below the lower limit goes to extinction
  - Very important in conservation

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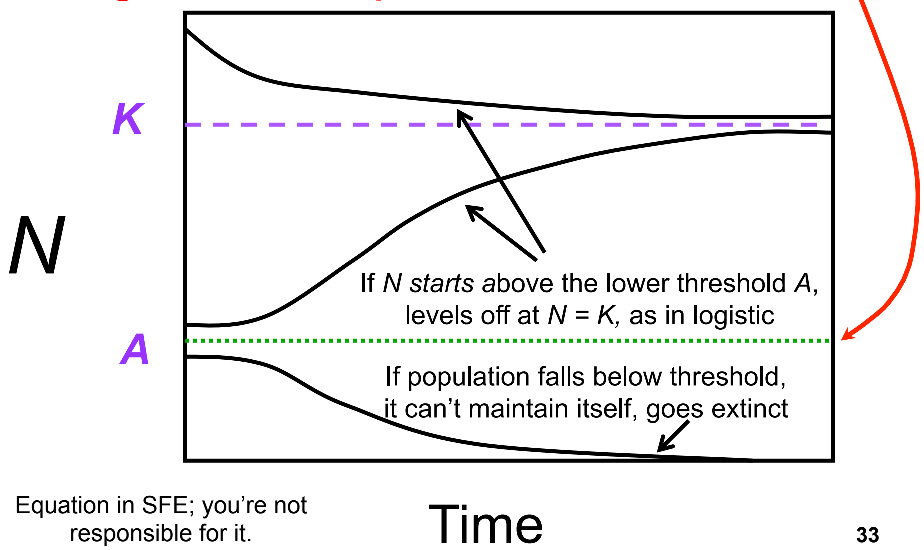
Adding an Allee threshold to the logistic: two possible outcomes



Equation in SFE; you're not responsible for it.

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Population growth

Geometric (discrete) vs Exponential (continuous) Growth Model

BUT growth unlimited

Logistic (density-dependent) Growth Model

Better BUT can be more realistic with:

Time lags

Allee threshold

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Relationships among models in BIO120

1. Basic models:

	Discrete time steps (difference equations, arithmetic)	Infinitesimal steps (differential equations, calculus)
Density independent	Geometric growth model	Exponential growth model
Density dependent	none	Logistic growth model

2. Extensions for greater realism:

Add age structure (Lecture 19)

Add time lags

Add Allee effects

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