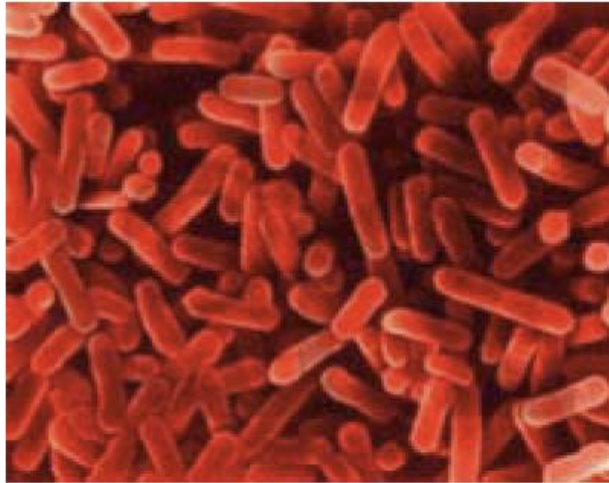


Computer Simulationspraktikum

Umweltwissenschaften

Ralf Schneider



The population bomb

Ecological modelling

- Explore how to model populations with dynamic models
- Density independent models
- Density dependent models
- Look at simple models for meta-populations
- Look at simple models for environmental stochasticity
- Look at harvesting from density dependent models – why is this interesting?
- What are key population processes for biology – birth, death, immigration and emigration
- Use Matlab throughout

The population bomb

- First one *E. coli* then 2, 4, 8, 16,...
- Divide every 20 mins, so after 32 h entire earth covered 1 m deep!
- Like compound interest – *E. coli* interest rate is 100% every 20 mins!
- Ecological interest rates rarely as high – most struggle to exist with rates ~ 0
- Ecological interest rates differ temporally and spatially

Why is it a population bomb?

- cf nuclear bomb – particles split and collide with other particles and continue splitting – chain reaction like exponential growth
- Rate of reaction not determined by number of particles present
- Growth rate (or ecological interest rate – i.e. birth and death rates) not dependent upon number of organisms - **Density independent**
- Geometric (discrete) and exponential (continuous) growth same process

Discrete time

- Time step anything convenient: day, month, year and census population at beginning of step

B = Number of births each animal has at beginning of time step that live to beginning of next time step

D = Probability an animal dies during time step

$$N_{t+1} = N_t + BN_t - DN_t$$

$$N_{t+1} = N_t(1 + B - D)$$

$$N_{t+1} = RN_t$$

$$R = 1 + (B - D)$$

Discrete time...

$$N_{t+1} = RN_t$$


N at $t = 0$ is N_0


$$N_1 = RN_0$$

$$\begin{aligned} N_2 &= RN_1 \\ &= R(RN_0) \\ &= R^2 N_0 \end{aligned}$$

$$N_t = R^t N_0$$

M 2.1  Let's plot discrete-time geometric growth equation

M 2.2  Plot represents an “explosion”, but more useful to plot on a semi-log scale

Ex 2.1  Show that slope of semi-log plot of population size vs time is $\log(R)$

Continuous time

- Counterpart of geometric growth in discrete time is exponential growth in continuous time


b = average birth rate per unit time per organism

d = average death rate per unit time per organism

$$\frac{dN}{dt} = bN - dN$$

birth and death usually combined into “intrinsic rate of increase”, $r = b - d$

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

Ex 2.2  Solve $\frac{dN}{dt} = rN$ where $N(0) = N_0$

Continuous time...

Compare continuous time with discrete time formulation

$$N(t) = N_0 e^{rt}$$

$$N_t = N_0 R^t$$

$$R = e^r$$

$$r = \log(R)$$


Continuous

Discrete

M. 2.3  Let's plot continuous-time exponential growth with

$$r = \log(R) = \log(2) \approx 0.69$$

Continuous time...

M. 2.4  Let's also plot this on a semi-log scale

Ex. 2.3  Show that slope of semi-log plot is r

- Geometric and exponential growth same thing, except how time kept
- Distinction biologically important when density dependence considered
 - Geometric and exponential growth linear as population size (N) never have N^2 term

Leslie Matrix for Discrete Data

- Describes population age groups (demography)
- Is population dominated by teeny boppers or old, wise individuals
- Easier and more useful in discrete time
- Simplest to have age-class width same as time-step (1-yr time step = 1-yr age class)
- All individuals from just born to 364 d old at census are age 1

Leslie Matrix with 3 Age Classes

F_x = fertility of an organism in age class x , where $x = 1, 2$ or 3
= number offspring born per parent of age class x surviving to census

P_x = probability individual starting age class x surviving entire step

$n_{x,t}$ = number of individuals of age class x at time step t

$$n_{1,t+1} = F_1 n_{1,t} + F_2 n_{2,t} + F_3 n_{3,t}$$

$$n_{2,t+1} = P_1 n_{1,t}$$

$$n_{3,t+1} = P_2 n_{2,t}$$

Leslie Matrix...

Written more compactly as:

$$\begin{pmatrix} n_{1,t+1} \\ n_{2,t+1} \\ n_{3,t+1} \end{pmatrix} = \begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \times \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix}$$

Here Leslie Matrix
constant over t

$$n_{t+1} = m \times n_t$$

m is Leslie matrix

All age 3 individuals die at end of each time step

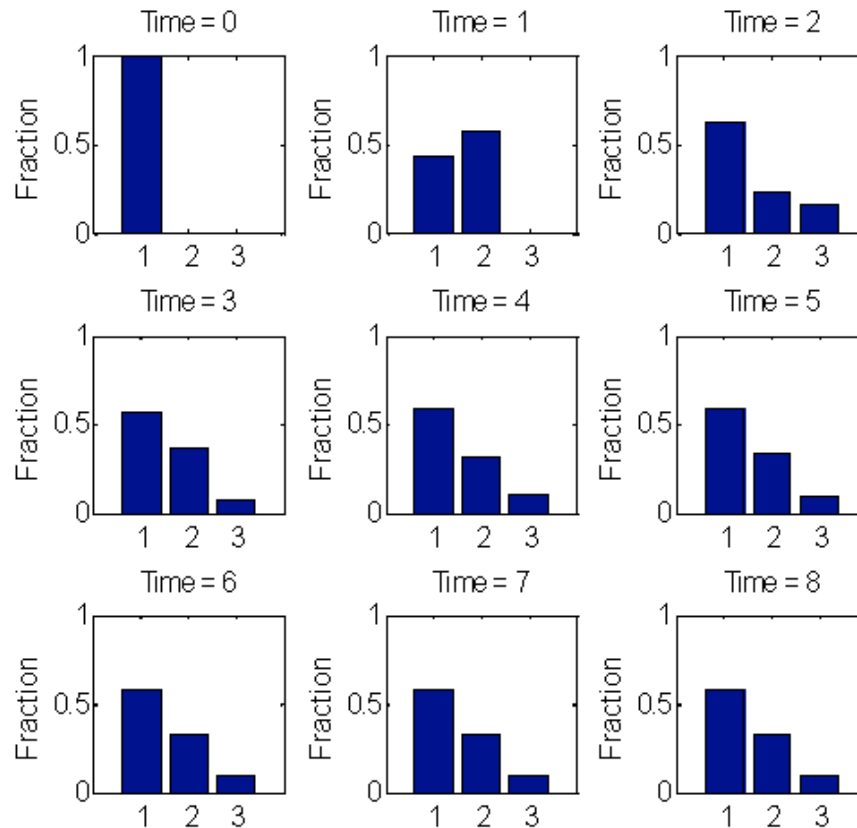
Leslie Matrix...

M. 3.1



- Let's try to code this:
 - Fecundities are 0.5, 1, 0.75 for 3 age classes
 - Survivorship is 0.6666 and 0.3333 for age classes 1 and 2
 - Initial number of individuals in each age class is 2, 0 and 0

Leslie matrix – further investigation



M. 3.2

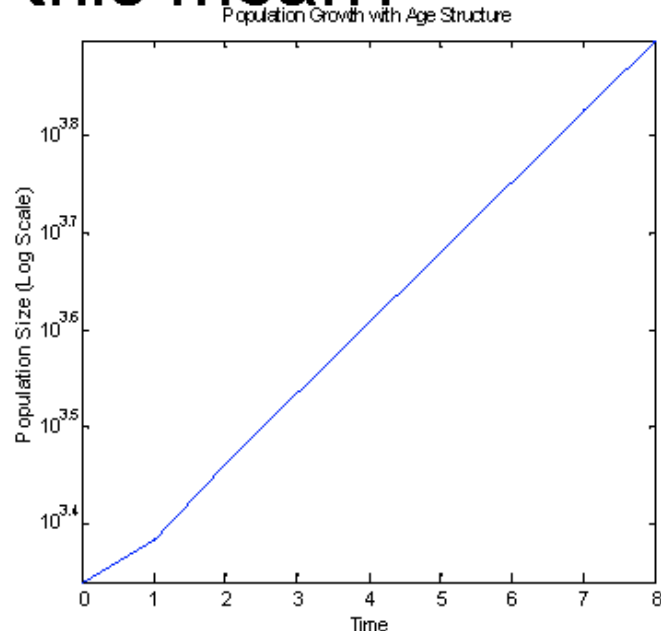


Ultimate age distribution called *stable age distribution*
What happens to this if change initial age class sizes?

Leslie matrix...

M. 3.3 

- Another regularity emerges – let's plot sequence of population sizes through time on a semilog plot
- What does this mean?



Leslie matrix...

- Once hits stable age structure have geometric increase or decrease, depending on P s and F s
- Geometric growth (R) from successive population sizes
- Once population at stable age structure then multiplying Leslie matrix by column vector n is to increase or decrease n by R
- i.e. Once components of n in stable age distribution, then just lengthening or shortening it by a scalar R
- A vector such that the action of multiplying it by a matrix lengthens or shortens it is called an eigenvector
- R can thus be computed directly using eigen analysis

Eigen analysis

$$\begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix} \times \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix} = R \times \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \end{pmatrix}$$

$$Ax = \lambda x$$

- where x (here n) is eigenvector of A (Leslie Matrix)
- *lambda* is eigenvalue (R)

M. 3.4  Let's see how this works...

Task 1

Loggerhead sea turtles (*Caretta caretta*) are spectacular marine predators that reach about 1 metre in length and weigh 115 kg on average. They are circumglobal, inhabiting continental shelves, bays, estuaries, and lagoons in temperate, subtropical, and tropical waters. They clamber up onto sandy beaches to bury their eggs in the sand. When the eggs hatch, the young turtles rush to the water and eventually swim far out into the ocean before returning to lay eggs on the same beaches some twenty years later.

Sadly these marine turtles have been dwindling in number and are now listed as an endangered species. One of the first approaches to protecting these animals was massive closure of the beaches where they lay their eggs, thereby protecting vulnerable newborn turtles from the disturbance and hazards associated with humans.

In the mid-1980s, a US postgraduate student Deborah Crouse decided to look at the conservation of this species rigorously – using the best available estimates of growth, reproduction and survival. She pieced together the following annual projection matrix, which depicts how a stage-structured turtle population changes from one year to the next (written in MATLAB format):

$$M = \begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix}$$

This matrix is nearly the same as a Leslie matrix, except that here the turtles are classified by their size rather than their age – this is called a “stage-structured” population as compared with an “age-structured” population. Here the elements of the matrix indicate that 67.5% of the turtles survive and grow large enough during one year to be promoted from the hatchling size class into the first juvenile size class, and the remainder die. Next, 70.3% of the turtles from the first juvenile size class remain in that size class after one year, while 4.7% grow large enough to join the second juvenile size class. The final two size classes are the mature classes. Each year, 1.9% of the turtles from the second juvenile class enter the first mature size class. Each of these produces 4.665 turtle hatchlings per year, on the average. 6.1% of these small mature turtles graduate to the largest graduate the largest mature size class while 68.2% remain in this class each year. Each large mature turtle produces 61.896 hatchlings per year, on the average, 80.91% of the large mature turtles survive the year and remain in this size class.

Start with an initial population of 300 hatchlings, 800 in the first juvenile size class, 50 in the second juvenile class, 50 in the first mature size class, and 50 in the final mature class.

Questions

1. What happens to this population over 30 generations? Plot the total population over this time on a semilog plot. Explain what is happening.
2. Using this information, what is the population geometric growth rate (R) and the stable age structure?

The geometric growth factor and the stable age distribution can be calculated directly from the Leslie matrix, without having to go through the iteration process. Once the stable age distribution has been attained, the only effect of multiplying the Leslie matrix by the column vector n is to increase the population size by the geometric growth factor. Another way to say this is that once the components of n are in the stable age distribution, thereafter the operation of multiplying the Leslie matrix by n is only to lengthen it or shrink it by the factor R . A vector such that the action of multiplying it by a matrix merely lengthens it or shrinks it is called an eigenvector of the matrix, and the factor by which it is lengthened or shrunk is called the eigenvalue of the matrix corresponding to that eigenvector. The most important eigenvector is the one that has the *biggest* eigenvalue. Using this terminology, the stable age distribution is an eigenvector of the Leslie matrix, and the geometric growth factor is the biggest of the eigenvalues. Although this sounds complicated, we can now easily calculate the stage age distribution and geometric growth factor directly from the Leslie matrix using eigen analysis.

3. Confirm that the population geometric growth rate (R) and the stable age structure calculated by conducting an eigenanalysis is the same as using the iterative procedure above. The necessary commands are:

```
[v,d]=eig(m)
```

```
R=max(max(abs(d))) % largest eigenvalue is R
```

```
c=v(:,5)/sum(v(:,5)) % Stable size structure. Note MATLAB's convention is to  
present eigenvectors with unit length, whereas we want vector's components to  
add to 1
```

4. Let's try and work out the merits of different conservation strategies by exploring permutations of the above Leslie matrix. Beach regulations have been put in place over recent decades to protect newly-born turtles – minimising building close to beaches where turtles lay eggs, trying to limit changes to the dune profile, removing cats and foxes in important hatchery areas, and reducing lighting behind dunes. Simulate these measures by increasing juvenile survivorship (currently 67.5%) to 100% (an impossible best-case scenario). What happens to the population?
5. Conduct “matrix experiments” to ascertain aspects of loggerhead demography that should be targeted by conservation biologists. Focus on the two mature size classes (note: put the juvenile survivorship back to 67.5%). Think up some possible measures that may be put in place to protect the loggerhead.

Leslie matrix...

- If Leslie matrix changes through time then have to iterate (can't use eigen) and use Leslie matrix for each time step

$$n_{t+1} = m_t n_t$$

- If males and females have different survivorship, analyse each sex separately (different Leslie matrices) and pretend males produce male offspring – sum to get population

Living through the good and bad

- All talk of population bomb might make you think that we are going to be taken over by an avalanche of organisms
- Why don't populations cover planet?
- Moist year is good for earthworms and population explode, followed by dry year when population crashes
- Populations have good and bad times, mainly due to environment, so R not constant (environmental stochasticity)
- Variation at low population levels because of chance (demographic stochasticity)

Environmental stochasticity

- Familiar with arithmetic mean – what about geometric mean?
- Nature uses geometric average when grading a population's success – here's why
- Growth year 1 is R_1 and growth rate year 2 is R_2

Separate population growth rate of $R = \sqrt{R_2 R_1}$

$$N_1 = R_1 N_0$$

$$N_1 = \sqrt{R_2 R_1} \times N_0$$

$$N_2 = R_2 N_1$$

$$N_2 = \sqrt{R_2 R_1} \times N_1$$

$$= R_2 R_1 N_0$$

$$= \sqrt{R_2 R_1} \times \sqrt{R_2 R_1} \times N_0 = R_2 R_1 N_0$$

Environmental stochasticity...

- Constant environment equivalent of fluctuating environment is geometric mean of R_s
- What does this mean for extinction?
- How can populations escape the “curse” of the geometric mean?

Metapopulations

- Spreading risk through dispersal!
- If distribution of R spatially same as R at single spot through time, then any point in time species enjoys arithmetic average R
- Metapopulations ~independent subpopulations connected by dispersal
- 2 versions of minimising extinction risk
 - R in each metapopulation independent
 - R in each metapopulation inverse
- Which is better?

Metapopulations

$$N_{1,t+1} = R_{1,t}((1 - m)N_{1,t} + mN_{2,t})$$

$$N_{2,t+1} = R_{2,t}((m)N_{1,t} + (1 - m)N_{2,t})$$

m = probability organism from subpopulation 1 disperses to subpopulation 2
and vice versa

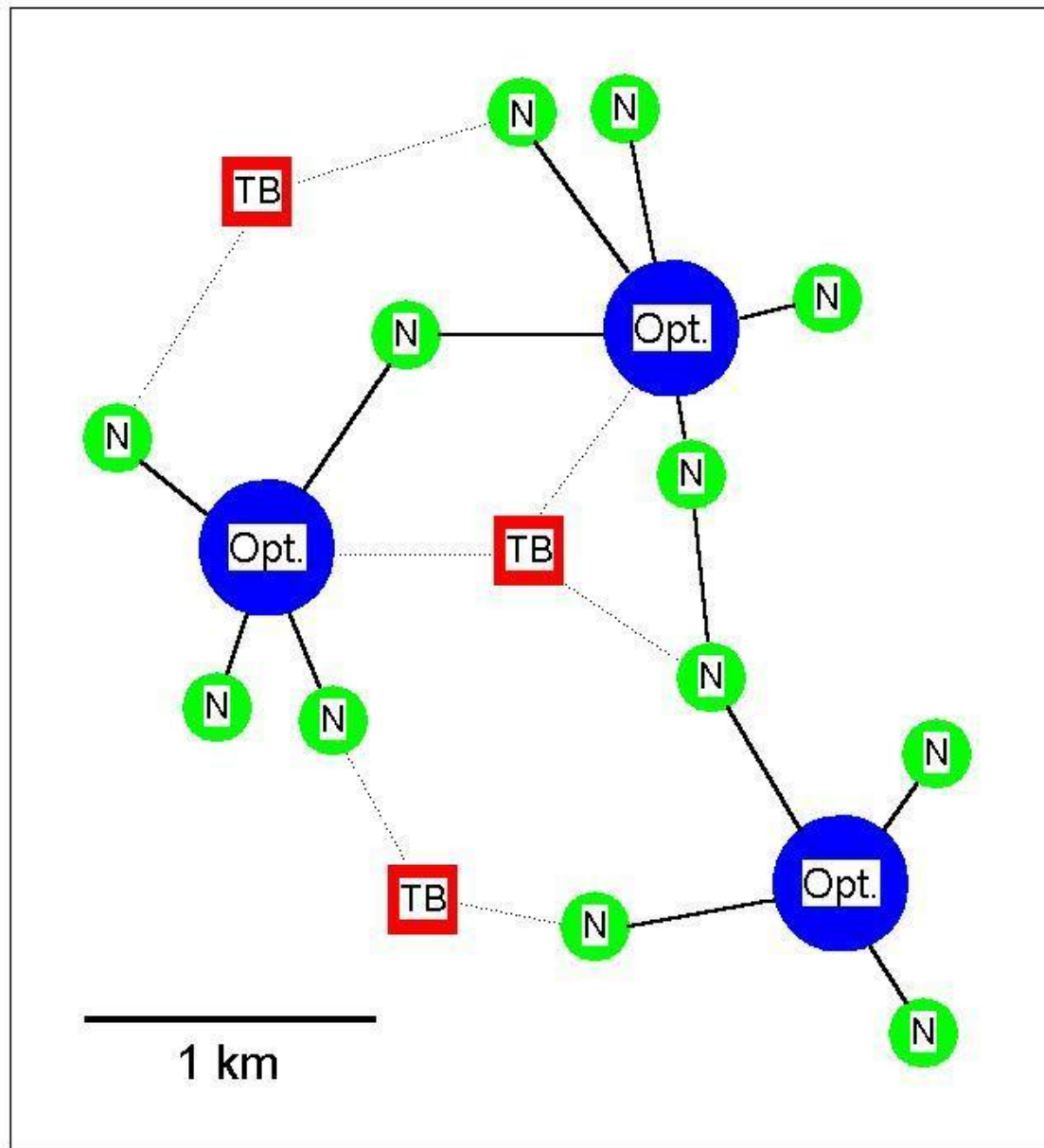
$1-m$ = probability organism stays at home

$N_{x,t}$ = number of individuals at time t in subpopulation at location x , where $x = 1, 2$

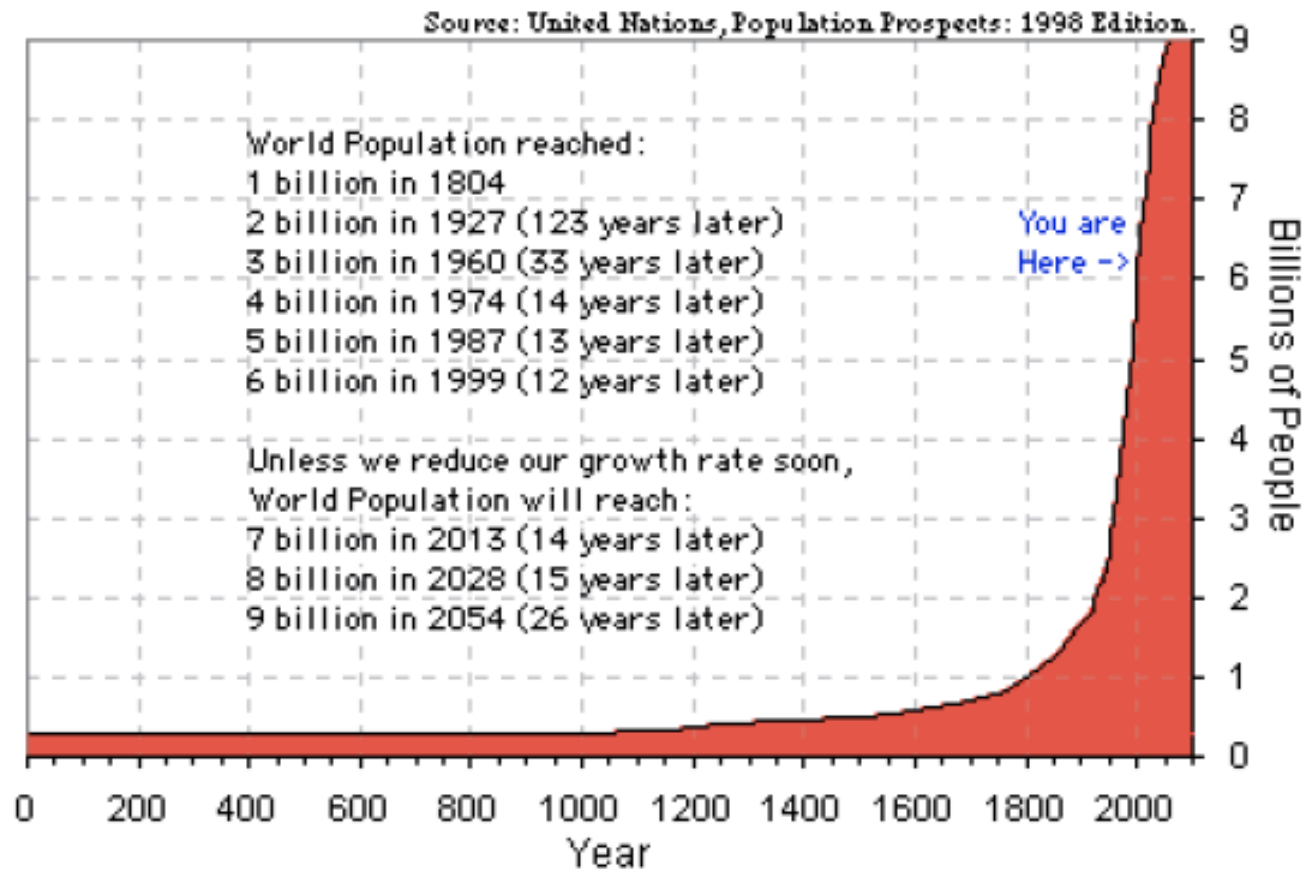
$R_{x,t}$ = Geometric growth factor in location x at time t

M. 3.5  Let's code this to see how metapopulations spread risk

What are the implications for conservation management?



Frogs



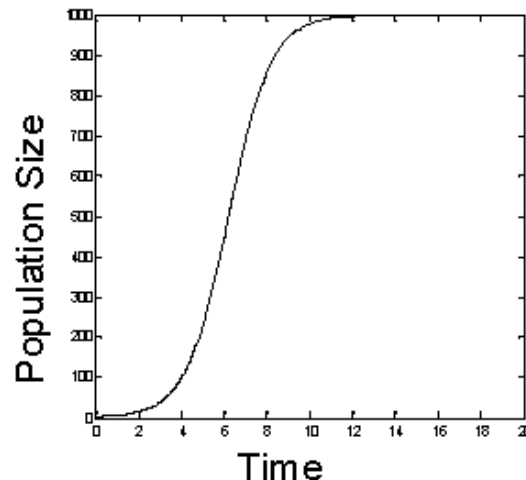
Where to stop?

Introduction

- Will *E. coli* cover world?
- One reason don't is consume resources, so per capita birth rate declines and death rate increases
- Population level off to steady-state size
- If average birth and/or death rate $f(\text{population size})$ then density dependent
- Are populations always limited this way?
- No - population bomb can be limited by natural fluctuations in environment (as we saw), without density dependence
- How to recognise density dependence and what models?
- Learn how many bald eagles or grizzly bears a particular habitat can support, or how many fish you can catch

Logistic Model of Limits to Growth

- Most elementary model of density dependence is logistic: S-shaped population curve



- 2 versions – discrete and continuous

Discrete Time Logistic

$$B(N) = B_0 - bN$$

Note signs of b and d

$$D(N) = D_0 + dN$$

$B(N)$ = number of births

$D(N)$ = number of deaths

B_0 = density independent birth rate

D_0 = density independent death rate

b = coefficient relating individual birth to population size

d = coefficient relating individual death to population size

Geometric model $N_{t+1} = BN_t + (1 - D)N_t$

My 4.1



Let's derive the discrete logistic equation

4.2 Logistic Equation

The **simple logistic equation** is a formula for approximating the evolution of an animal population over time. Many animal species are fertile only for a brief period during the year and the young are born in a particular season so that by the time they are ready to eat solid food it will be plentiful. For this reason, the system might be better described by a discrete difference equation than a continuous differential equation. Since not every existing animal will reproduce (a portion of them are male after all), not every female will be fertile, not every conception will be successful, and not every pregnancy will be successfully carried to term; the population increase will be some fraction of the present population. Therefore, if " A_n " is the number of animals this year and " A_{n+1} " is the number next year, then

$$A_{n+1} = rA_n$$

where " r " is the **growth rate** or **fecundity**, will approximate the evolution of the population. This model produces exponential growth without limit. Since every population is bound by the physical limitations of its surrounding, some allowance must be made to restrict this growth. If there is a carrying-capacity of the environment then the population may not exceed that capacity. If it does, the population would become extinct. This can be modeled by multiplying the population by a number that approaches zero as the population approaches its limit. If we normalize the " A_n " to this capacity then the multiplier $(1 - A_n)$ will suffice and the resulting logistic equation becomes

$$A_{n+1} = rA_n(1 - A_n)$$

or in functional form

$$f(x) = rx(1 - x).$$

Discrete Time Logistic...

$$\Delta N = rN(1 - \frac{N}{K})$$

NOTE: r and K summary parameters lumping information on individual births and deaths

- N as stock or asset (natural capital)
- ΔN as interest (earnings) or growth (production) on capital (units number of organisms)
- ΔN is thus natural production function

Discrete Time Logistic...

M 4.1  Let's plot ΔN ...

Ex. 4.2  What are roots of the equation?

Ex. 4.3  Peak production is MSY – what is its equation?
Maximum sustainable yield

- Ecologically optimal stock size, not economically optimal stock size (see later...)

Discrete Time Logistic...

- Logistic model also used to forecast population growth through time
- Simply iterate:

$$N_{t+1} = \Delta N + N_t$$


M 4.2  Let's plot logistic through time...

Continuous Time Logistic


- Continuous version same as discrete version except ΔN is replaced by $\frac{dN}{dt}$

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

- Main difference: birth continuous production of offspring; death continuous loss of individuals

My 5.1 
$$N(t) = \frac{K}{1 + \left[\frac{K}{N(0)} - 1\right]e^{-rt}}$$

Continuous Time Logistic

M5.1  Now lets plot continuous over discrete version...

- Why don't curves coincide?
- Continuous time compounded; discrete time only compounded end of each time step

Continuous Time Logistic...

Exponential growth $N(t) = N_0 e^{rt}$

Over one interval, for continuous logistic :

$$\text{so } \Delta N = N_0 e^{r(t+1)} - N_0 e^{rt} = N_0 e^{rt} (e^r - 1)$$

By compounding at end of period

$$r_{\text{discrete}} = e^{r_{\text{continuous}}} - 1$$

$$\text{And } r_{\text{continuous}} = \log(r_{\text{discrete}} + 1)$$

M5.2  Let's plot continuous curve with discrete r

- Continuous matches discrete only at bottom
- Continuous approaches K with grace, not discrete

Logistic Model with Data

- When would you use discrete or continuous version?
- For what animals/plants?
- Which parts of the world?

Logistic Model with Data...

- Classic set of experiments by GF Gause in 1934 with *Paramecium*

M5.3  First thing – is there density dependence?

- Two approaches to estimate r and K
 - fit natural production to stock size
 - fit logistic model through time
- Which is better? When?
- Should we use discrete or continuous logistic?

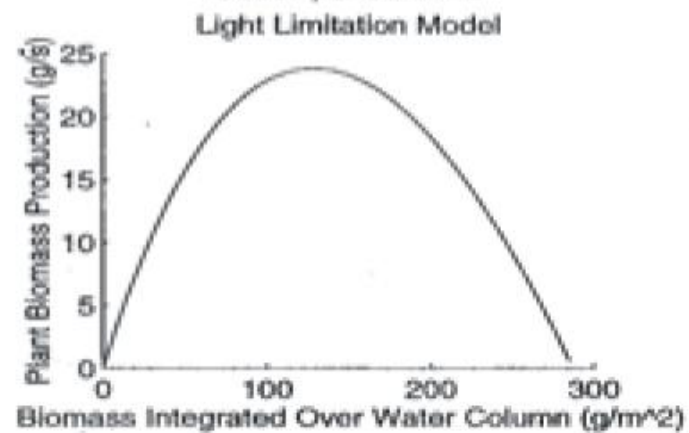
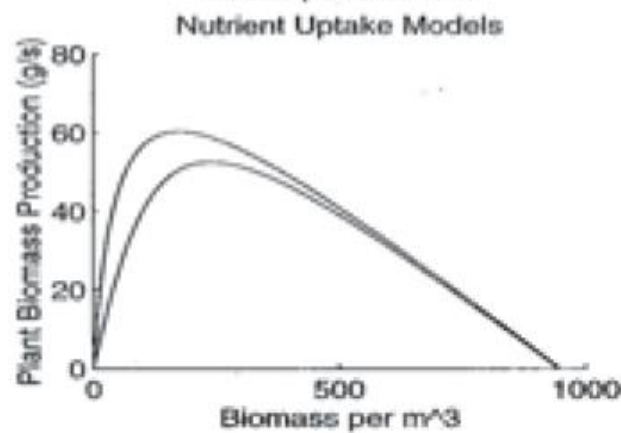
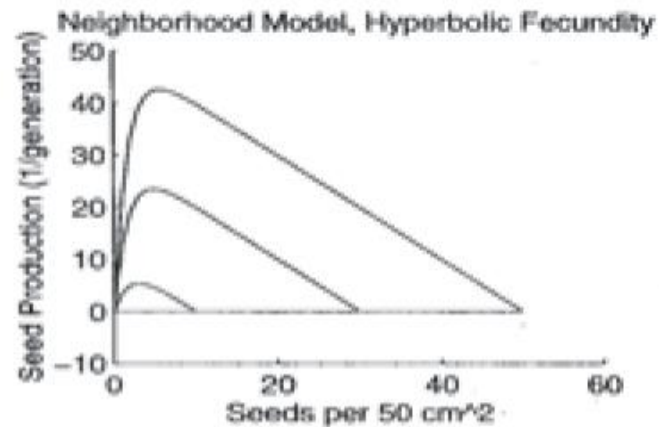
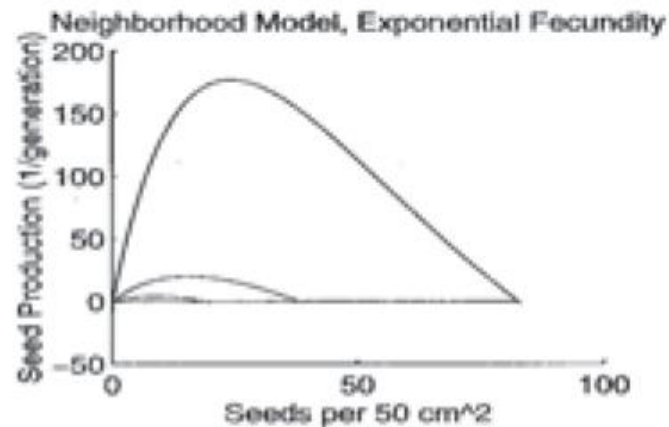


M5.4  Let's do it in MATLAB

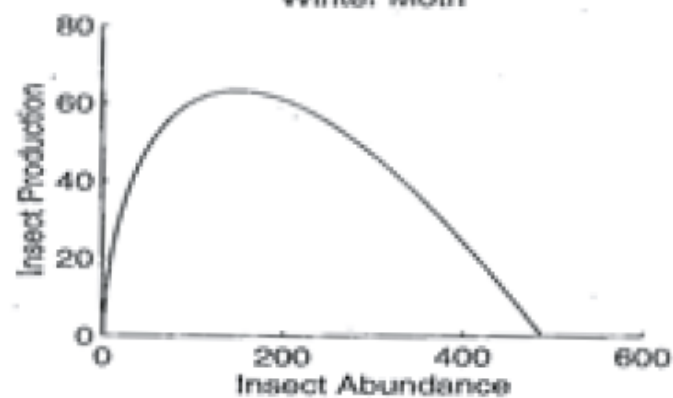
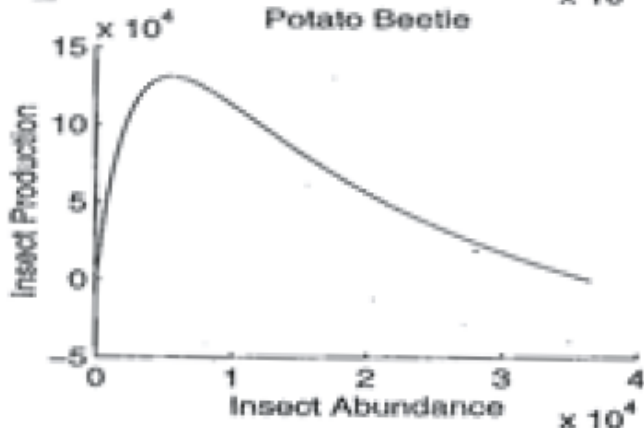
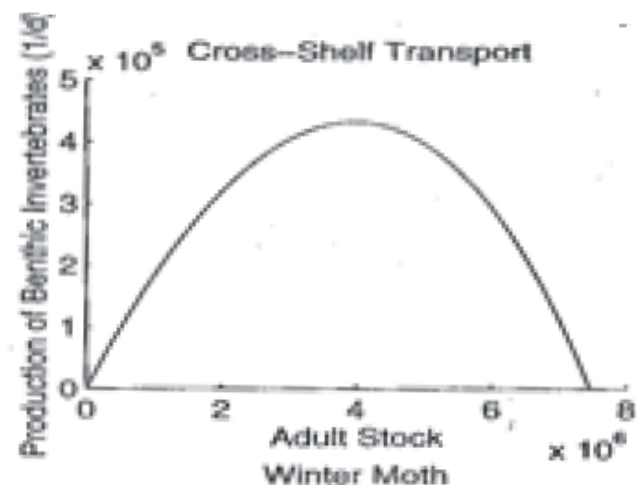
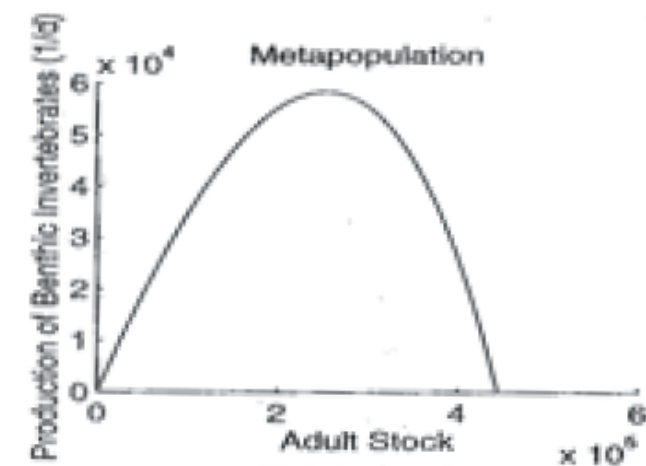
Comparing Logistic with Other Models

- Is the whole world logistic?
- Logistic when birth decreases linearly and death increases linearly with N
- What about seed production dependent on number of neighbours, nutrients and light?
- Combining with death rates is a population dynamic model
- Based on how individuals function is IBM

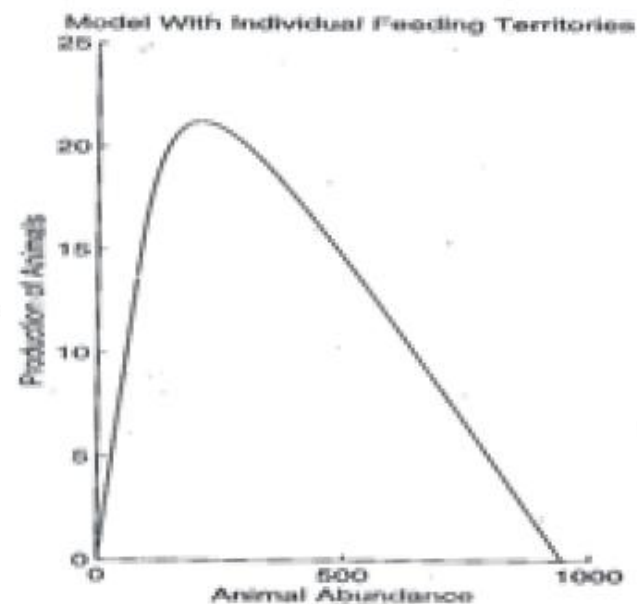
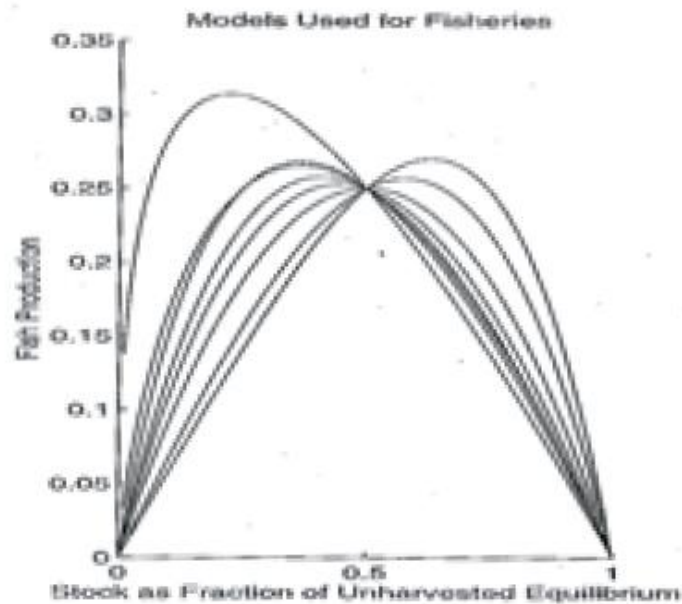
Comparing Logistic with Other Models

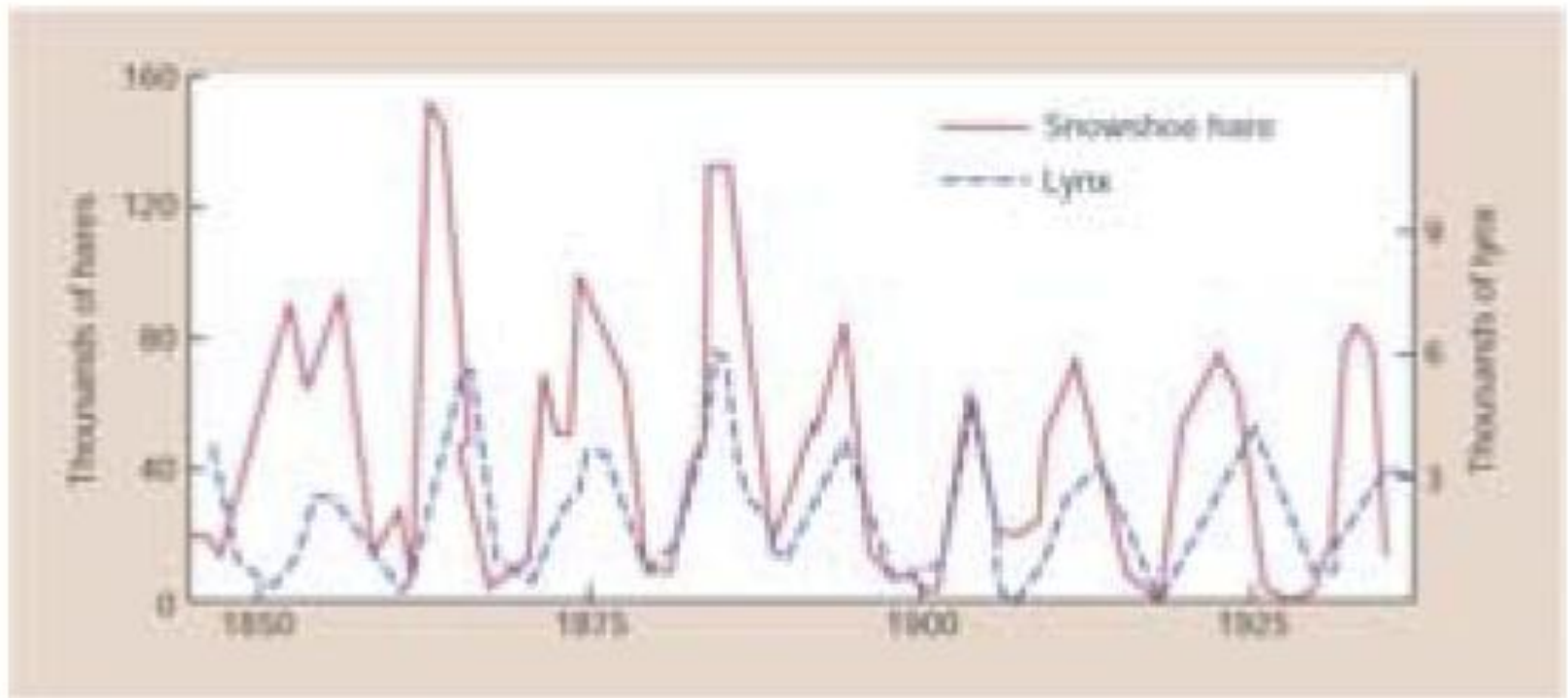


Comparing Logistic with Other Models...



Comparing Logistic with Other Models...





Ecological stability

Ecological Stability

- Concept of stability – a marble in a bowl on a table
- Stable equilibrium
- Unstable equilibrium
- Neutral equilibrium
- Does an equilibrium mean that the world is constant?

Testing Stability

- Production function of population in continuous t

$$\frac{dN}{dt} = F(N)$$

$F(N)$ generally non-linear For logistic, $F(N) = rN(1 - \frac{N}{K})$

Step 1: Find all equilibrium points Set $F(N) = 0$

Step 2: Check stability of each equilibrium point

Step 2: Checking Stability

Let \hat{N} denote an equilibrium (so $F(\hat{N}) = 0$)

Let n denote a small deviation from equilibrium

$$n = N - \hat{N}$$

- Aim is to see if n grows (unstable equilibrium) or diminishes (stable equilibrium)

Rearranging : $N = n + \hat{N}$

$$\frac{dN}{dt} = F(N)$$

$$\frac{d(n + \hat{N})}{dt} = F(n + \hat{N})$$

Now \hat{N} is a constant so $\frac{d\hat{N}}{dt} = 0$

$$\frac{dn}{dt} = F(n + \hat{N})$$

Difficult to solve explicitly because $F(N)$ generally non-linear

Step 2: Checking Stability...

if n small then

$$F(n + \hat{N}) \approx F(\hat{N}) + F'(\hat{N})n \quad \text{Note: } F'(\hat{N}) \approx \frac{F(n + \hat{N}) - F(\hat{N})}{n}$$

$$\frac{dn}{dt} = F(\hat{N}) + F'(\hat{N})n$$

Now $F(\hat{N}) = 0$ (equilibrium point)

$$\frac{dn}{dt} = F'(\hat{N})n$$

Now let $\lambda = F'(\hat{N})$

$$\text{So } \frac{dn}{dt} = \lambda n$$

$$n(t) = n(0)e^{\lambda t}$$

Step 2


- Let λ denote slope of $F(N)$ at equilibrium point
- If λ negative, n decreases through t , **stable**
- If λ positive, n increases through t , **unstable**
- If $\lambda=0$ do not know (rare)


Logistic Model Without Harvesting

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

Step 1: Find all equilibrium points

We know these...

Ex. 6.1  Step 2: Check stability of each equilibrium point

M. 6.1  What does this mean for populations growing according to the logistic equation?

Logistic Model with Harvesting

- Suppose logistic model describes a harvestable resource – e.g. fish or trees
- How much should you take? Control harvest rate h
- Need policy decision on best h
 - MSY. Stock size N is $K/2$ then growth $rK/4$.
 $h=rK/4$ is one management target
 - Other management targets?

Logistic Model with Harvesting


- Resource owned by firm or managed by government
- Economically, goal to maximise resource revenue
- Imagine stock “natural capital”, each organism say \$1 value
- Dollar may be hypothetically invested as natural capital or invested in bank earning ρ
- Allocate capital between natural and financial stock
 - Each \$ in savings account earns ρ
 - Each \$ invested as an organism earns rate of natural production function $F(N)$, which varies with density dependence

Ex. 6.2



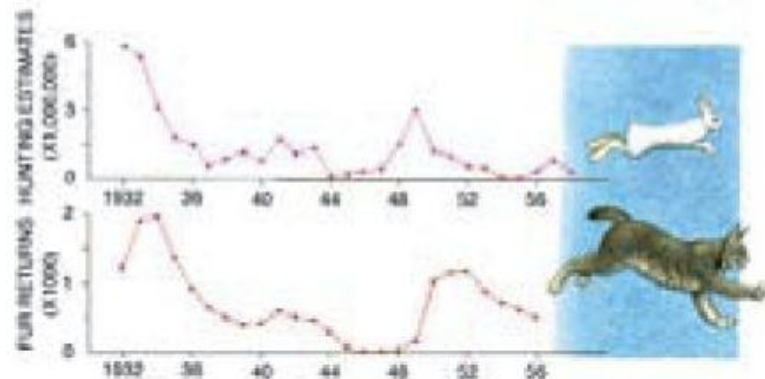
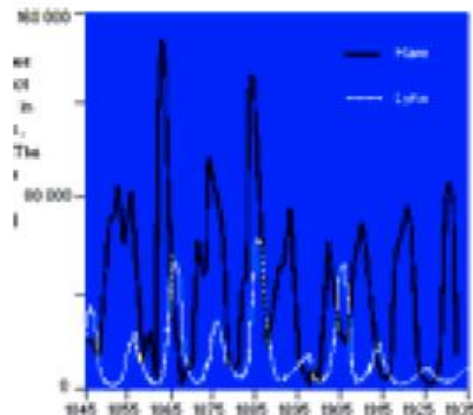
What is best allocation?

Logistic Model with Harvesting...

M. 6.2  Let's illustrate the economically optimal harvest strategy

Predator-Prey Interaction

- Many big predators but most small
- Predators often liked more than prey???
- Questions
 - How many predators can prey sustain?
 - How much predation can the prey tolerate?
 - Are there cycles?



Volterra Predator-Prey Model

- 1st predator-prey model in ecology by Vito Volterra in 1920s
- Prey grow exponentially in absence of predator; predators die exponentially in absence of prey
- No density dependence
- Predators contact prey by “random collision”

Volterra Predator-Prey Model

$$\frac{dN_1}{dt} = rN_1 - aN_1N_2$$

$$\frac{dN_2}{dt} = baN_1N_2 - dN_2$$

N_1 Number of prey

N_2 Number of predators

r Intrinsic rate of prey increase

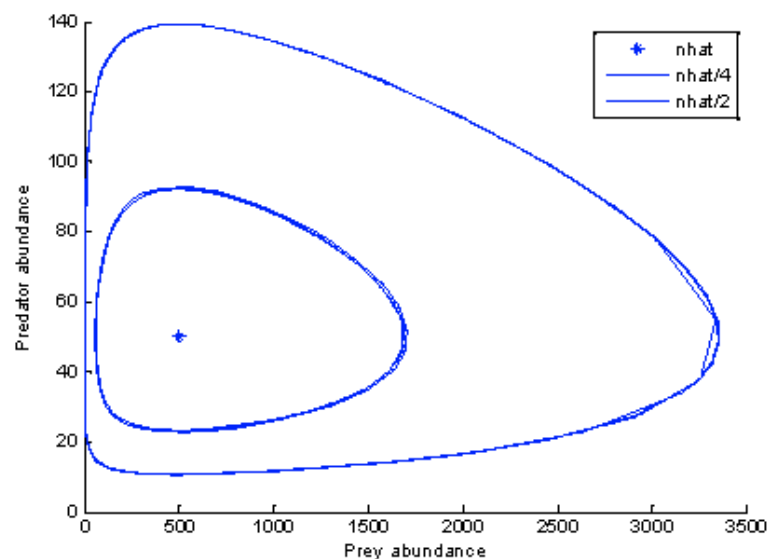
a Coefficient relating prey capture to predator-prey collisions

b Coefficient relating prey capture to predator births

d Death rate of predator

Volterra Predator-Prey Model

- What does this model tell us?
- What are equilibria of these equations?
- What does your answer mean?
- 🔺 Let's plot system of equations and see what it looks like



Volterra Predator-Prey Model

- 5 main lessons
 1. Predators can control exponential prey growth
 2. Any prey population can support a predator population
 3. Formula for equilibrium abundances give estimate of average abundances through time
 4. Predator-prey interaction has tendency to oscillate
 5. The Volterra Principal: General pesticides ineffective controlling prey when usually controlled by predators

Adding Density Dependence to Prey

$$\frac{dN_1}{dt} = rN_1 \left(1 - \frac{N_1}{K}\right) - aN_1N_2$$

$$\frac{dN_2}{dt} = baN_1N_2 - dN_2$$

$$\hat{N}_1 = \frac{d}{ba}$$

$$\hat{N}_2 = \frac{r}{a} \left(1 - \frac{d}{baK}\right)$$

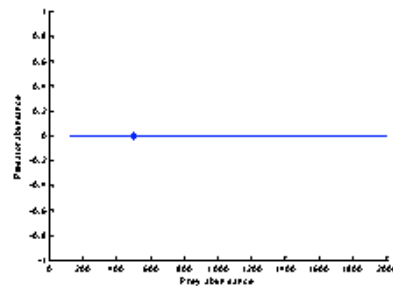
How big does K of prey have to be to support the predator?

Volterra Predator-Prey with Density Dependence



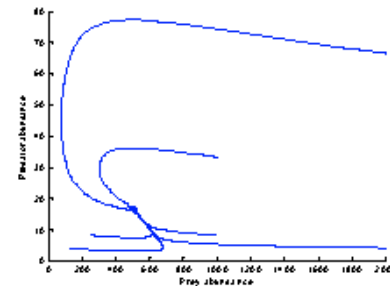
Let's plot system and see what it looks like

- Density dependence has large effect on dynamics
- Value of K critical for coexistence



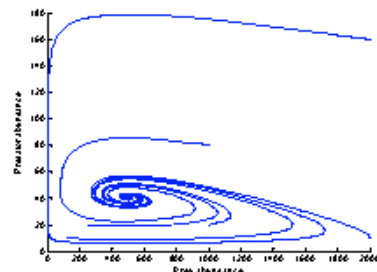
$$K \leq \frac{d}{ba}$$

No Predators



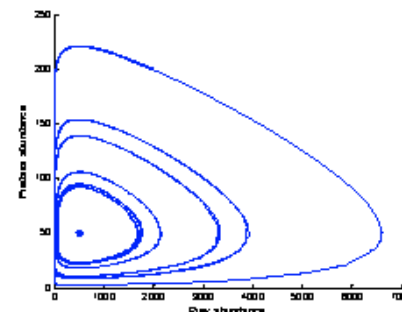
$$K > \frac{d}{ba}$$

Stable, but no cycles



$$K \gg \frac{d}{ba}$$

Stable focus, spiral cycles



$$K \gg \gg \frac{d}{ba}$$

Neutral equilibrium

Volterra Model with Predator Satiation and Density Dependence

- Term for feeding is

$$aN_1N_2 = (aN_1)N_2$$

Linear feeding term

- Can use non-linear feeding term – e.g. $c(1 - e^{\frac{-aN_1}{c}})$

📌 What does this feeding term look like?

Volterra Model with Predator Satiation and Density Dependence

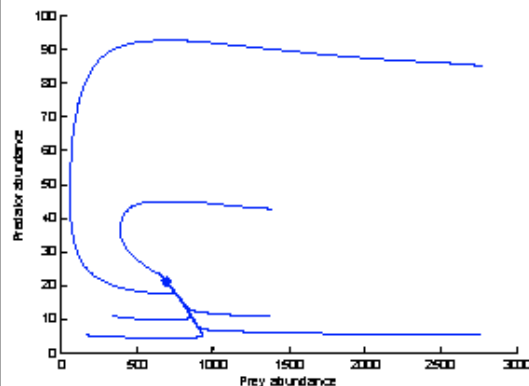
$$\frac{dN_1}{dt} = rN_1 \left(1 - \frac{N_1}{K}\right) - c \left(1 - e^{-\frac{aN_1}{c}}\right) N_2$$

$$\frac{dN_2}{dt} = bc \left(1 - e^{-\frac{aN_1}{c}}\right) N_2 - dN_2$$

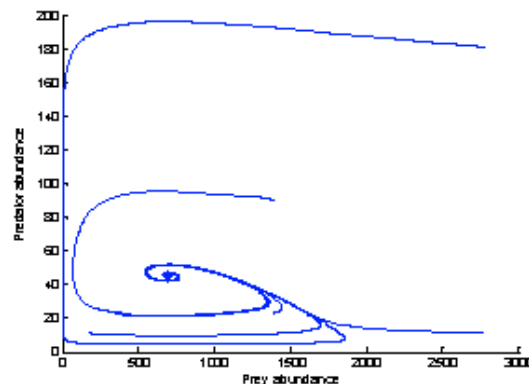


What does this system of equations look like?

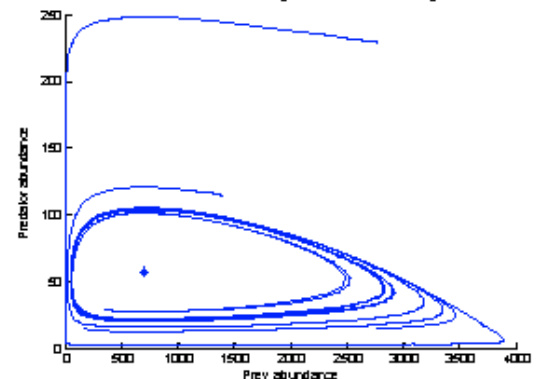
$K = 1000$, Stable node



$K = 2000$, Stable focus



$K = 4000$, unstable focus surrounded by limit cycle



Task 2

Models of population growth under resource limitation discussed so far have considered a constant carrying capacity. In reality, of course, carrying capacity varies from year-to-year, because it depends on factors such as rainfall, frequency of frosts, and so forth. This year-to-year weather-driven variation does not undermine the basic principles of resource-limited population growth, although it may obscure the clarity of density-dependent trends.

A simple but useful extension of logistic population growth modelled with weather-driven variation has been applied to the Serengeti wildebeest populations. Wildebeests are regularly poached, and because their populations are currently quite large, Serengeti park officials would like to legalise a limited amount of harvesting. In allowing harvesting, park officials seek some compromise between maximising harvest and minimising the risk of wildebeest extinction (or herd collapse).

The problem is complicated by the fact that wildebeest demography is tightly connected to rainfall (because rainfall determines the amount of plant material produced each year as food), and rainfall varies unpredictably among years. A simple way of incorporating this complication is to define the wildebeests' carrying capacity as a function of rainfall; in particular the relation $K = \text{rainfall} \times 5532$ has been shown to describe the dynamics of past wildebeest populations exceedingly well.

This K is plugged into what is called the Beverton-Holt model for resource limited growth. The Beverton-Holt model is one of a variety of different equations that qualitatively behave like the logistic equation, although their details vary. That is, at low population densities, the per-capita reproduction rate is the highest; and when carrying capacity is exceeded, the per-capita net reproduction rate falls to below 1 (so that the population shrinks). The Beverton-Holt equation for resource-limited growth is:

$$N_{t+1} = \frac{RN_t K}{K + (R - 1)N_t}$$

Where R is the maximum geometric growth factor achieved as N goes to zero and K is the carrying capacity.

Q1. Using MATLAB, plot the Beverton-Holt equation showing population size vs time for a constant carrying capacity of $K=1,000,000$ and $R=1.1323$ over 100 years (including the initial year). Make two separate runs: one with initial population size of 200,000 and the other with 2,000,000 wildebeests. Explain what is happening.

Now let's incorporate a variable carrying capacity and harvest rate so we can use MATLAB to investigate the management issue of harvesting in a variable environment. We now treat K simply as a variable governed by the equation for rainfall, with rainfall drawn as a random variable from a list of past rainfalls recorded for the Serengeti. The idea then is to simulate future scenarios with different degrees of harvesting, where h represents the fraction of population harvested. The complete model is thus:

$$N_{t+1} = \frac{RN_t K}{K + (R - 1)N_t} \times (1 - h)$$

First create an array of actual observed rainfalls from the Serengeti,

```
rain=[100, 38, 100, 104, 167, 167, 165, 79, 91, 77, 134, 192, 235, 159, ...  
      211, 257, 204, 300, 187, 84, 99, 163, 97, 228, 208, 83, 44, 112, 191, ...  
      202, 137, 150, 158, 20];
```

and then generate the carrying capacities associated with each year of rainfall with

```
K=5532*rain;
```

Q2. Run the model with an initial population size of 200,000, but with a modified carrying capacity each year (i.e. choose the rainfall level each year randomly, and its associated K). Choose the rainfall level each year randomly, and its associated K . Re-run the model with an initial population size of 2,000,000. Explain what happens.

Now let's consider a range of harvest rates,

```
h=0:0.02:0.2;
```

Using this information and the Beverton-Holt model you already have coded (including variable rainfall), write a Matlab programme to simulate the fate of wildebeest for each harvest level. Set the initial population size to be 200,000. Set a lower threshold of 25,000 wildebeests as a collapsed stock (this number is nearly the record low for the Serengeti herd).

Q3. Plot a graph of the wildebeest population through time under the different harvest rates. Explain what is happening. About what harvest rate can the population sustain? Re-run your model again and explain why you have different a different answer.

Q4. Illegal hunting decreases the number of Serengeti lions, a major predator of wildebeest, and thus decreases wildebeest populations. How could you easily simulate predation with the model that you have? Using the model that you have built, what effect does reducing hunting of lions have on the harvesting rate that is sustainable?

Q5. Much of Africa is forecast to have lower rainfall under future climate change scenarios. Assume that rainfall declines by 50% of its present value in the future (and assume illegal lion hunting continues). What will have to happen to the potential harvest rate under climate change?

Q6. With a stochastic model, each model run will be different. Describe how you would extend your programme to confirm that the patterns that you've reported in this assignment hold and are not due to random variation? (HINT: use a Monte Carlo simulation).