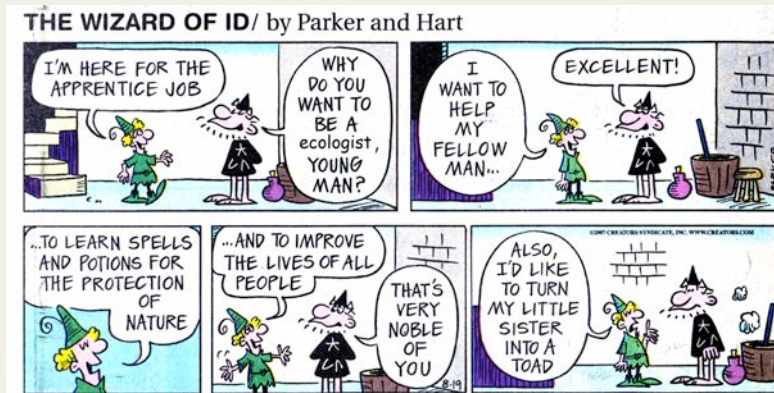


## Part 2: Quantitative Modeling

### Population Growth: Single State Variable Models



S.R. Borrett

Bio534  
Meeting #5  
Fall 2011

## Announcements & Assignments

### Lab

- I should have the lab assignment posted by Wednesday; I will send an email when this is ready.

### Homework

- Read Gotelli Ch2

# Conceptual Modeling Homework

Construct an adjacency matrix for the following diagram. Please use a flow from column to row orientation. (1 HWK pt)

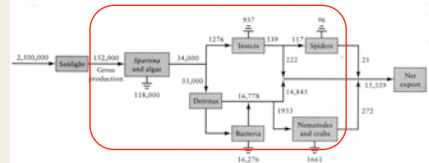


FIGURE 8.15 Energy-flow diagram for a Georgia salt marsh; units are  $\text{kJ m}^{-2} \text{yr}^{-1}$ . The striated arrow represents respired energy lost from the system. From D.S. McLusky, *The Estuarine Ecosystem*, Wiley, New York (1981).

### Adjacency Matrix

Relationship: Energy Flux  
 Currency: energy ( $\text{kJ m}^{-2} \text{yr}^{-1}$ )  
 matrix orientation: flow from column to row

Species	Symbol	$X_1$	$X_2$	$X_3$	$X_4$	$X_5$	$X_6$	gain	# of within system inputs to $X_i$
Spartina & Algae	$X_1$	0	0	0	0	0	0	1	0
Insects	$X_2$	1	0	0	0	0	0	0	1
Spiders	$X_3$	0	1	0	0	0	0	0	1
Detritus	$X_4$	1	0	0	0	0	0	0	1
Bacteria	$X_5$	0	0	0	1	0	0	0	1
Nematodes & Crabs	$X_6$	0	0	0	1	1	0	0	2
Environment	loss	1	1	1	1	1	1	0	0

# of within system losses from  $X_j$

2	1	0	2	1	0
---	---	---	---	---	---

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 \end{bmatrix}$$

$$A' = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 1 & 1 & 1 & 1 & 1 & 1 & 0 \end{bmatrix}$$

# Conceptual Mod

Original network issues

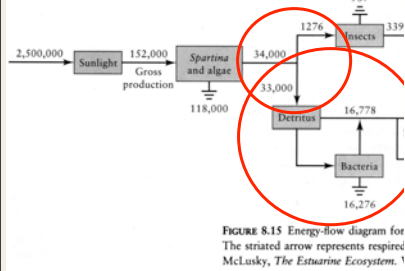


FIGURE 8.15 Energy-flow diagram for the salt marsh. The striated arrow represents respired energy lost from the system. From D.S. McLusky, *The Estuarine Ecosystem*, Wiley, New York (1981).

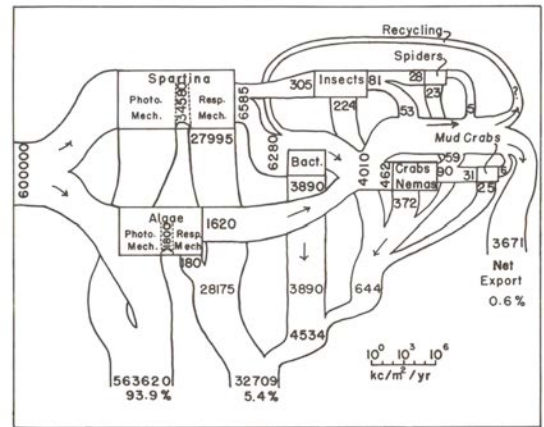


FIG. 4. Energy-flow diagram for a Georgia salt marsh. Teal 1962

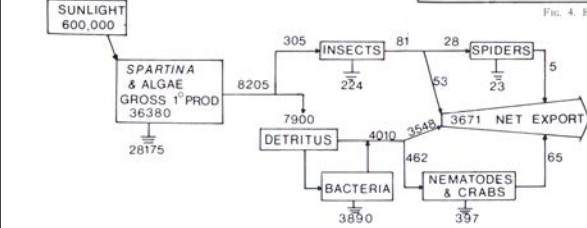


Figure 2.3 Energy-flow diagram for a Georgia salt marsh. Units are  $\text{kcal m}^{-2} \text{yr}^{-1}$ . (After Teal, 1962.)

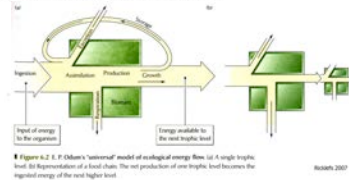


Figure 4.2 P.O. Umeki's 'universal' model of ecological energy flow. (a) A single trophic level. (b) Representation of a food chain. The net production of one trophic level becomes the respired energy of the next higher level. Rosen 2007

McLusky 1981

## Learning Objectives

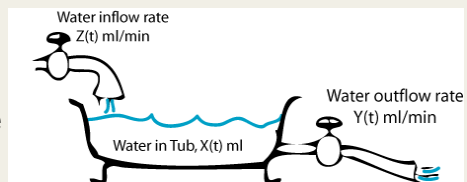
At the end of today's discussion, you should be able to:

- **Diagram** a simple population model
- Distinguish between and identify the elements of the
  - “law” of **autocatalytic growth**
  - **Discrete time** and **continuous time models**
  - **exponential** and **geometric growth** models
- Define a **specific rate**
- Explain the importance of the four major **assumptions** in the exponential growth model.
- Find **equilibriums** and calculate population **doubling times**.
- Describe how to use models to **project future population size**
- Express the equivalence between  $r$  and  $\lambda$ .

Consider a **system** with a **single state variable** of interest

### I. Non-Living

Entity = Bathtub  
State Variable = Water Volume



### II. Living

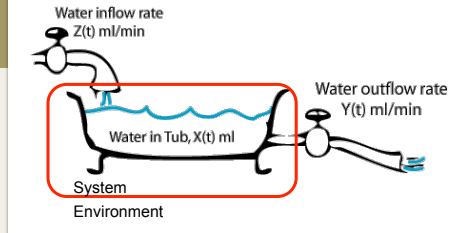
Entity = population  
State Variable =  
population ecology = individual abundance or density  
ecosystem ecology = biomass  $g\ C\ m^{-2}$



How can we model the **change** in  $X$   
[where  $X$  = **water volume** or **population density**]  
with respect to **time**?

# I. Bathtub

- Q<sub>1</sub>: What is the water volume in the bathtub at time  $t$ ?
- Q<sub>2</sub>: What processes influence the water volume?



1. Bound the system, define the state variable(s)  
 $X = \text{Water (ml)}$
2. What processes effect the amount of water in the bathtub?  
Water flows into the bathtub at a constant rate  $Z \text{ ml H}_2\text{O min}^{-1}$   
Water flows out of the bathtub at a constant rate  $Y \text{ ml H}_2\text{O min}^{-1}$

3. Then we can describe the change in water volume as

$$\begin{aligned}
 X(t + \Delta t) &= X(t) + \text{Inflow} - \text{Outflow} \\
 &= X(t) + Z * \Delta t - Y * \Delta t
 \end{aligned}$$

Future state
Current state

Where  $\Delta t$  is a constant time step Discrete Time Equation

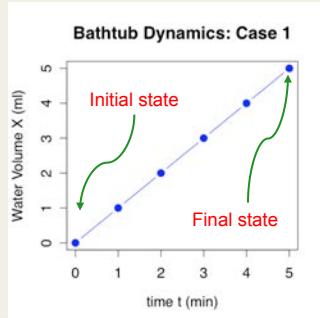
Check Units → Dimensional Analysis

# Bathtub Dynamics

$$\begin{aligned}
 X(t + \Delta t) &= X(t) + Z\Delta t - Y\Delta t \\
 \text{let } \Delta t &= 1
 \end{aligned}$$

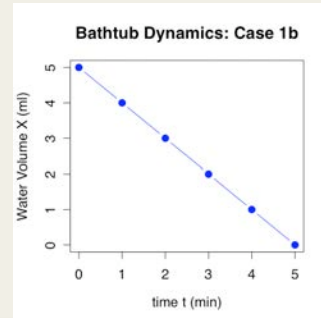
$Z > Y$

t	Z	Y	X
0	--	--	0
1	2	1	1
2	2	1	2
3	2	1	3
4	2	1	4
5	2	1	5



$Z < Y$

t	Z	Y	X
0	--	--	5
1	1	2	4
2	1	2	3
3	1	2	2
4	1	2	1
5	1	2	0



## From Discrete to Continuous Time

1. Our **discrete time** model was

$$X(t + \Delta t) = X(t) + Z\Delta t - Y\Delta t$$

2. First lets rearrange the equation using a bit of algebra

$$X(t + \Delta t) = X(t) + \Delta t(Z - Y)$$

$$X(t + \Delta t) - X(t) = \Delta t(Z - Y)$$

$$\frac{X(t + \Delta t) - X(t)}{\Delta t} = Z - Y$$

3. Now, lets let  $\Delta t$  decrease in size until it is infinitely small,  $\Delta t \rightarrow 0$

(recall definition of a limit from calculus)

4. Then our resultant, **continuous time** equation can be written as,

$$\frac{dX}{dt} = Z - Y$$

which is a **differential equation**.

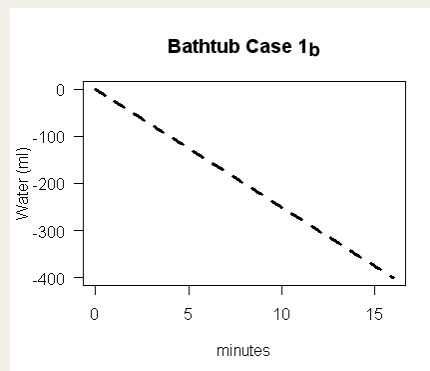
Q<sub>1</sub> What are the units of the equation?

Q<sub>2</sub> What is the meaning of a derivative?

## Bathtub Dynamics: Case 1



Inflow = 75 ml min<sup>-1</sup>  
Outflow = 50 ml min<sup>-1</sup>

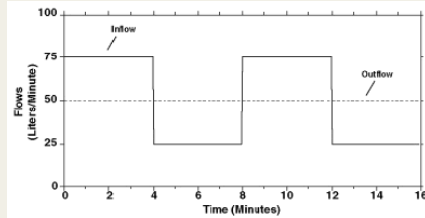


Inflow = 25 ml min<sup>-1</sup>  
Outflow = 50 ml

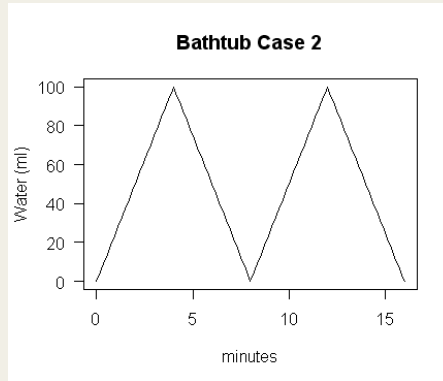
Do these results make physical sense? (see Case 3)

## Bathtub Dynamics: Case 2

Variable Input, constant output



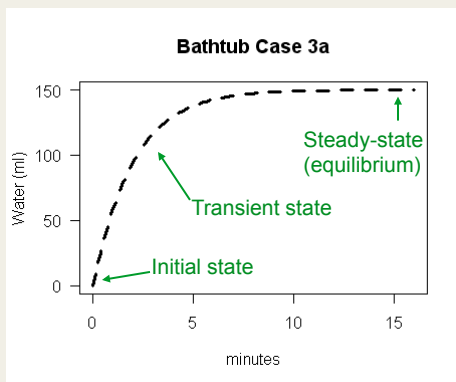
Time	Inflow	Outflow	Water (L)
0	0	0	0
1	75	50	25
2	75	50	50
3	75	50	75
4	75	50	100
5	25	50	75
6	25	50	50
7	25	50	25
8	25	50	0
9	75	50	25
10	75	50	50
11	75	50	75
12	75	50	100
13	25	50	75
14	25	50	50
15	25	50	25
16	25	50	0



Q: What is wrong with this?

Notice:  
The problem was carefully engineered, but we have not addressed the problem raised in Case 1b.

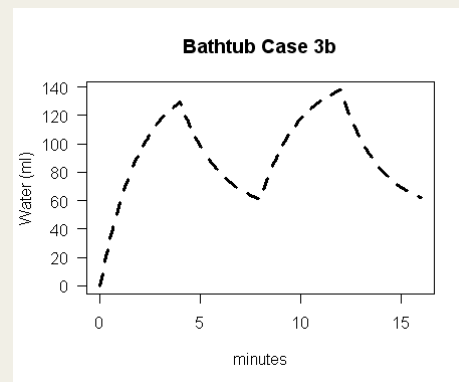
## Bathtub Dynamics: Case 3



Inflow = 75 ml min<sup>-1</sup>  
Outflow = 0.5 min<sup>-1</sup> \* X ml.

$$\frac{dX}{dt} = Inflow - Outflow$$

$$= 75 - 0.5 * X$$



Inflow = as in Case 2  
Outflow = 0.5 min<sup>-1</sup> \* X ml.

“donor controlled”

No longer can lose more than what is physically available

## II. Building a Population Model

### Population

a group of individuals of the same species living in the same place and time

Let  $N$  represent the number of individuals

What processes determine  $N$ ?

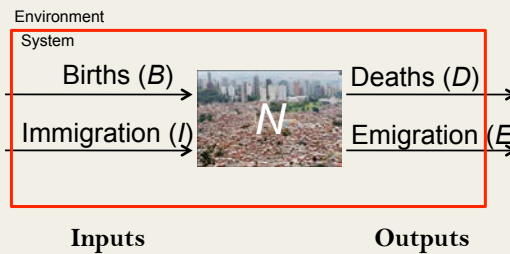
### Equation

$$N_{t+1} = N_t + \overset{\text{Inputs}}{B + I} - \overset{\text{Outputs}}{D - E}$$

Demographic Balance Equation

Autocatalytic Growth

### Conceptual Diagram



## Simplifying Assumptions

Assume: **Closed Population**

$$\Delta N = B - D$$



Assume: **Continuous Time** – continuous growth processes

Use an ordinary, continuous differential equation

$$\frac{dN}{dt} = B - D$$

Instantaneous population growth rate

What are B and D?

## Instantaneous Process Rates

$$\frac{dN}{dt} = B - D$$

Let:  $B = bN$       and       $D = dN$

$b$  and  $d$  are **specific rates** of births and deaths, respectively. For example,  $b$  implies that the population grows by  $b$  individuals for each individual in the original population per time step and has units of  $\frac{\text{individuals m}^{-2}}{\text{individuals m}^{-2} \times t} = t^{-1}$

Assume:  **$b$  and  $d$  are time and density independent**

Assume: **no time lag (instantaneous)**

$$\begin{aligned} \frac{dN}{dt} &= bN - dN \\ &= (b - d)N \\ &= rN \end{aligned}$$

$r =$  intrinsic growth rate

$r$  defines three possible dynamics

$r > 0 \Rightarrow$  exponential increase

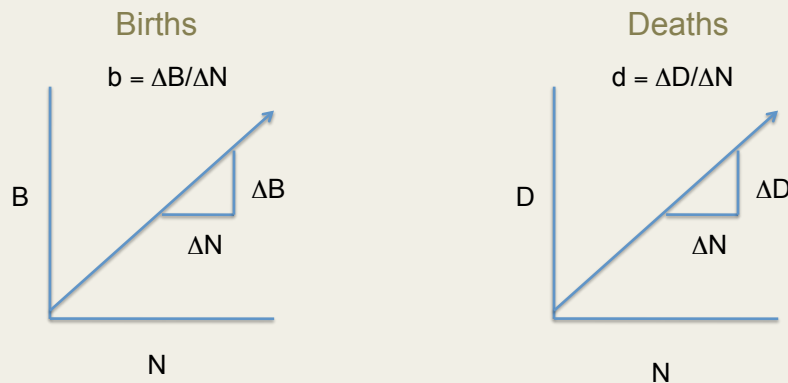
$r = 0 \Rightarrow$  no change

$r < 0 \Rightarrow$  exponential decline

Check Units  $\rightarrow$  Dimensional Analysis

Exponential Growth

## Linear Process Formulation



As defined, the processes are a linear function of population density

## Model Use & Analysis: Finding the Equilibriums

When will the population not grow?

We can find the **equilibrium points** of the model – where the population will not change by setting the differential equation to zero and solving it.

$$\begin{aligned} \frac{dN}{dt} &= 0 \\ 0 &= rN \end{aligned}$$

This equation can only be true if  
(1)  $r = 0$ , or  
(2)  $N^* = 0$

What happens if  $N$  is negative?

This is a very common analytical technique for analyzing Diff Eq models

## Model Use & Analysis: Projecting Population Size

How do we use the exponential growth equation to forecast future population?

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

Integrate it to find the following **exact solution**

$$N_t = N_0 e^{rt}$$

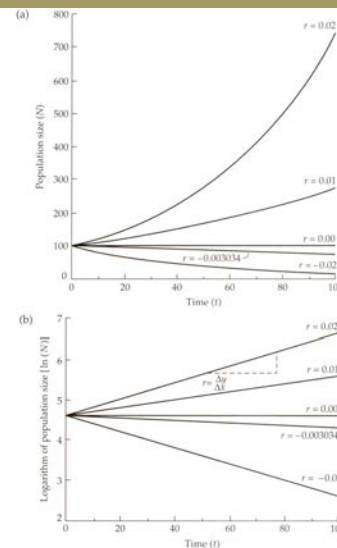
Where Initial state

$N_0$  = initial population size ←

$e$  = base of natural logarithm

$r$  = intrinsic growth rate

$t$  = future time of interest



**Figure 1.1** (a) Trajectories of exponential population growth, calculated from a starting population size of 100 individuals. The estimated  $r$  of  $-0.003034$  [individuals/(individual  $\times$  year)] corresponds to the projection for the grizzly bear (*Ursus arctos horribilis*) population of Yellowstone National Park (see Figure 1.6). (b) Exponential growth curves plotted on a semilogarithmic graph. The same data are used as in (a), but the y axis (population size) shows the natural logarithm (base  $e$ ) of population size. In this type of graph, an exponential curve becomes a straight line; the slope of that line is  $r$ , the intrinsic rate of increase.

## Model Use & Analysis: Doubling Time

A feature of a population that we can calculate from the model

$$N_{t_{\text{double}}} = 2N_0$$

substitute  $2N_0 = N_0 e^{rt_{\text{double}}}$

solve  $t_{\text{double}} = \frac{\ln(2)}{r}$

### Example Doubling Times

Table 1.1 Estimates of  $r$  and doubling times for different organisms.

Species	Common name	$r$ (individuals / (individual • day))	Doubling time
T phage	Virus	300.0	3.3 minutes
<i>Escherichia coli</i>	Bacterium	58.7	17 minutes
<i>Paramecium caudatum</i>	Protozoan	1.59	10.5 hours
Hydra	Hydra	0.34	2 days
<i>Tribolium castaneum</i>	Flour beetle	0.101	6.9 days
<i>Rattus norvegicus</i>	Brown rat	0.0148	46.8 days
<i>Bos taurus</i>	Domestic cow	0.001	1.9 years
<i>Avicennia marina</i>	Mangrove	0.00055	3.5 years
<i>Nothofagus fusca</i>	Southern beech	0.000075	25.3 years

From Fenchel (1974).

Gotelli 2008

## Assumptions

### Closed Population – no $I$ or $E$

- Alternative = metapopulation models (Ch4)

### Constant $b$ and $d$

- Density independent vs dependent (Ch2)
- Time independent vs. time varying
- No environmental constraints
- No demographic or environmental stochasticity

### No genetic structure

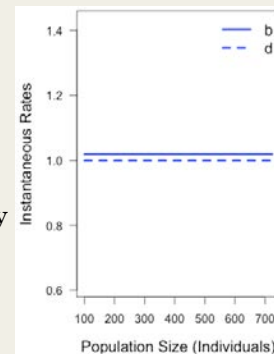
- Identical individuals (or average individual)

### No age or size structure

- Alternative = structured population models (Ch3)

### Continuous growth, no time lags

- Alternative = discrete time with delay, delay differential equations



## Discrete Time: non-overlapping generations

Given

$$N_{t+1} = N_t + r_d N_t = N_t(1 + r_d)$$

Where

$r_d$  = discrete growth factor

Let

$$\lambda = 1 + r_d$$

Then

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

$$N_1 = \lambda N_0$$

$$N_2 = \lambda N_1 = \lambda(\lambda N_0) = \lambda^2 N_0$$

And in general

$$N_t = \lambda^t N_0$$

If we let our time step be 20 min, this would match the growth rate of the record for bacterial reproduction

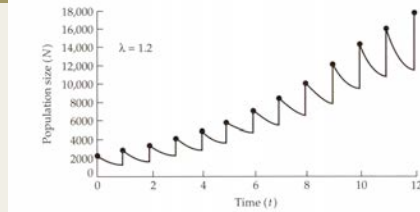
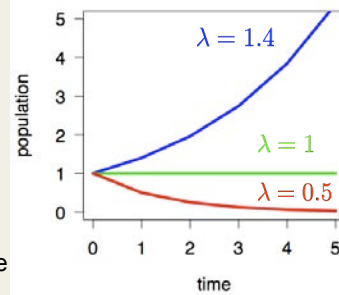


Figure 1.2 Discrete population growth. In this example, births are pulsed at the beginning of the year, and deaths occur continuously. Gotelli 2008



“Geometric Population Growth”

## Equivalence between $r$ and $\lambda$

“the continuous model essentially ‘connects the dots’ of time in the discrete model” (p. 13)

Thus, there must be an equivalence between  $r$  and  $\lambda$ . What is it?

$$e^r = \lambda$$

$$r = \ln(\lambda)$$

$\lambda$  is a dimensionless ratio (no units), but it is time step dependent

$$r > 0 \leftrightarrow \lambda > 1 \Rightarrow \text{population increases}$$

$$r = 0 \leftrightarrow \lambda = 1 \Rightarrow \text{population at steady state}$$

$$r < 0 \leftrightarrow \lambda < 1 \Rightarrow \text{population decreases}$$

## Stochastic Models

A **stochastic model** is one that contains at least one random variable

Used when there is uncertainty in a processes

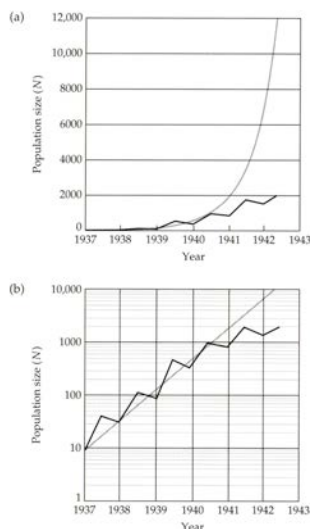
Each time the modeled process is executed, the random variable can have a different value. This implies that the model will give an different prediction each time.

- Use *Monte Carlo* techniques to describe model behavior
- simulate a large number of times
- describe the ensemble of solutions (mean, range, variance)

In population models we can introduce stochasticity in many ways:  
Environmental vs. Demographic Stochasticity

Gotelli provides a couple of examples of modeling environmental and demographic stochasticity.

## Pheasants of Protection Island



**Figure 1.5** Growth of pheasant (*Phasianus colchicus torquatus*) population introduced to Protection Island. The thin line shows the hypothetical exponential growth curve, with  $r = 1.3217$  individuals / (individual  $\cdot$  year); the thick line shows the observed population size. For comparison, population sizes are plotted on a linear scale in (a) and a logarithmic scale in (b). Note that the logarithmic scale is base 10, not base  $e$ . (Data from Lack 1967.)

Gotelli 2008

Model projection compared to empirical data

Model seems to “fit” the data for a period of time, and then it fails to adequately predict the population dynamics.

Why does might this model have ultimately failed here?

