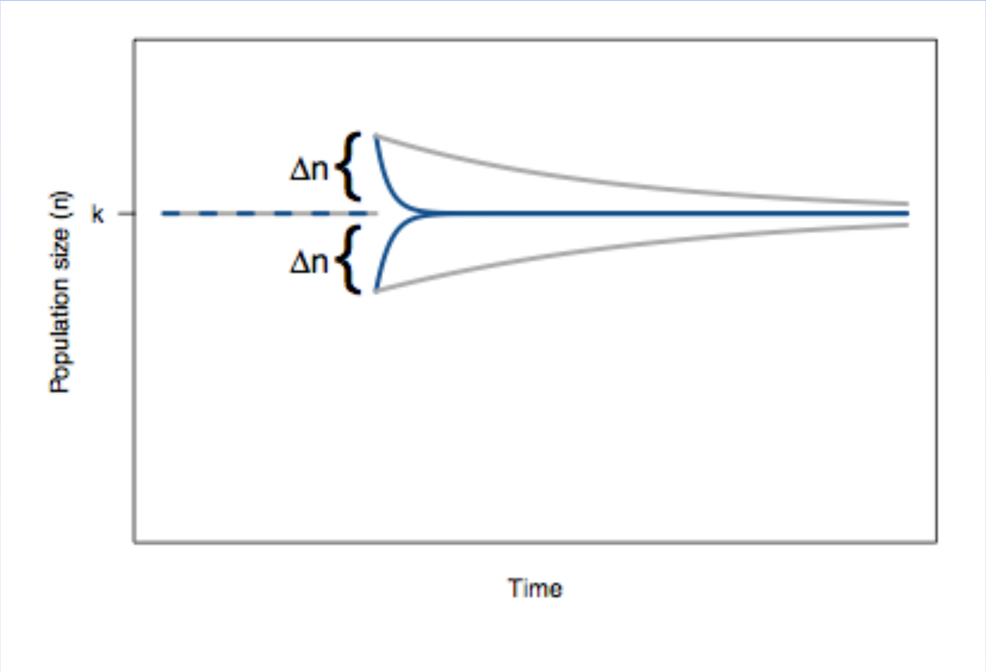
Density Dependence, Stability & Allee effects

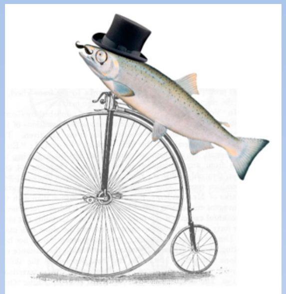
ECOL 4000/6000

Quiz1: For each statement, write True or False
e.g. A: True, B: True



A: intrinsic growth rate for “gray” population > intrinsic growth rate for “blue” population
B: “blue” population is more resilient than “gray” population

Quiz2 – which of the following are plausible reasons for the non-cycling of salmon populations?



A) Insufficient harvesting of salmon population (~5%)
B) Lack of severe density dependence
C) Presence of severe density dependence
D) Considerable harvesting of salmon population (~40%)

Answer all that apply – partial credit available

Key Concepts

- Bounded growth
- Carrying capacity
- Equilibrium
- Stability
- Population dynamics in continuous time (revisited)
- Allee effects

Muskox on Nunivak Island

Ovibos moschatus

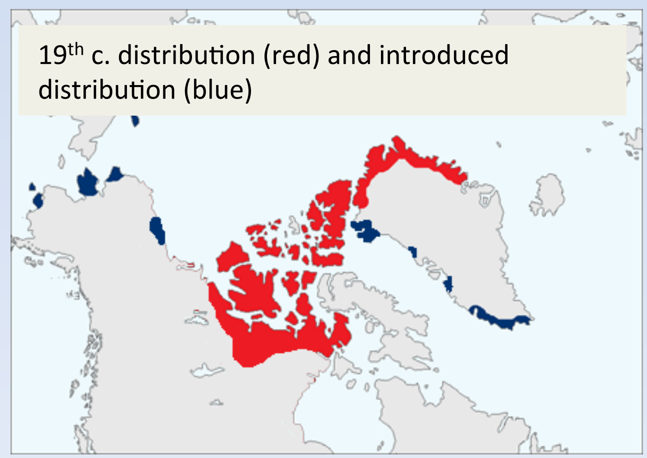
- Related to goats and sheep
- Large-bodied herbivore

 -200 cm in length

 -285 kg in weight

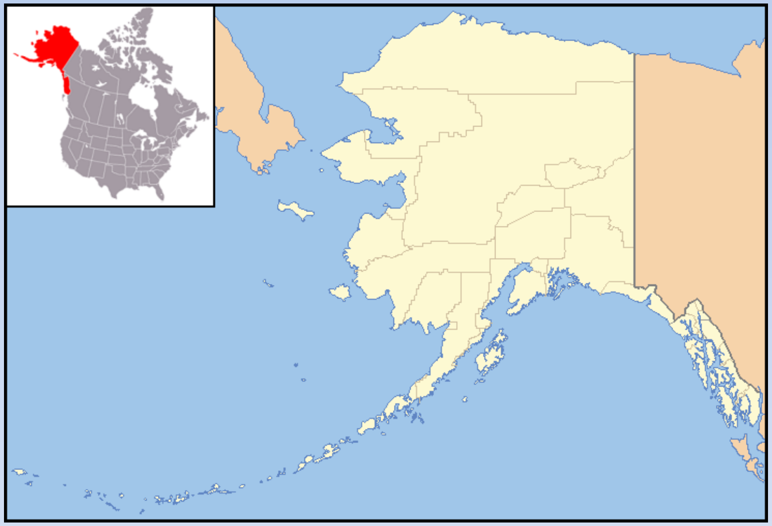
- Migrated to North America during Pleistocene (contemporary of Wooly Mammoth)

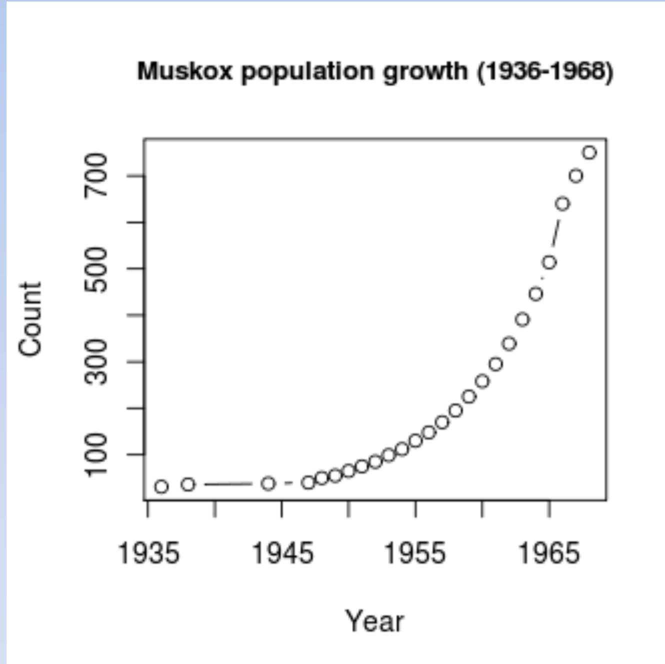
Muskox exhibiting social defense behavior



19th c. distribution (red) and introduced distribution (blue)

Muskox on Nunivak Island



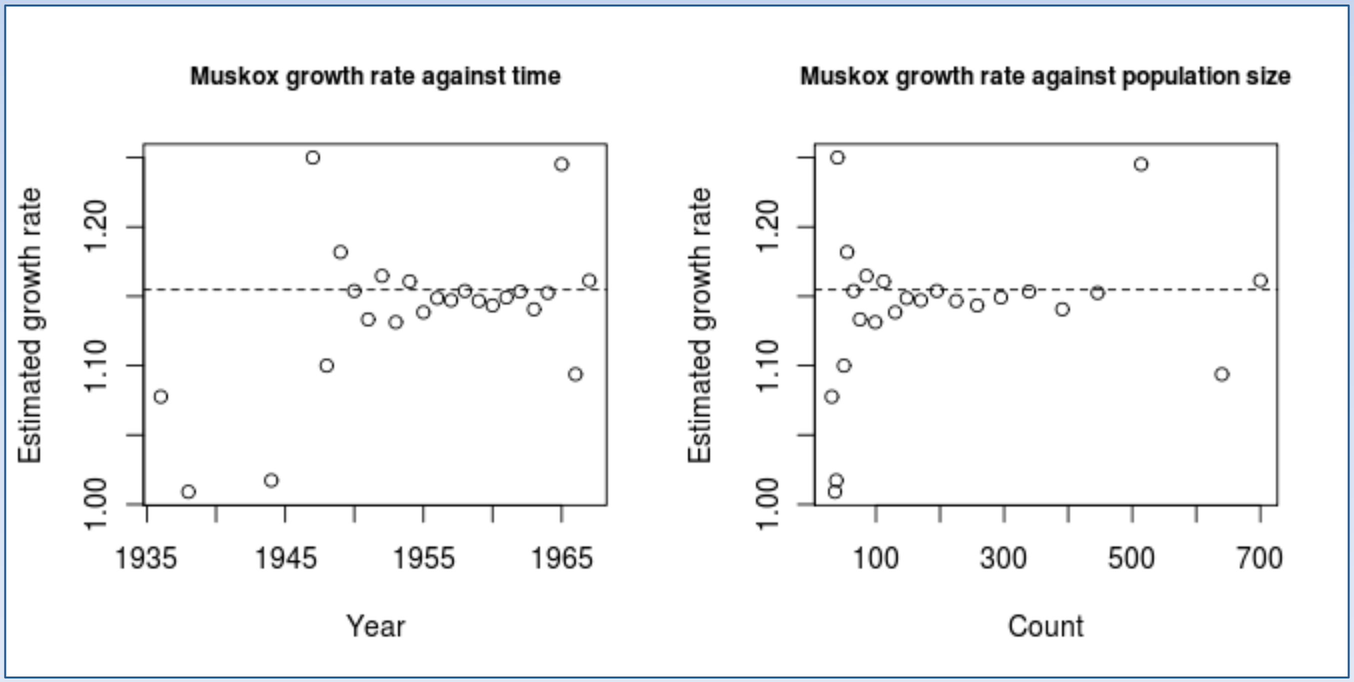


- Extirpated in 19th c.
- 31 animals introduced in 1936 by USFWS
- ~650 animals in 1970

Muskox on Nunivak Island

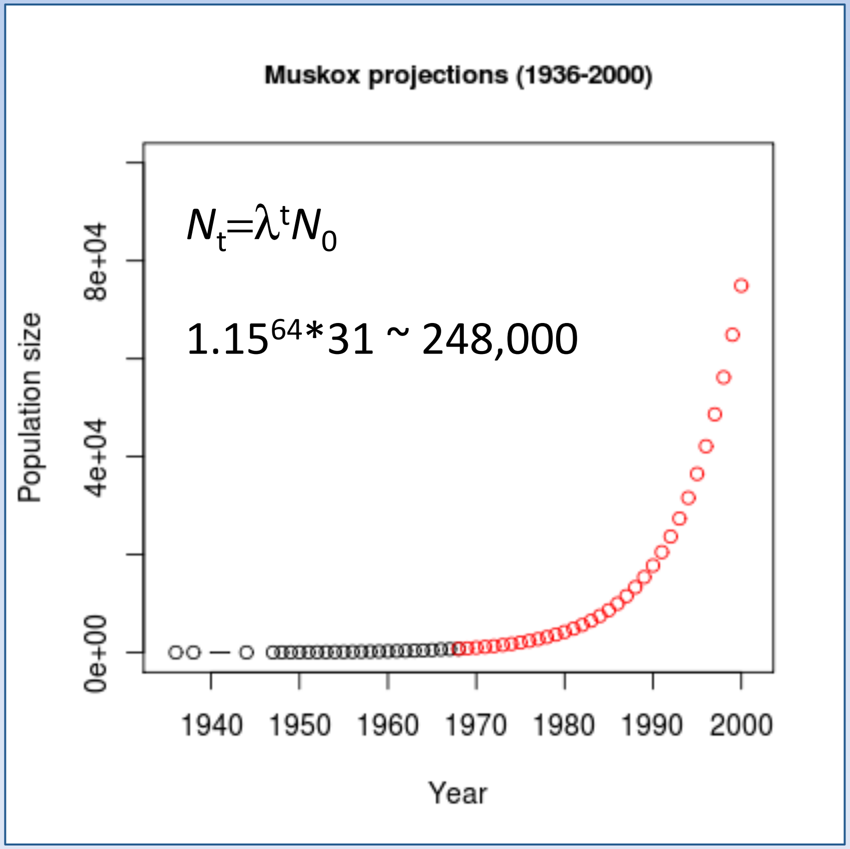
$$e^{\frac{\log(N_t/N_0)}{t}} = \lambda$$

(1) Estimate year-to-year growth rate from formula derived in first class
(2) Average estimated growth rate is λ=1.15
(3) Plot alternately against time and population size



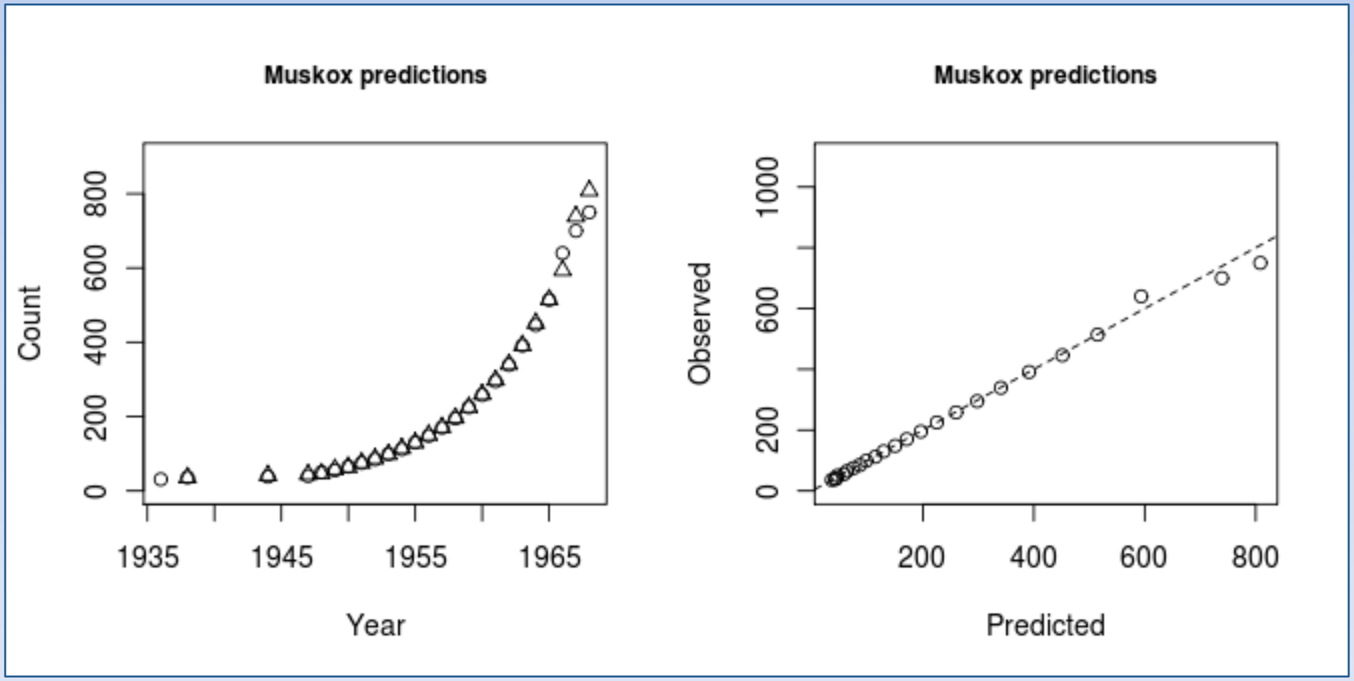
How many muskox do you suppose there are on Nunivak Island now?

Muskox on Nunivak Island



Muskox on Nunivak Island

Two ways to compare the model and observations



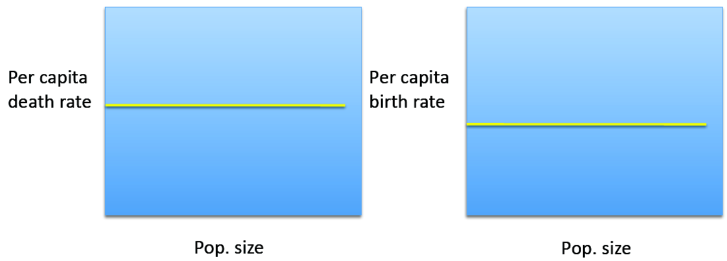
What do these plots say about Muskox population dynamics?

Review: geometric growth

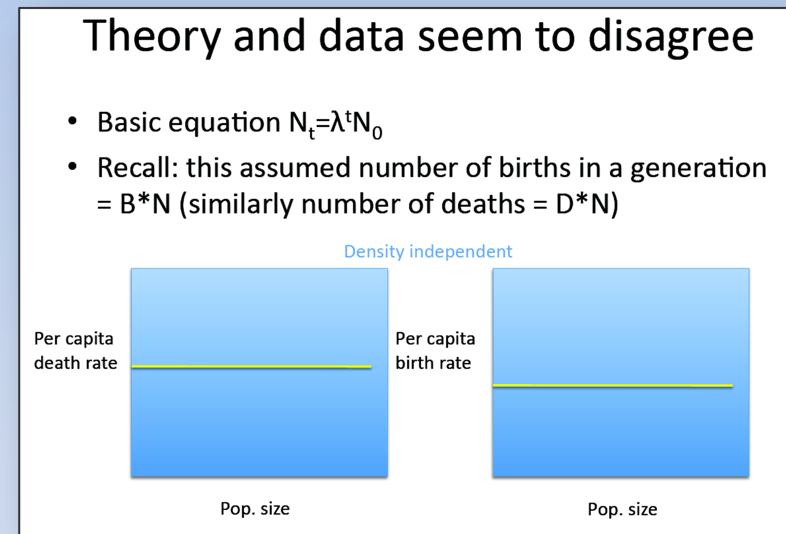
Theory and data seem to disagree

- Basic equation $N_t=\lambda^t N_0$
- Recall: this assumed number of births in a generation = B*N (similarly number of deaths = D*N)

Density independent



Review: geometric growth



$$N_t = \lambda^t N_0$$

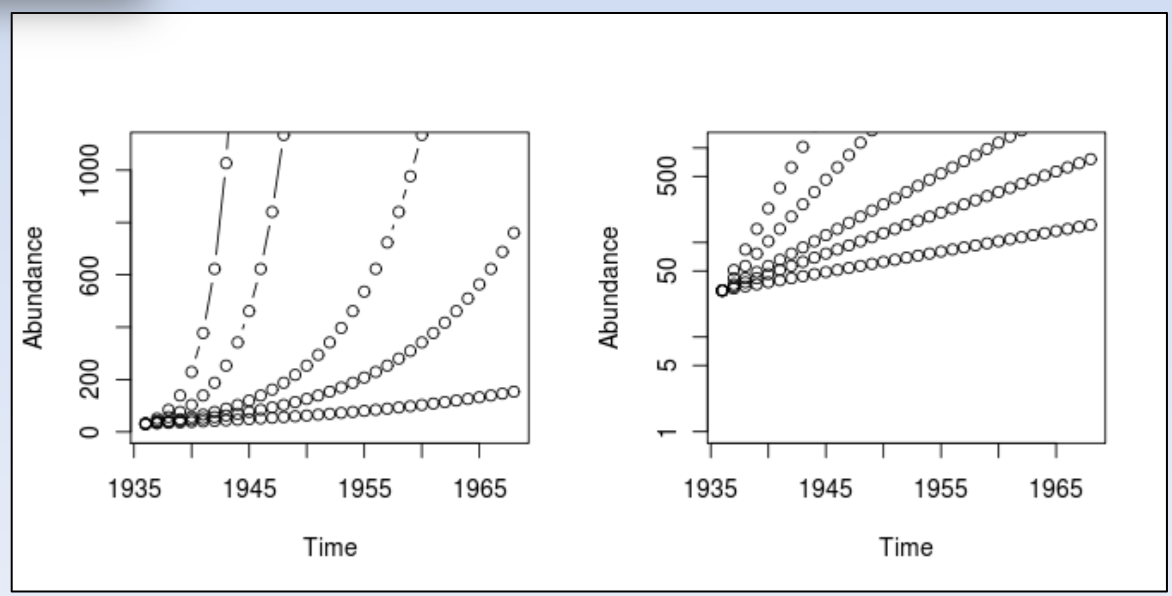
$$\log(N_t) = \log(\lambda^t N_0)$$

$$\log(N_t) = \log(\lambda^t) + \log(N_0)$$

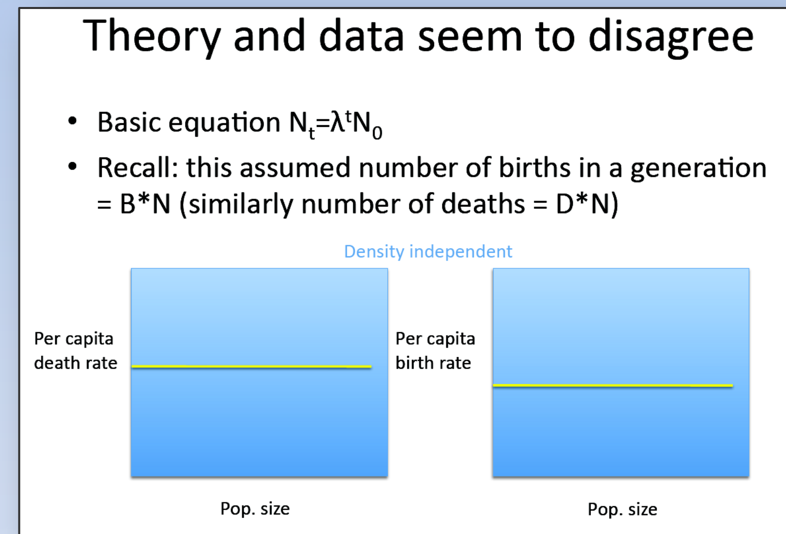
$$\log(N_t) = t\log(\lambda) + \log(N_0)$$

Log-transform to make it linear

$$\log(N_t) = t\log(\lambda) + \log(N_0)$$



Review: geometric growth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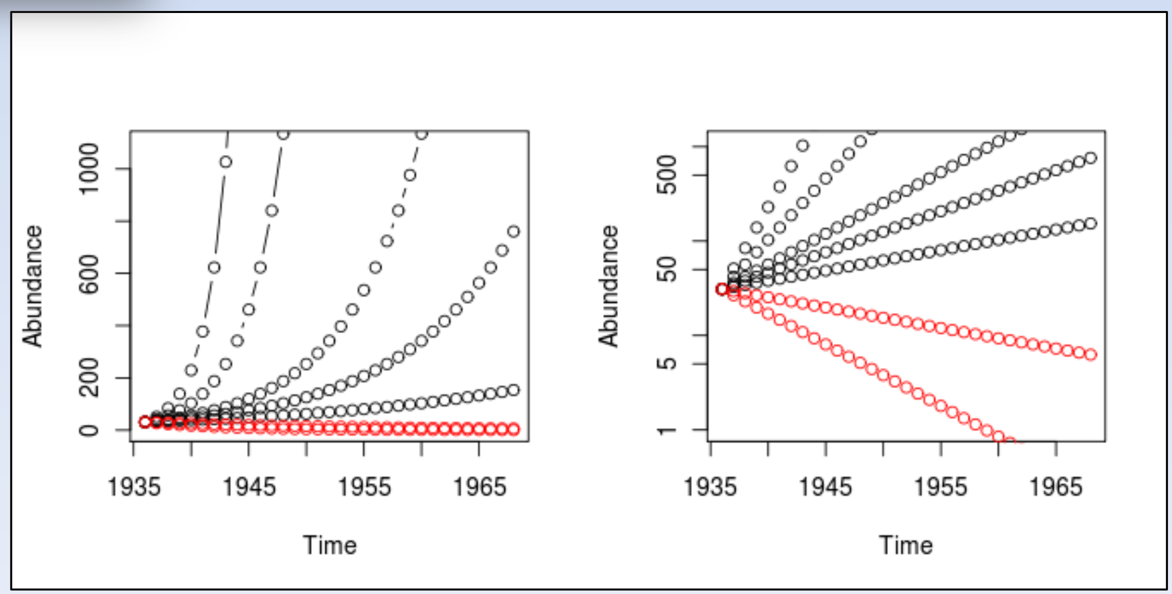
$$\log(N_t) = \log(\lambda^t) + \log(N_0)$$

$$\log(N_t) = t\log(\lambda) + \log(N_0)$$

Even works for *declining* populations

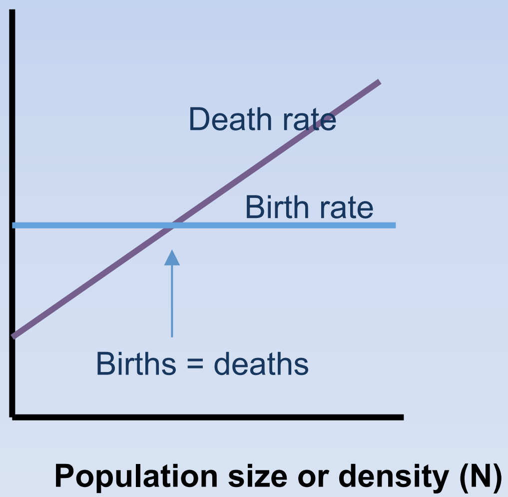
Under what biological conditions would populations decline?

How is this reflected in the fundamental equation?

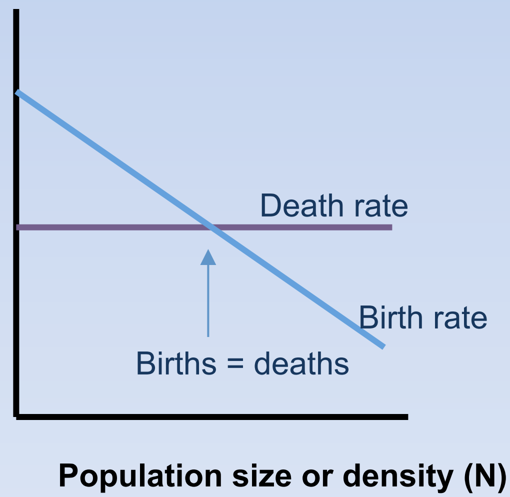


Density dependence

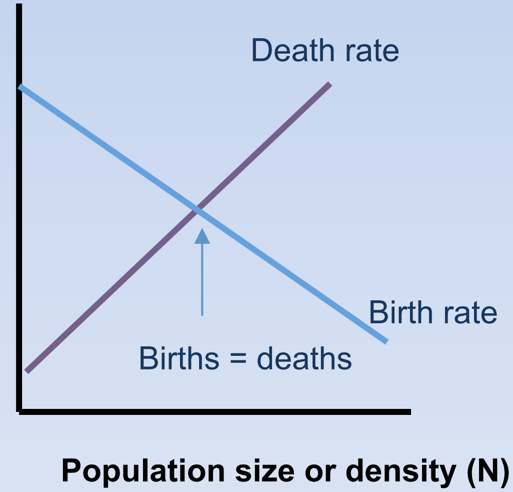
Density dependent death rate



Density dependent birth rate



Density dependent birth & death rate



Relationship between population size and per capita birth rate/per capita death rate could be linear or nonlinear

Adding density dependence

Define λ as a function of *N* and substitute for the old constant growth rate

$$N_{t+1} = \lambda\{N_t\} N_t$$

Recall: In the first lecture λ was defined by $\lambda = B - D + 1$

Note: It may no longer be easy (or even possible) to find a general expression for N_t. But, we can always iterate the model on a computer.

What function should we use?

Three models for density dependence

$$\lambda(N) = \frac{R}{1 + aN_t}$$

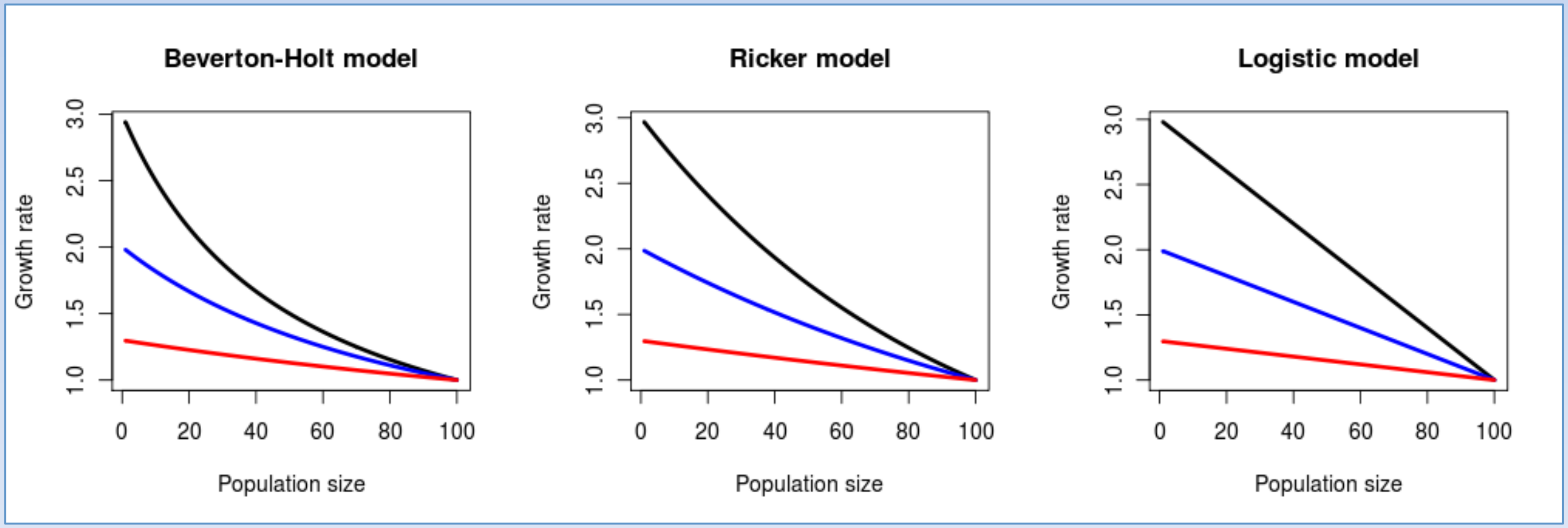
$$N_{t+1} = N_t \frac{R}{1 + aN_t}$$

$$\lambda(N) = \lambda_0 e^{bN_t}$$

$$N_{t+1} = N_t \lambda_0 e^{bN_t}$$

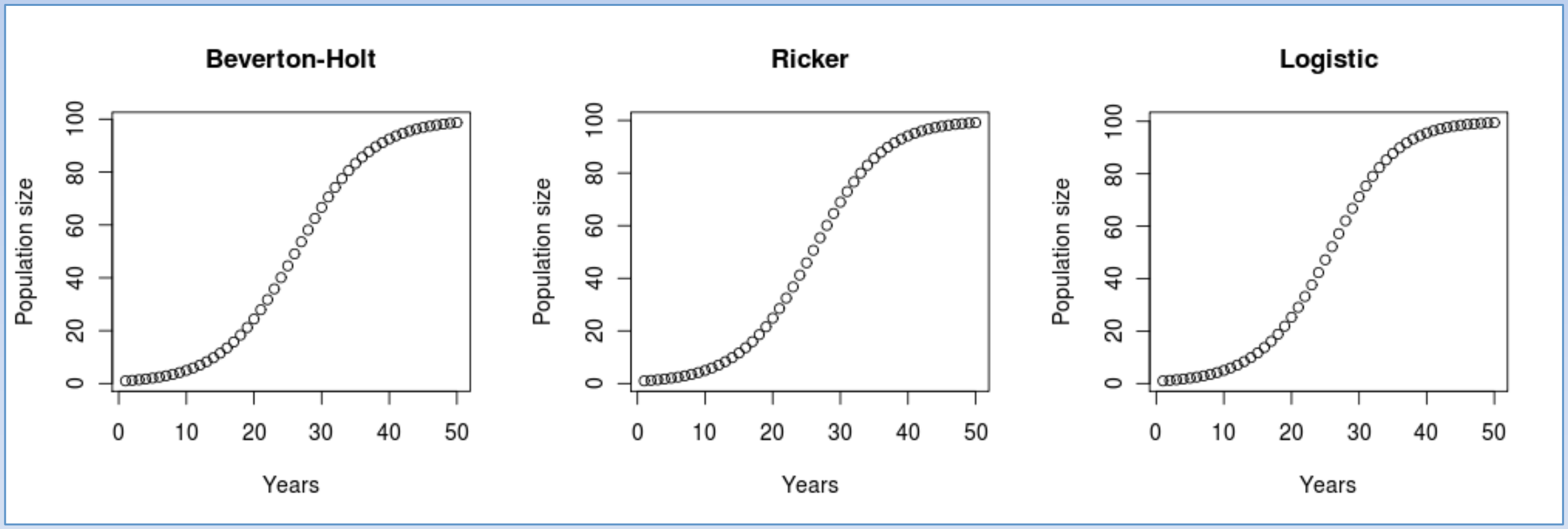
$$\lambda(N) = R(1 - N/K)$$

$$N_{t+1} = N_t R(1 - N/K)$$



How do these models differ?
What do solutions of these models looks like?
(What do we mean here by "solutions"?)

Solutions of these models



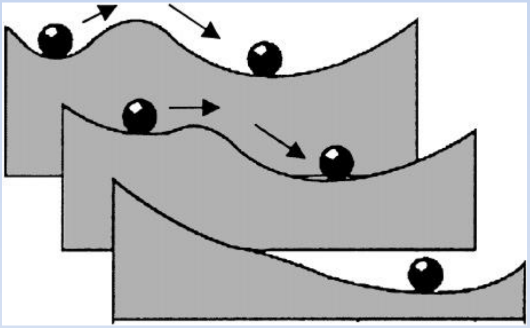
How are these trajectories different from density-independent growth?

- Growth is *bounded* (a necessary condition for *regulation*)
- Population size reaches a *carrying capacity*

Equilibrium

Carrying capacity is a special case of *equilibrium*

What is an equilibrium?



Challenge question: What are the carrying capacities of our three models of density dependent dynamics?

Practice question (previous exam question)

Consider a population with density-dependent growth given by the Beverton-Holt model with growth rate ,

$$\lambda(N) = \frac{R}{1 + aN_t}$$

parameters R=2.3, and a=0.005 , and initial population size N_0=80. What will the population size be after 2 years (i.e. what is N_2)? What is the carrying capacity of this population? Is the carrying capacity stable?

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N_1~131, N_2~182

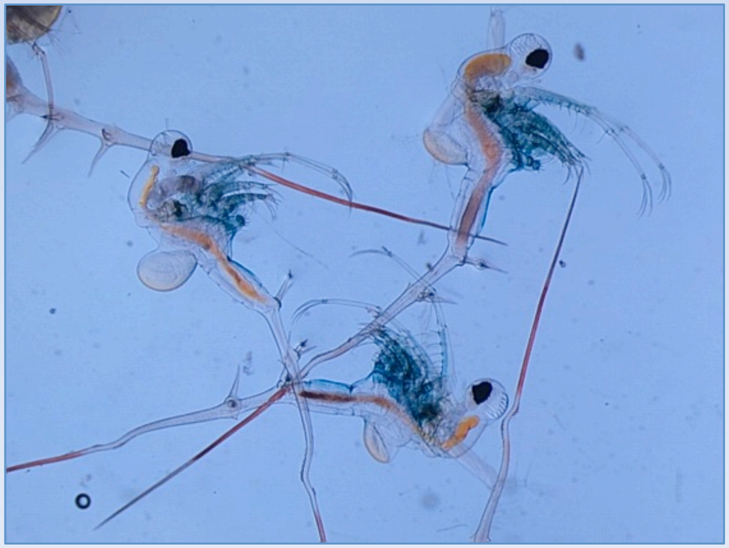
Review so far

- Density dependence in reproduction and survival give rise to density-dependent population growth
- Three models for density-dependent population dynamics are the *Beverton-Holt* model, the *Ricker* model, and the *logistic map*
    - These differ with respect to the *curvature* of density dependence
    - Each has a positive equilibrium called a *carrying capacity* and another equilibrium corresponding to *extinction*
    - The stability of the equilibria of these models depends on the *parameters*

Continuous population growth

- To now we have mostly been concerned with *annualized* (or *discretized*) reproduction and survival
- What about species that reproduce continually rather than in specific breeding seasons?
  - Many species of vertebrates and plants (especially in tropics)
  - Plankton
  - Microbes

Daphnia magna



Bythotrephes longimanus

Continuous population growth

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

A differential equation

Define a new variable→ $$r = b - d$$

And substitute→ $$\frac{dN}{dt} = rN$$

Continuous population growth

$$\frac{dN}{dt} = rN$$

$$\frac{1}{N}dN = rdt$$ Separation of variables

$$\int \frac{1}{N}dN = \int rdt$$ Integrate

$$\log N = rt + C$$ General Solution

$$e^{\log N} = e^{rt+C}$$ Algebra

$$N = e^{rt}e^{C}$$

$$N = Ae^{rt}$$ What is A?

Continuous population growth

$$N = Ae^{rt}$$

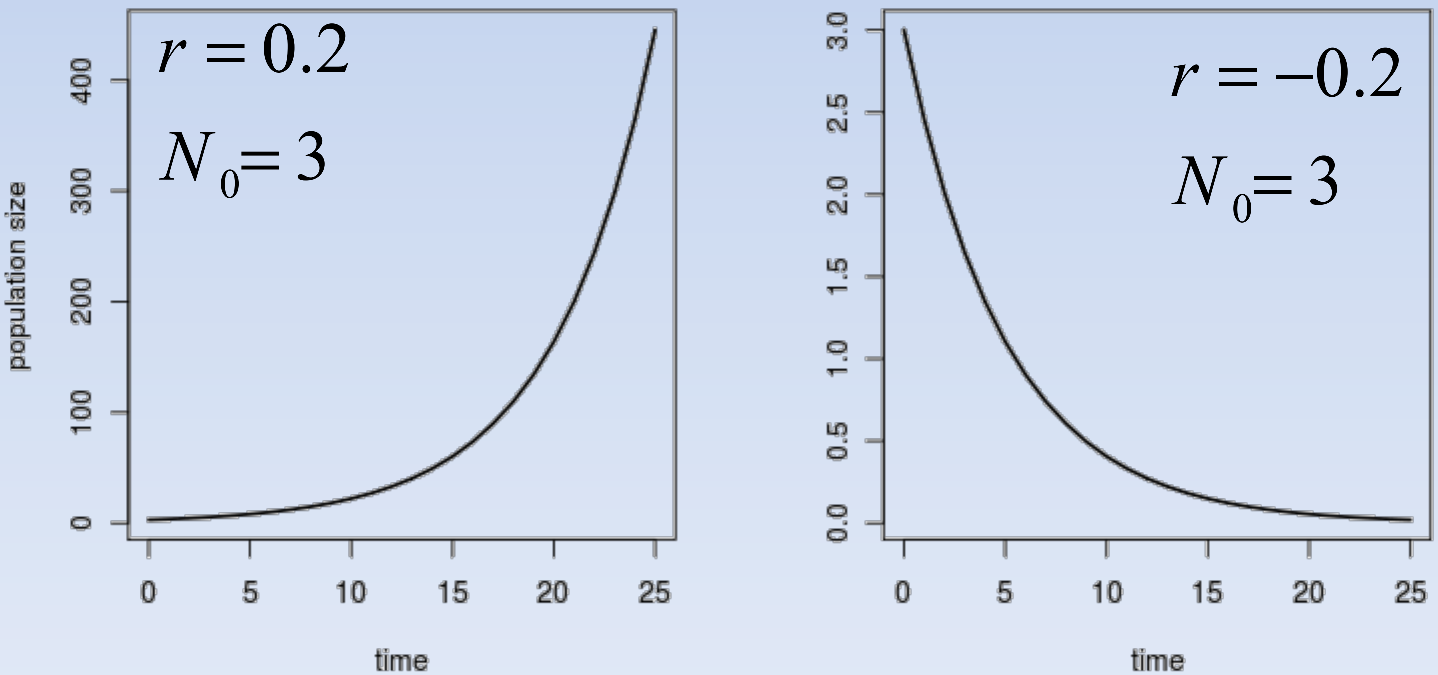
$$N_0 = Ae^{r(0)}$$

$$N_0 = A \Leftrightarrow A = N_0$$

So…

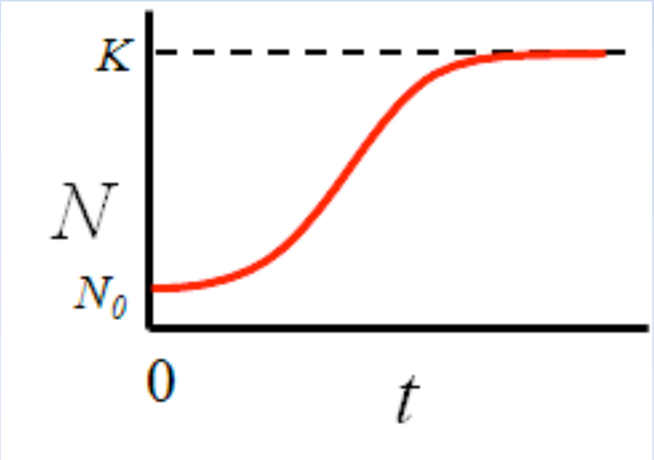
$$N_t = N_0 e^{rt}$$ ← Remember this

Continuous population growth
Numerical examples



Calculus recap

- dN/dt>0 means N increases over time
- dN/dt<0 means N decreases over time
- dN/dt=0 means N doesn't change over time



What is dN/dt doing over the range of time in this example?

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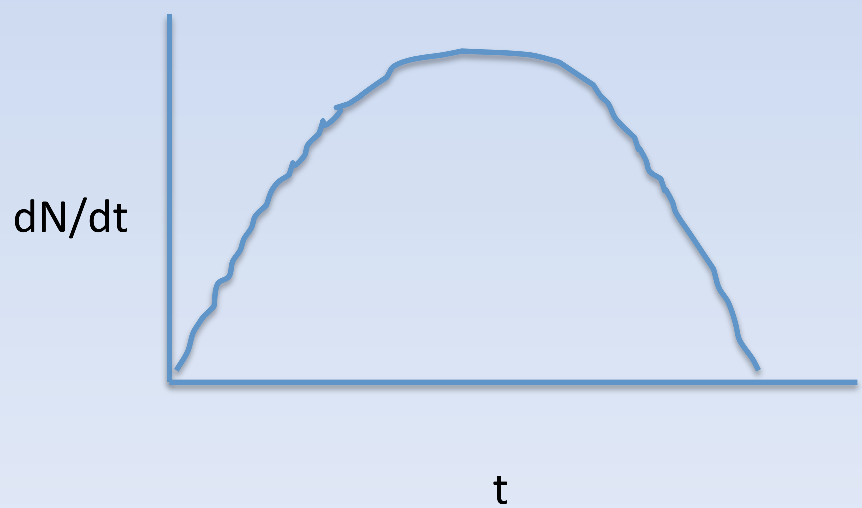

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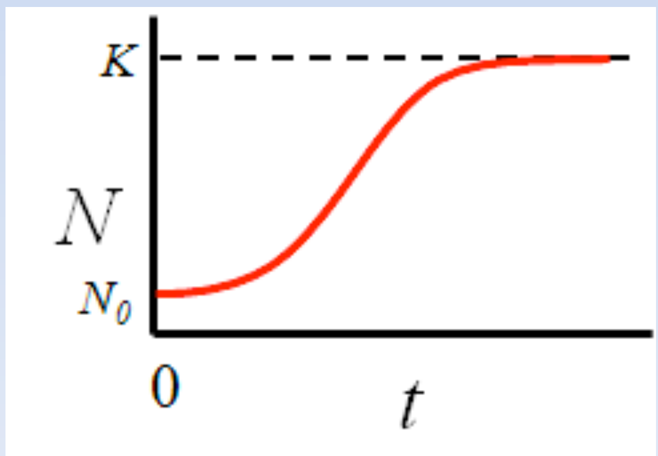

What is dN/dt doing over the range of population densities (N) in this example?

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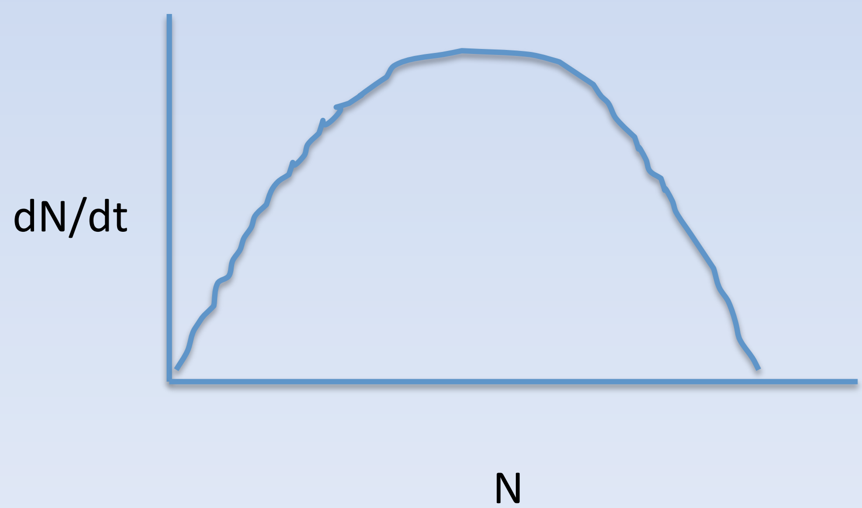


What is dN/dt doing over the range of population densities (N) in this example?

Density dependence in continuous time

$$\frac{dN}{dt} = \big(b(N) - d(N)\big)N$$ ←Start here

Add density dependence→
$$b(N) = b_0 - aN$$
$$d(N) = d_0 + cN$$

$$\frac{dN}{dt} = \left(b_0 - aN - d_0 - cN\right)N$$

Rearrange→
$$\frac{dN}{dt} = \left(b_0 - d_0\right)N\left(1 - \left(\frac{a+c}{b_0 - d_0}\right)N\right)$$

Linear density dependence

$$\frac{dN}{dt} = (b_0 - d_0)N\left(1 - \left(\frac{a+c}{b_0 - d_0}\right)N\right)$$

Define some new variables→

$$r = b_0 - d_0$$

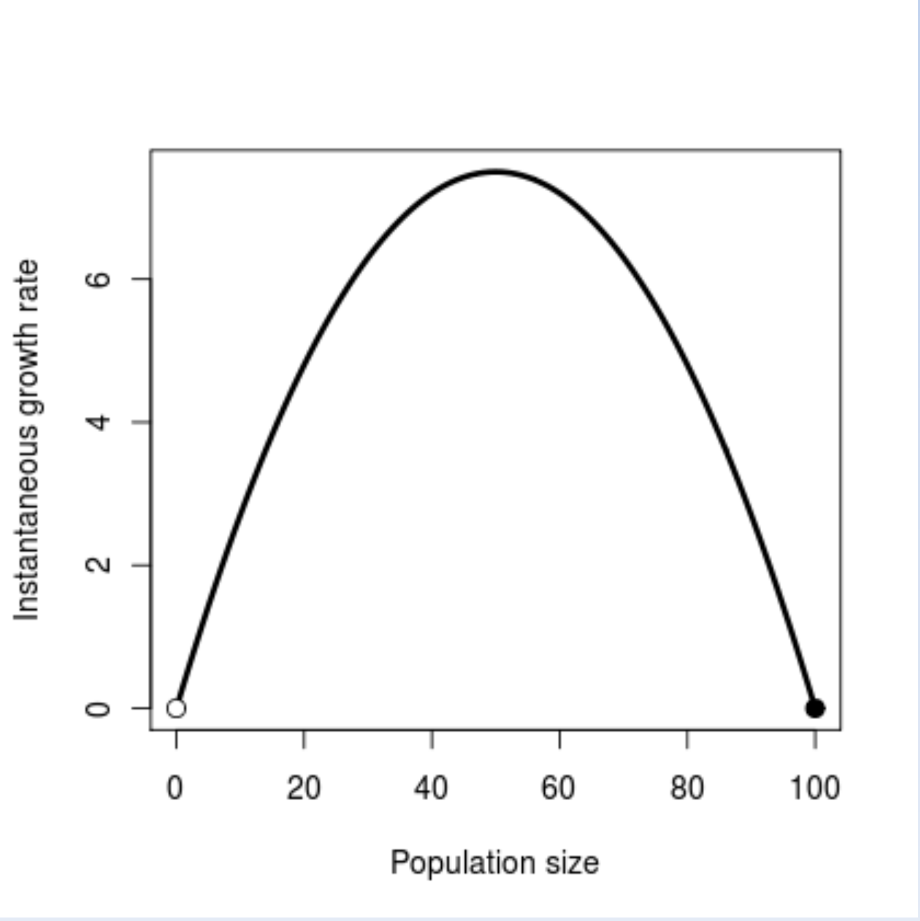
$$K = \frac{b_0 - d_0}{a+c}$$

$$\frac{dN}{dt} = rN(1 - N/K)$$

←Substitute, and you have the logistic equation for regulated population growth

Linear density dependence

A way to visualize density dependent growth rate

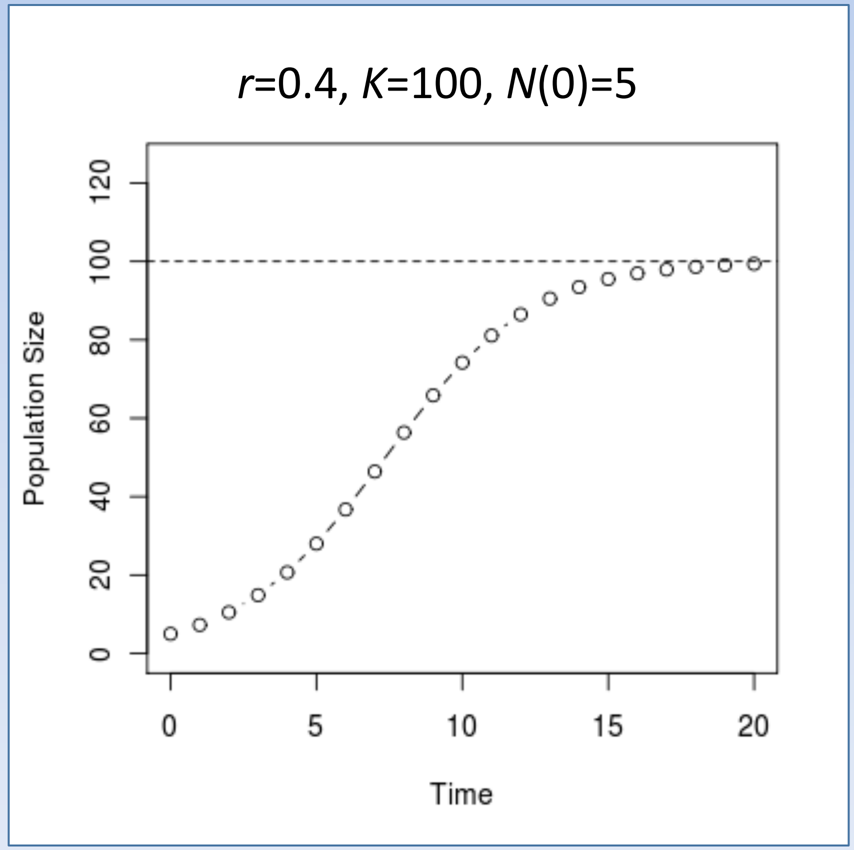


Analytical/numerical solutions

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

What are the equilibria?

- $N=K$ (carrying capacity)
- Not all equilibria are parameters of the model
- $N=0$



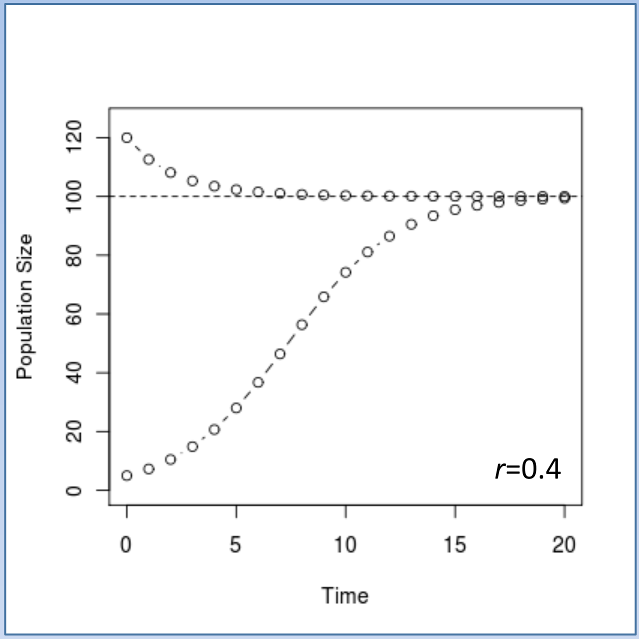
Questions

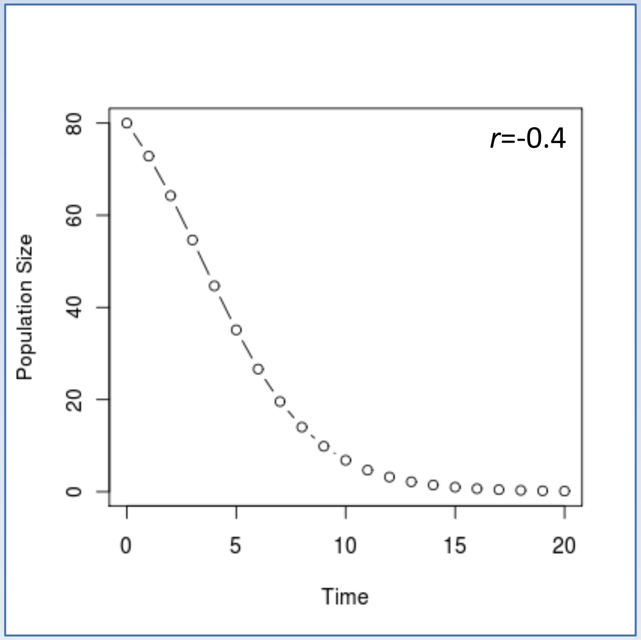
- Is carrying capacity stable?

$$\frac{dN}{dt} = rN(1 - N/K)$$

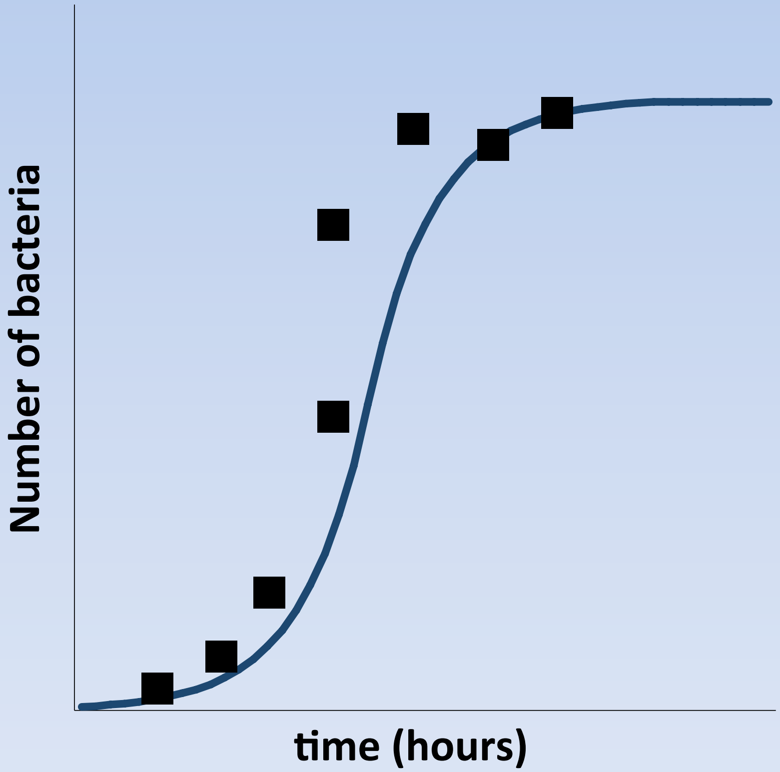
- What happens where *r*<0?
- Is *N*=0 stable?

N=0 and *N*=*K* are the equilibria of the logistic model
- If *r*>0, *N*=0 is unstable and N=K is stable
- If *r*<0, *N*=0 is stable and N=K is unstable
- If *r*=0, all values of N are neutrally stable





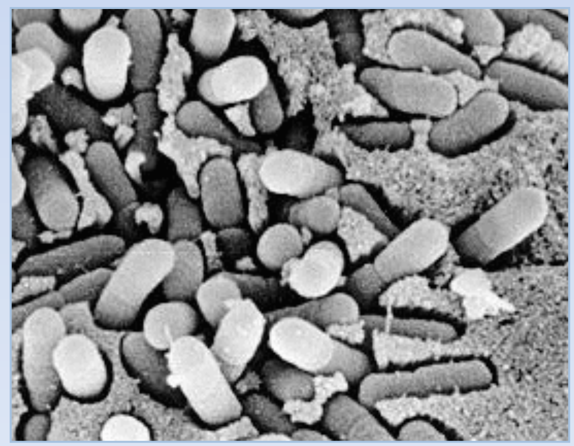
Escherchia coli



Bacteria: divide by simple binary fission

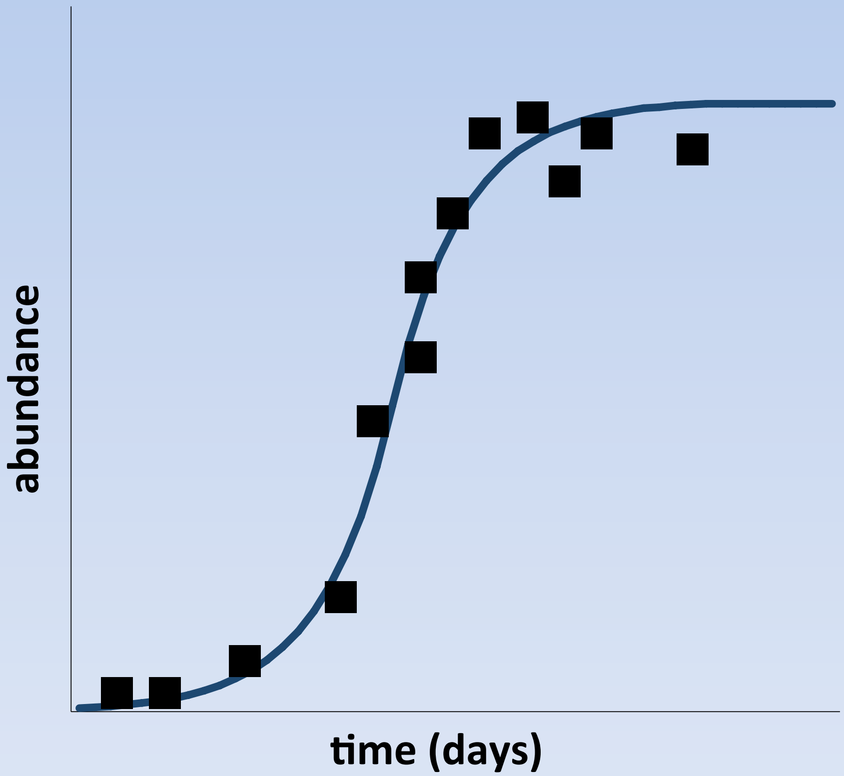
3 phases: slow, maximum, and reduced acceleration

Not a bad fit to the model



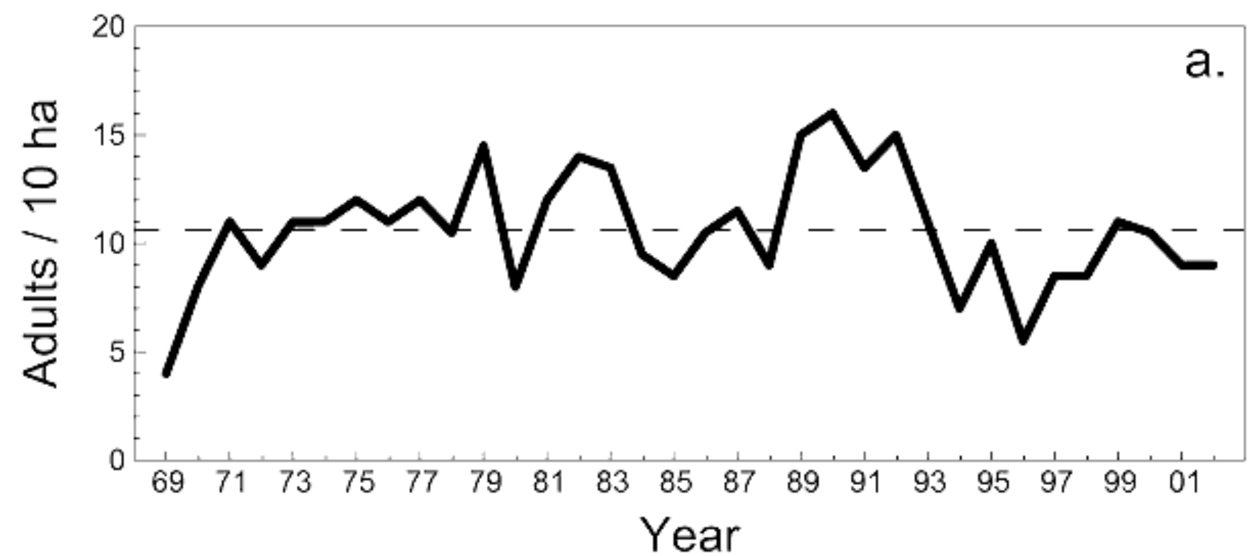
MCKENDRICK, A. G., AND PAI, M. K. 1911 The rate of multiplication of microorganisms. A mathematical study. *Proc. Roy. Soc*. Edinburgh, 31, 649-655.

Paramecium aurelia



- Gause (1934) *The struggle for existence*
- 20 *Paramecium*
- Added constant number of bacteria every day

Smithsonian
National Zoological Park



Population trends of Black-throated Blue Warblers within a 10-ha census plot at Hubbard Brook Experimental Forest, New Hampshire, USA. The number of adults has remained relatively stable for at least three decades, 1969 - 2002. The dashed line indicates mean population density on the study area; the slope of linear regression was not significantly different from 0 (R^2 = 0.0001, P = 0.94).

Smithsonian
National Zoological Park

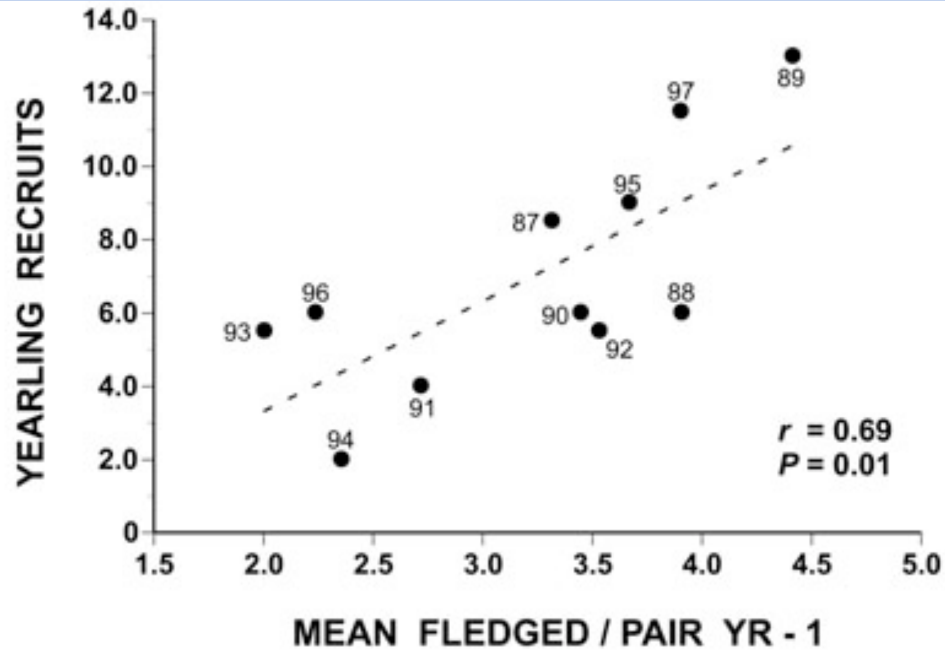


Fig. 1. Number of yearling male Black-throated Blue Warblers recruited into the breeding population is positively correlated with mean number of young fledged per pair in the previous year. Data from a 64 ha plot at Hubbard Brook.

Smithsonian
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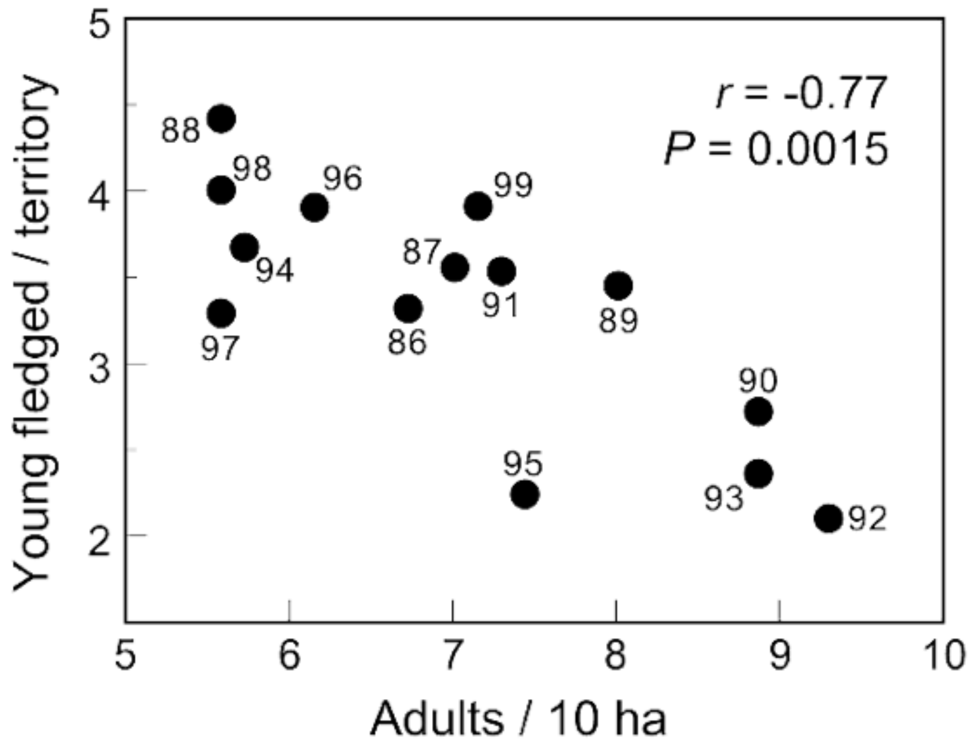

Figure 2. Annual fecundity of black-throated blue warblers declined as density of breeding adults increased on a 64-ha plot used for demographic studies at the Hubbard Brook Experimental Forest, New Hampshire, USA, 1986 - 1999. Numbers by points indicate year. First-order temporal autocorrelation in model residuals was not significant (Durbin - Watson d > 1.61, P = 0.19).

Smithsonian
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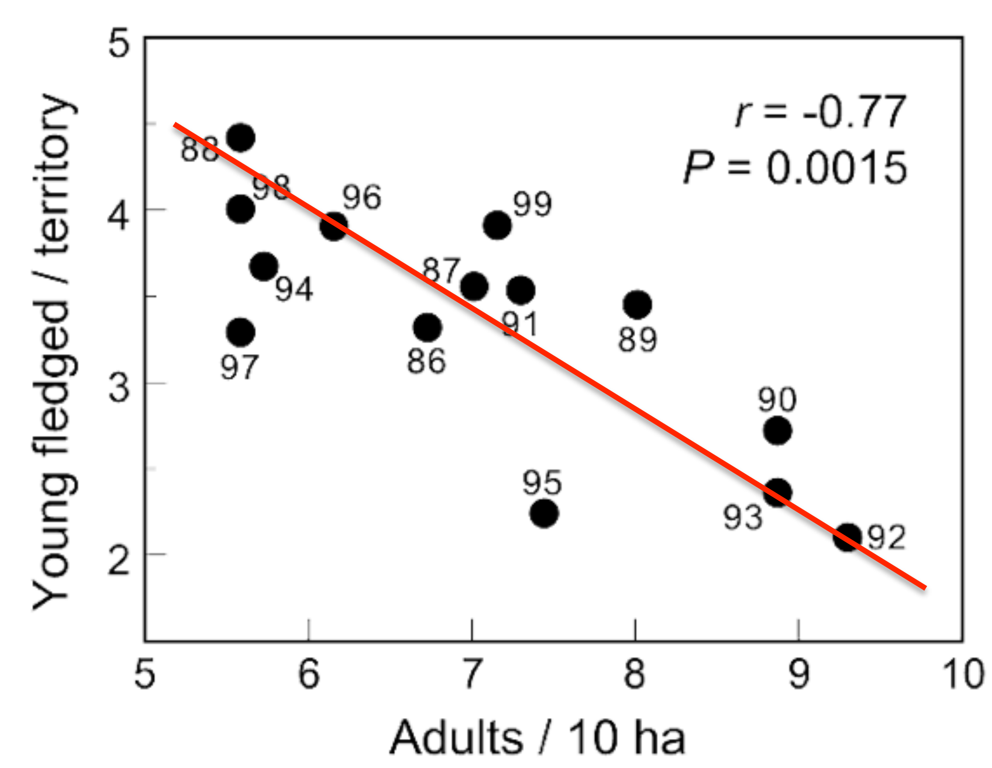

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Overview

- Bounded growth
- Carrying capacity
- Equilibrium
- Stability
- Population dynamics in continuous time
- Detecting density dependence in data (terns)

Homework: due by 5pm, Thursday September 8th
All: Ch2 Q2, Q3, Q5; Ch3 Q1, Q2, Q3
ECOL 6000 (bonus ECOL 4000): Ch2 Q7; Ch3 Q4, Q5
Bonus All: Ch2 Q6; Ch3 Q6