Example 1. Predator-prey system

- Basics of population dynamics models
- A practical question in pest management
- Extend the basic model to address the question
- Results and uses of the model

Basics of population dynamics models

Model for population, discrete time interval

- N=size of population
  - Total number or number/unit area
- Δt = time interval
- ΔN/ Δt = change in population in a time interval
- Dynamic model: model describes how variables change over time

- Often change in population is proportional to size of population. Model is
- $\Delta N/\Delta t = rN$
  - r is change in time interval per individual in population (=growth rate)
  - e.g. Population increases by 10% in a year. r=0.1/year.
  - r is net result, births - deaths

To calculate population at any time

- $N_{\Delta t} = N_{t=0} + (\Delta N / \Delta t)_{t=0}$
- $N_{2\Delta t} = N_{\Delta t} + (\Delta N / \Delta t)_{\Delta t}$
- $N_{3\Delta t} = N_{2\Delta t} + (\Delta N / \Delta t)_{2\Delta t}$
- etc.

- e.g. Initial population $N_{t=0}$ = 1000 and r=0.1/year
  - N_1=1100
  - N_2=1210
  - etc

Continuous time model

- Now model specifies dN/dt
  - Like ΔN/Δt but with infinitesimal time increments
  - dN/dt=instantaneous rate of change
  - To get N at any time, integrate equation (usually numerically)

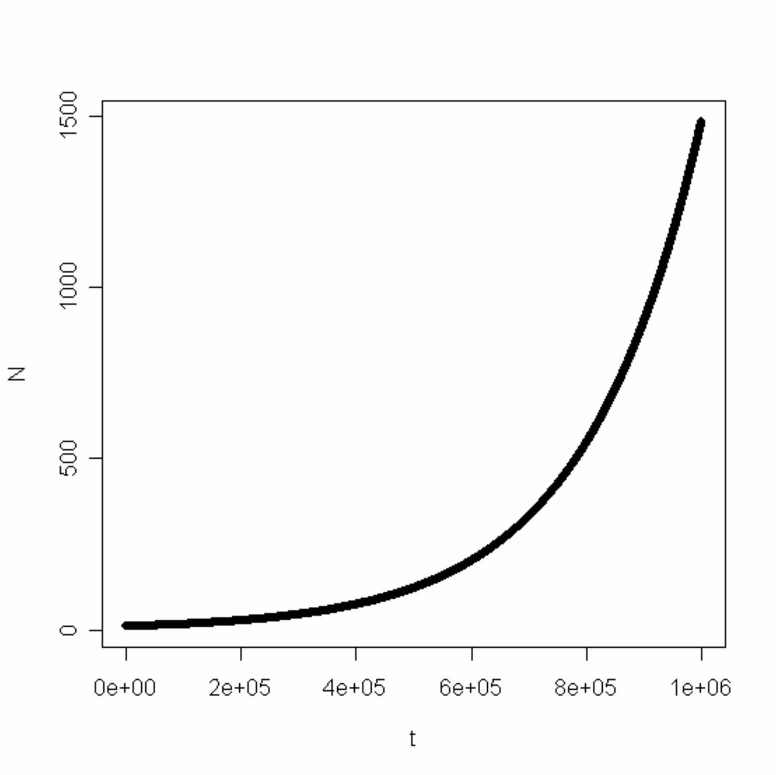
Exponential growth

- rate of change in population is proportional to size of population
- $dN/dt=rN$
  - r is relative growth rate

- In this case, we can solve equation analytically
- $N(t)=N(0)\exp(rt)$

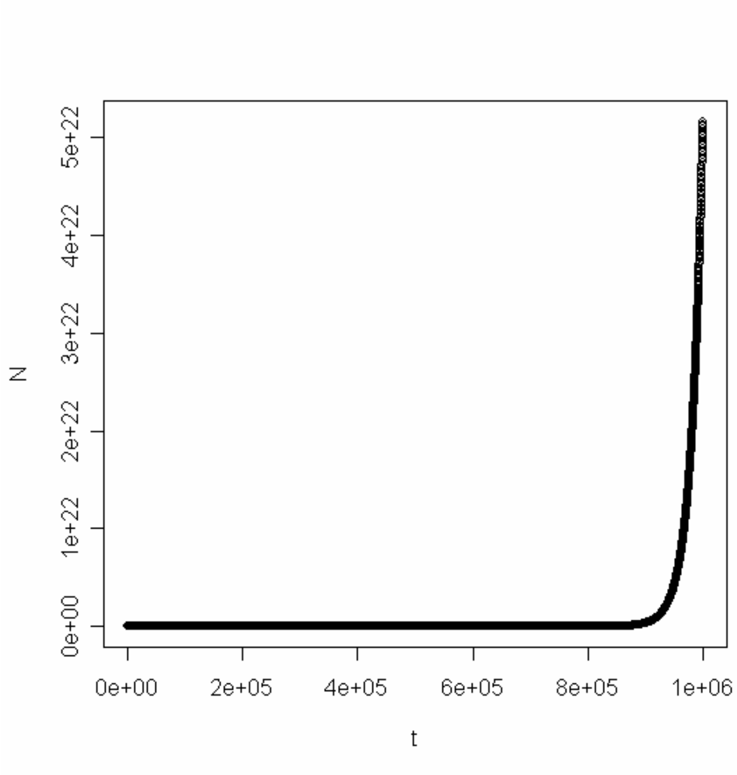
Initial population=10

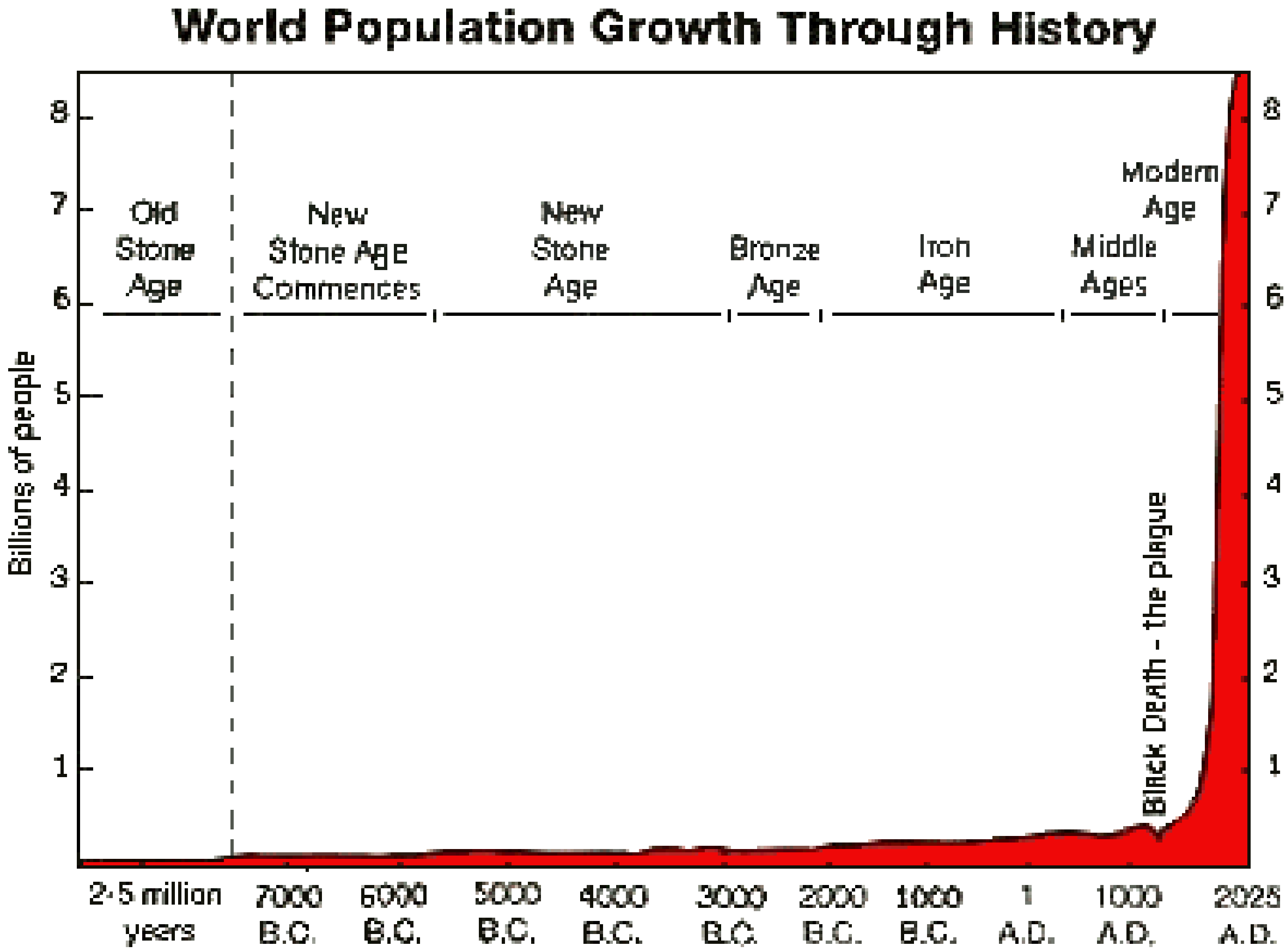
R=0.000005



Initial population=10

R=0.00005





World Population Growth Through History
Billions of people
8
7
6
5
4
3
2
1
Old Stone Age
New Stone Age Commences
New Stone Age
Bronze Age
Iron Age
Middle Ages
Modern Age
Black Death - the plague
2-5 million years
7000 B.C.
6000 B.C.
5000 B.C.
4000 B.C.
3000 B.C.
2000 B.C.
1000 B.C.
1 A.D.
1000 A.D.
2025 A.D.

Limits to exponential growth

- Is exponential growth sustainable?
- No, eventually some limiting factor intervenes
  - Limits of food
  - Limits of area
- Population reaches some limit
- Simple model for limited growth? dN/dt=?

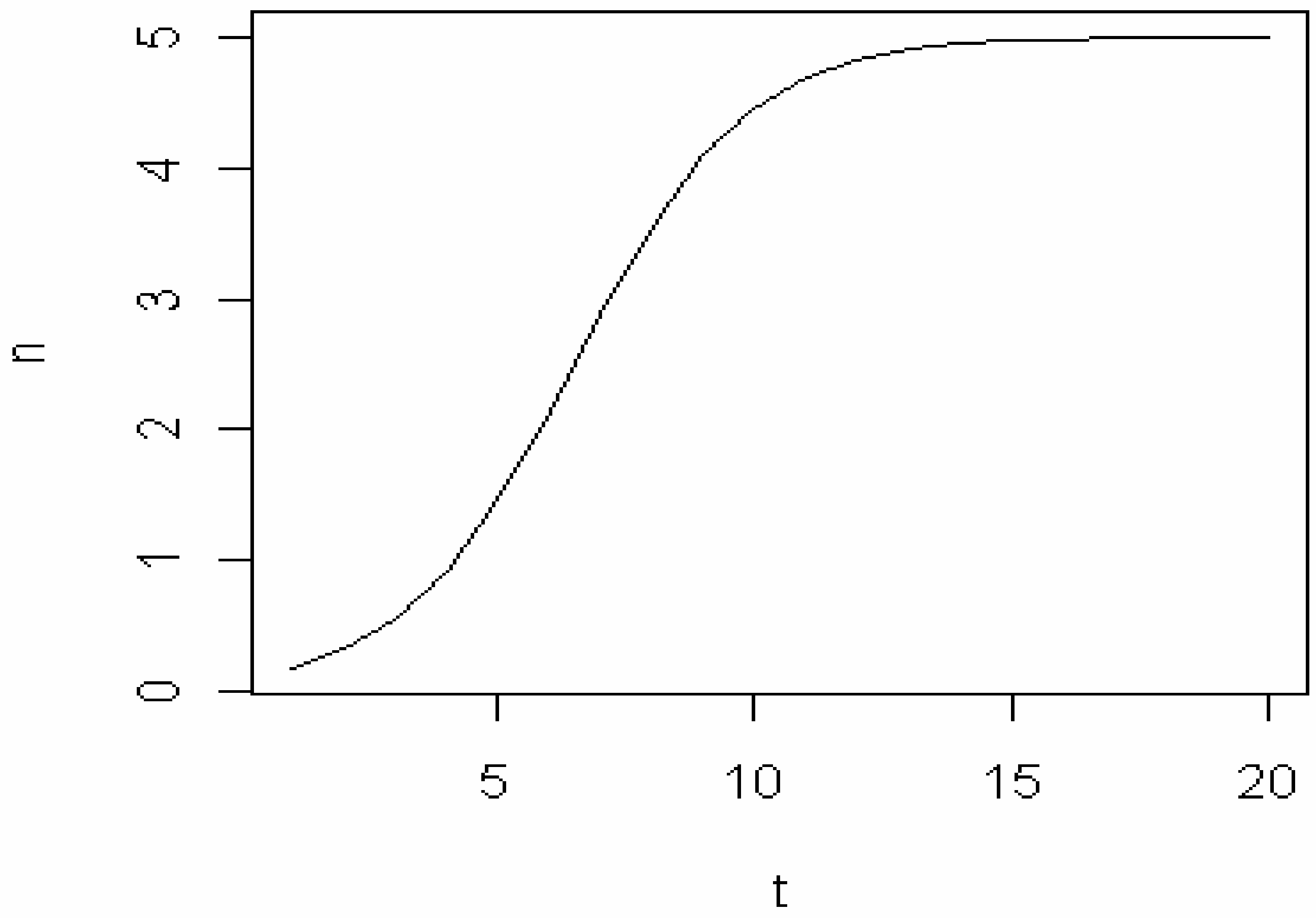
Logistic model of population growth

- $dN/dt=rN(1-N/K)$

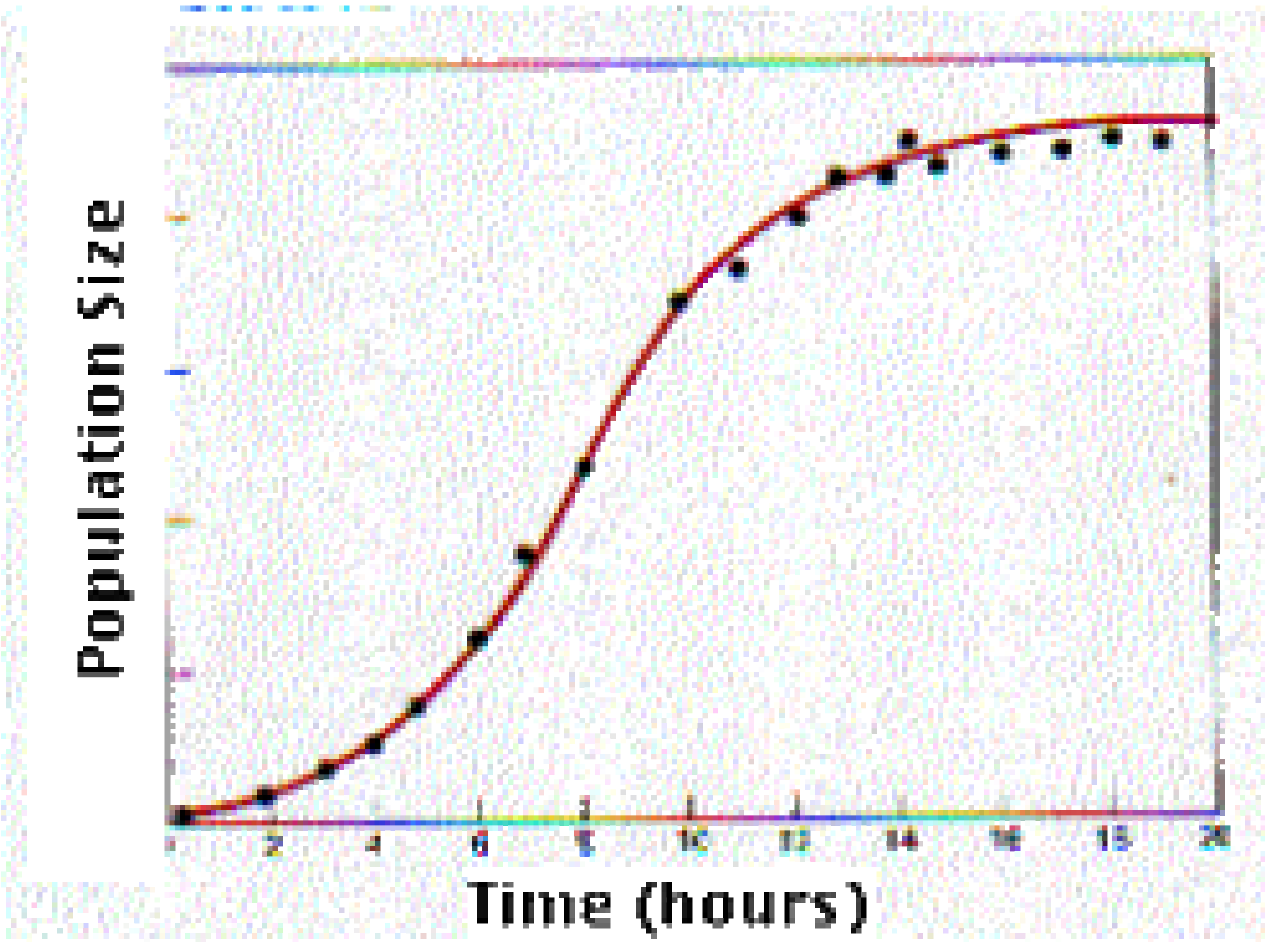
  r = relative growth rate

  K = carrying capacity

N0=0.1 r=0.6   K=5



Yeast population growth



Two interacting populations

Types of interaction

– Mutualism (+ +)
– Commensalism (+ 0)
– Neutralism (0 0)
– Amensalism (0 -)
– Predation parasitism (+ -)
– Competition (- -)

Predator prey interaction

Predator prey model

- Treat as dynamic system
  - two interacting populations
  - equations describe evolution over time
- Two state variables are:

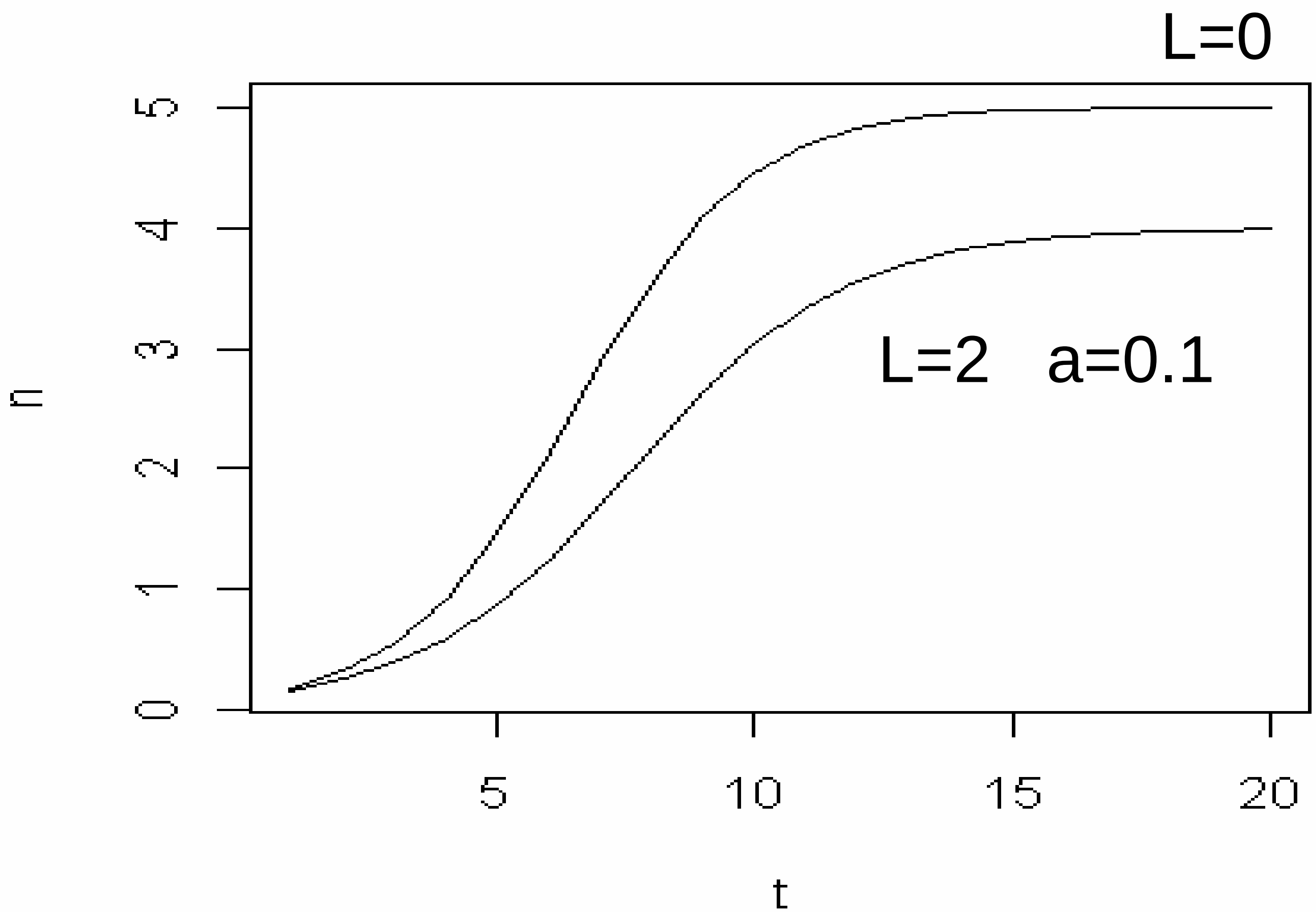
A(t)=number of individuals of prey at time t (or just write A)

L(t)=number of individuals of predator at time t (or just write L)

Model for prey

- Prey have logistic growth, plus mortality due to predation
- dA/dt=r*A*(1-A/K)-PR*L
- Form for PR=rate of predation/predator?

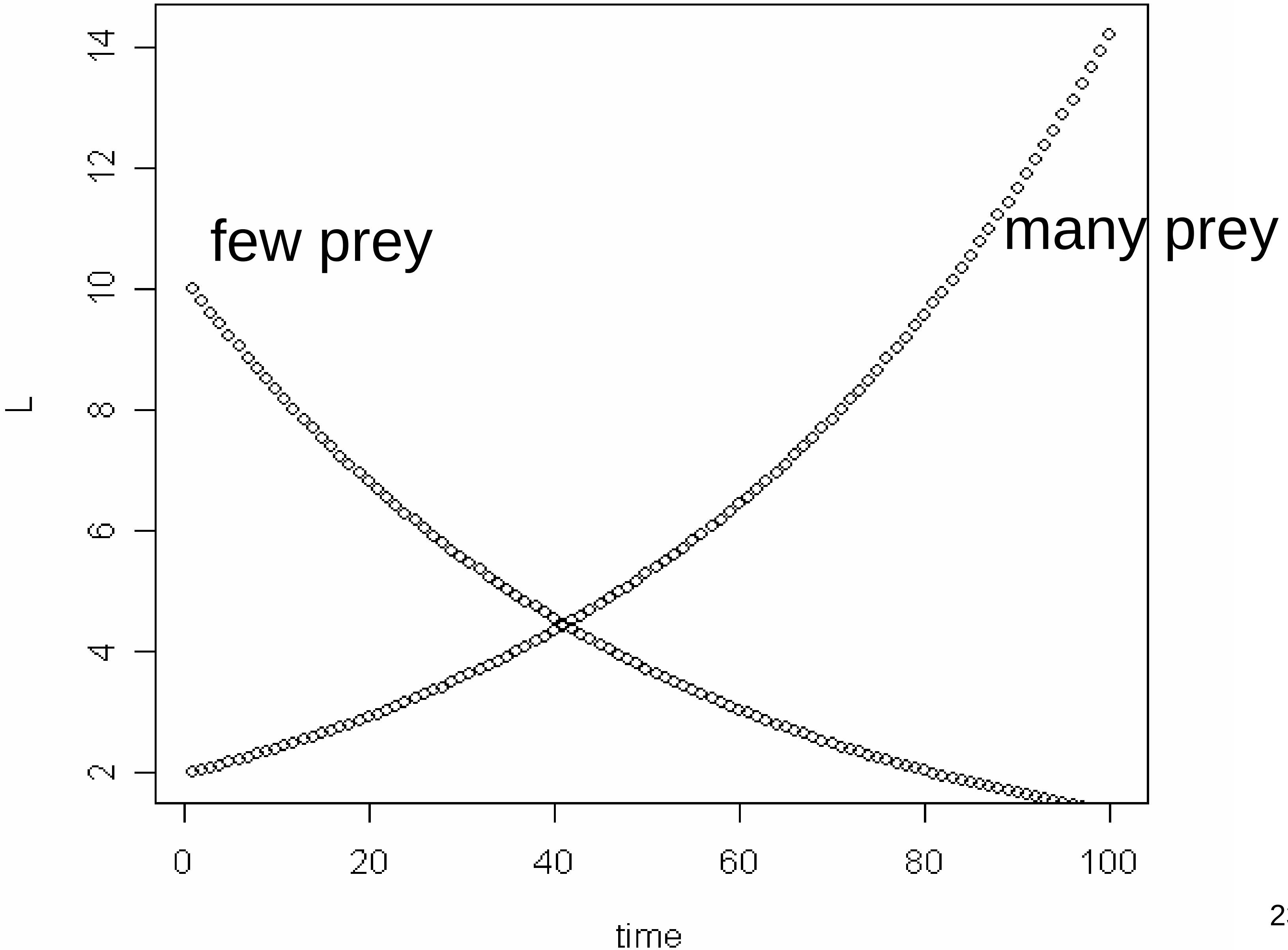
- Predation proportional to A
- PR=a*A



L=0
L=2 a=0.1
n
t
0
1
2
3
4
5
5
10
15
20

Model for predator

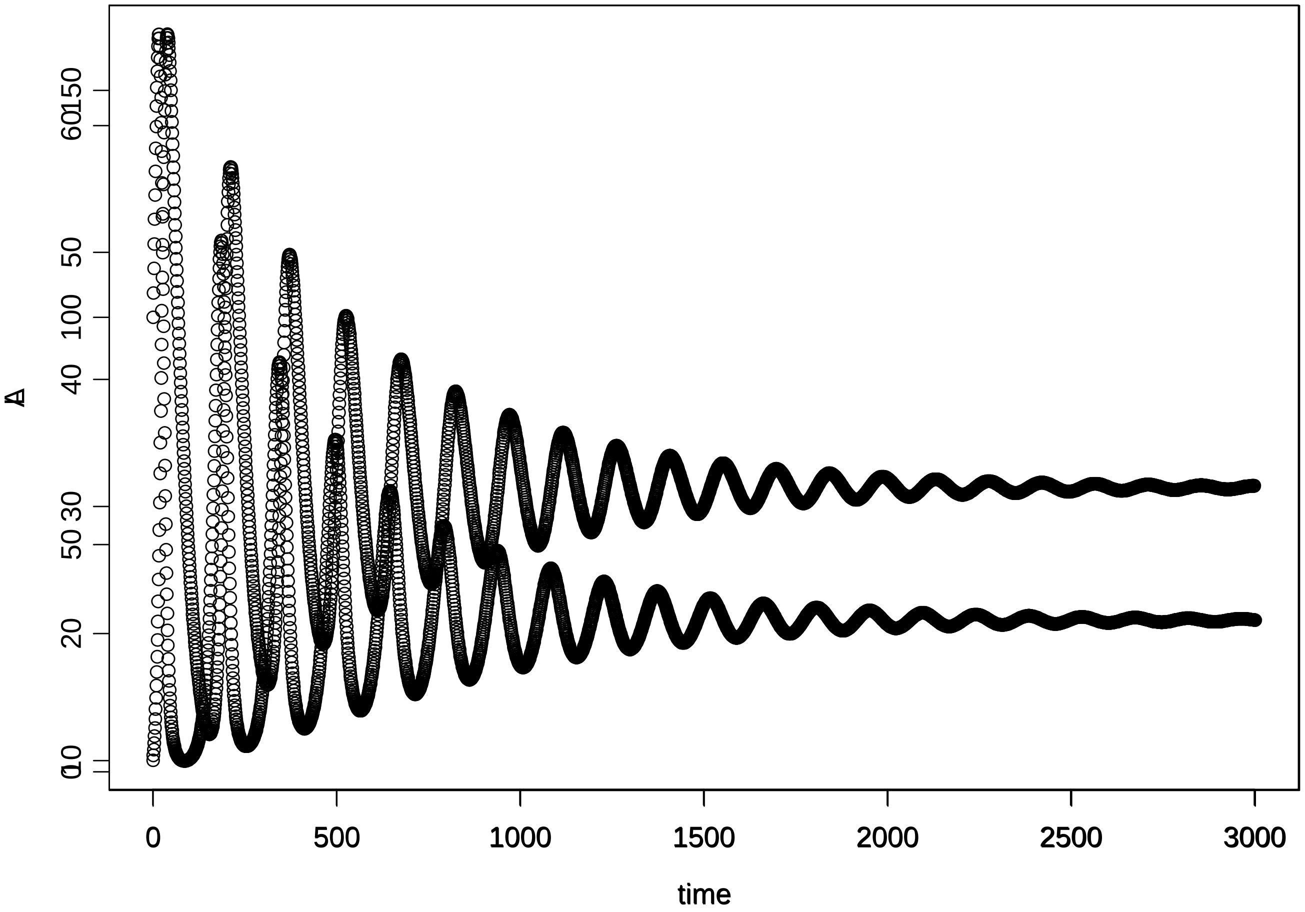
- Rate of increase depends on rate of predation
- Mortality is proportional to L
- $dL/dt= b*A*L - m*L$

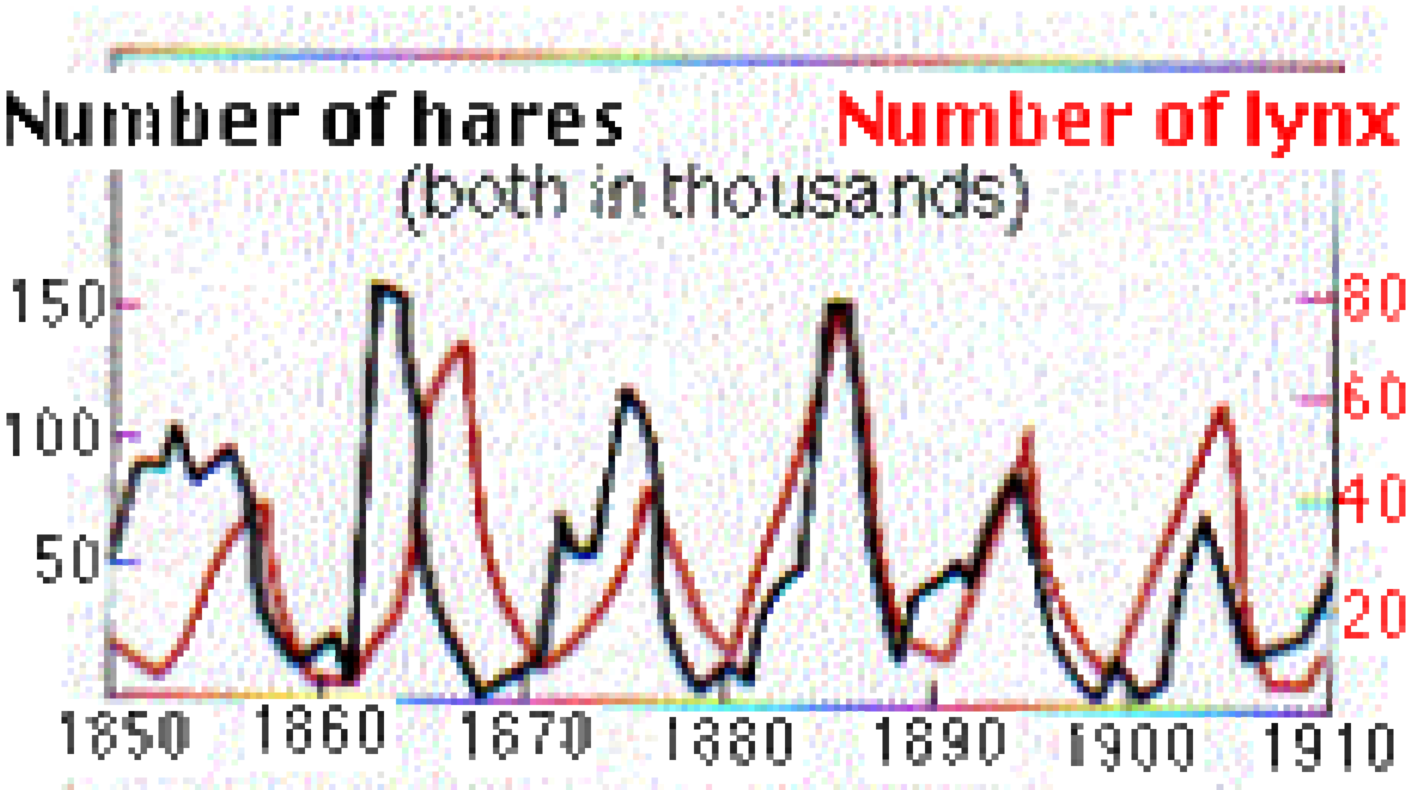

few prey
many prey
L
time
0
20
40
60
80
100
2
4
6
8
10
12
14

Predator and prey together

- Previously prey with fixed number of predators
- Predators with fixed number of prey
- What will two populations together look like?

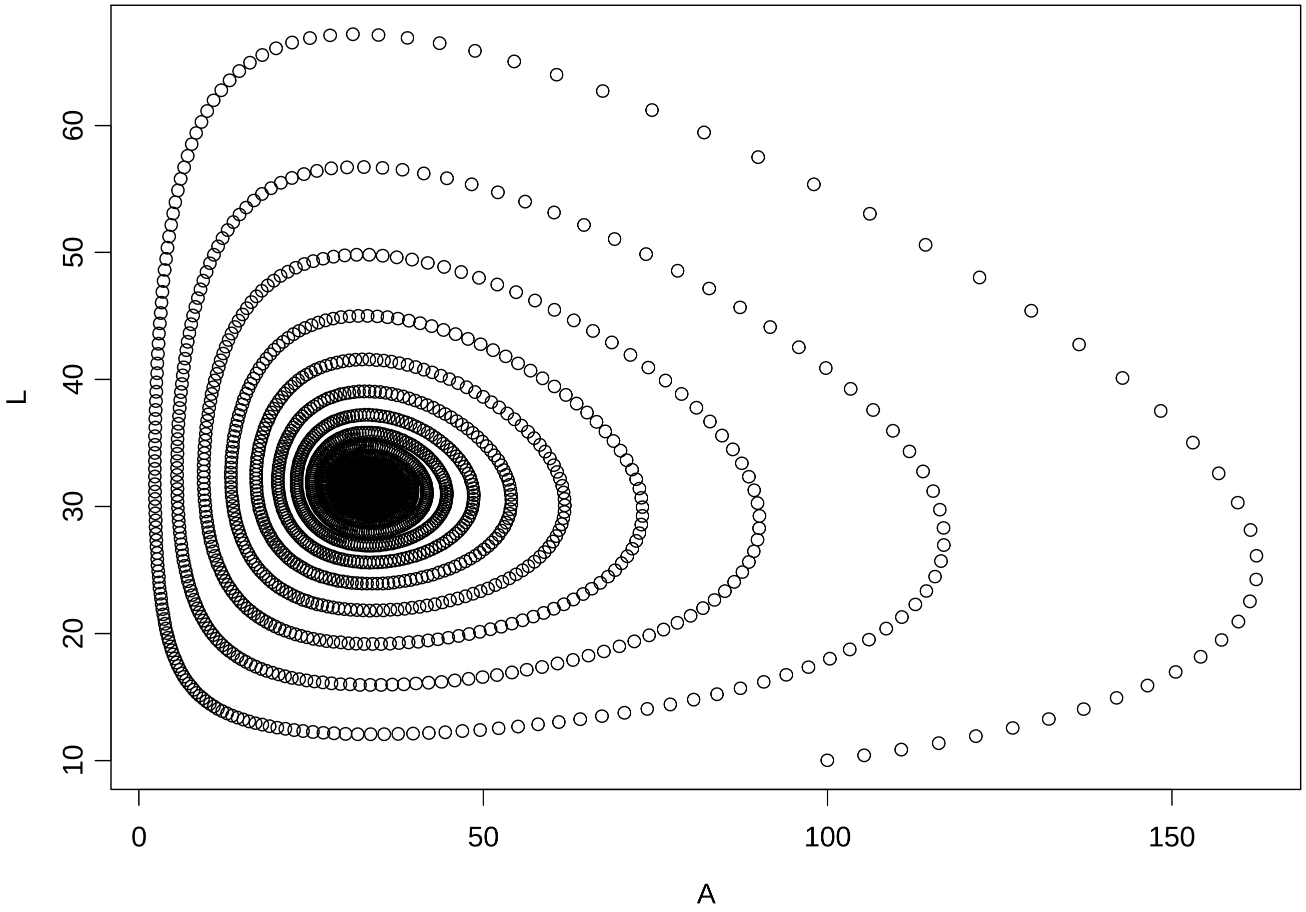
Predator and prey oscillations





Number of hares
Number of lynx
(both in thousands)
150
100
50
80
60
40
20
1850
1860
1670
1880
1890
1900
1910

Predator as function of prey



What is the use of the predator-prey model?

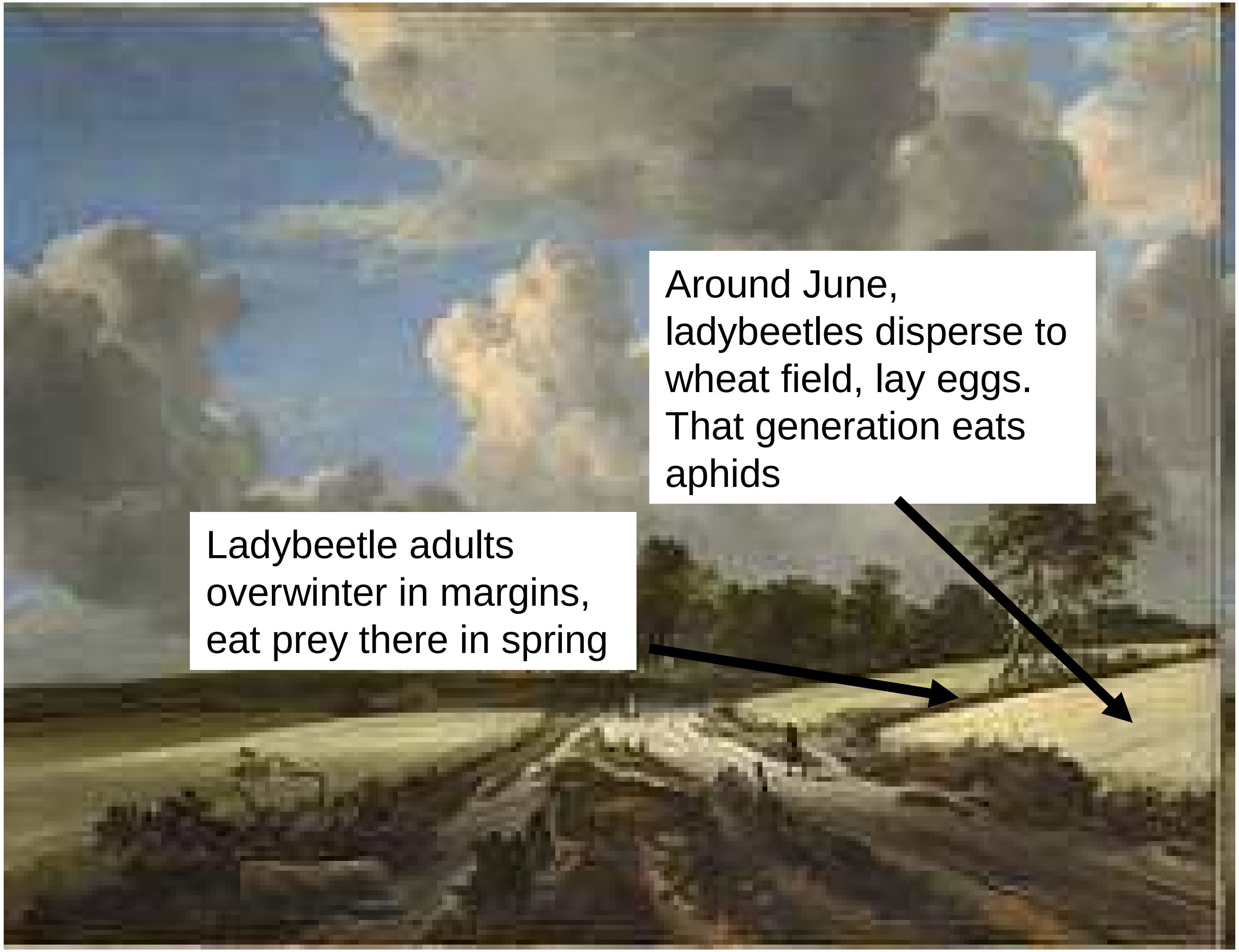
- Better understanding of real world
  - Use model to study system behavior
    - Identify behavior that we hadn't thought to study (cycles).
    - If behavior exists in real world
      - We have identified new phenomenon
      - Model provides provisional explanation.
      - But does this mean that model is "true"?
- Basis for more complex (realistic) models

A model to treat a practical problem in pest management

- Biological control of aphids in wheat
- Control using ladybeetles (predators of aphids)
- How can we increase predation?

- Bianchi, F. J. J. A. and van der Werf, W. 2004. Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes. Ecological Modelling 171, 177-193.

Describe system



Wheat fields 1670 Jacob van Ruisdael (Dutch, 1628/29–1682)

Proposed control strategy

- Increase prey in margins (artificial release). What effect will that have?
  - That should increase fecundity
  - Ladybeetles will lay more eggs in wheat field, will control wheat aphids better.
  - But less dispersal?

Questions

- Will extra prey in field margins help?
  - How much?
  - What does success depend on?

Could we study this question experimentally?

- Concerns large area (several fields and margins). Hard to experiment.
- Many possible conditions
  - Different numbers of prey in margins
  - Different aphid infestations in wheat
  - Different geometries, climates
  - Etc.
  - Would require many treatments
- So use a model

Model

- What are essential features to add to simple predator-prey model?
  - Three species: ladybeetles, prey in margins, aphids in wheat.
  - Take into account development stages of ladybeetles
    - Eggs, 4 larval stages, pupa, adult
  - More realistic model
    - Effect of temperature, effect of food on eggs, predation function
  - Take into account dispersal

Prey state variables

- Density of prey in margins
- Density of aphids in wheat

ladybeetle state variables

- Legg=density of ladybeetle eggs (number/m^2)
- LL1,…,LL4 = density of ladybeetle larvae stages L1,…nL4
- LPupa=density of pupae
- Ladult=density of adults

Ladybeetle development stages

- http://www.youtube.com/watch?v=6zrDGh2DIRU

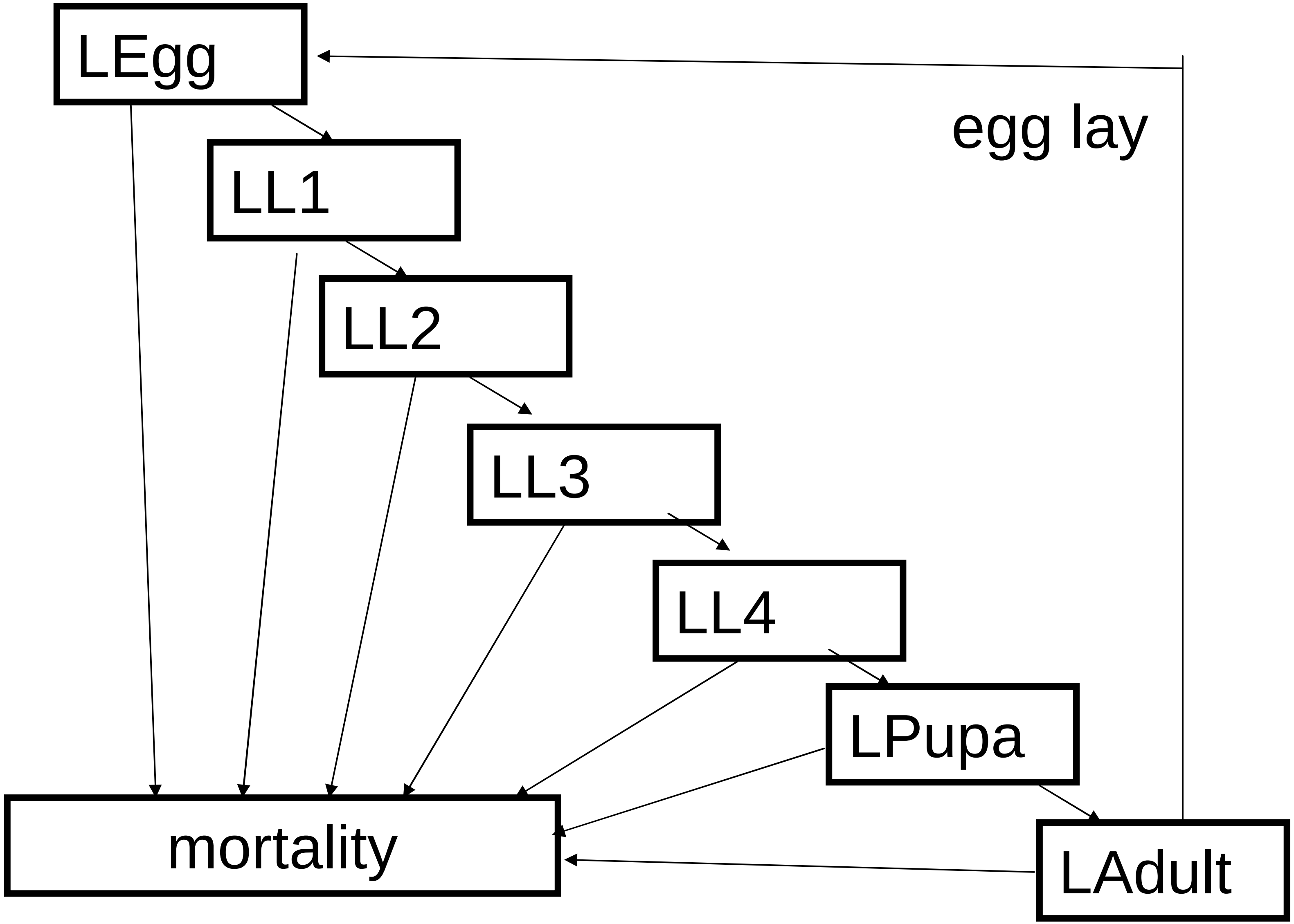
Prey dynamics

- New model for prey populations.
  - $\Delta A/\Delta t = r*A*(1-A/K)-\Sigma PRi*Li$ ($PRi=ai*A$)
  - (Use discrete time intervals Δt =10 minutes)
  - Sum is over ladybeetle stages
  - Same model, different parameters for two prey populations

Predator dynamics

What processes affect population of each ladybeetle stage?

- Eggs
  - increase depends on fecundity which depends on predation
  - Decrease because of mortality
  - Decrease because of hatching
- Other stages up to adults
  - Increase depends on input from previous stage
  - Decrease because of mortality
  - Decrease because of passage into next stage
    - Except adults. For them, just mortality


LEgg
egg lay
LL1
LL2
LL3
LL4
LPupa
mortality
LAdult

Predator model

- Egg stage
- ΔLegg/Δt = (eggs laid/day)*Ladult
  - megg*Legg
  - (fraction eggs hatched per day)*Legg

- For other stages i=L1, L2, L3, L4, pupa, adult
- ΔLi/Δt = (fraction leaving stage i-1 per day)*L(i-1)
  -mi*Li
  -(fraction leaving stage i per day)*Li

Data concern development times for various temperatures

- E.g. at 15°, development times are
  - Egg 9 days
  - L1 9 days
  - L2 8 days
  - L3 8 days
  - L4 14 days
  - Pupa 16 days

We need fraction leaving each stage

- Fraction leaving/Δt = (1/development time)* Δt
- Example

  10 minutes at 15° (development time 9 days)

  then 10 minutes at 20°.(development time 6 days)

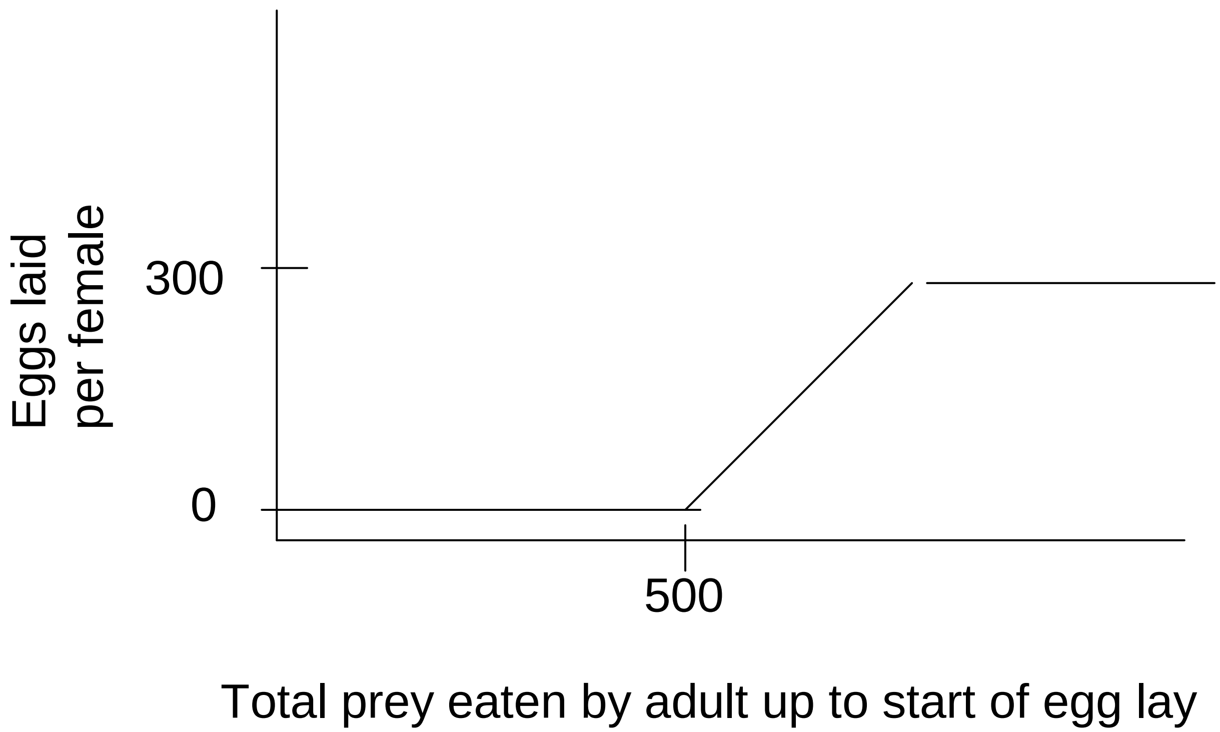
  What fraction of population leaves egg stage?

  10 minutes =0.0069 days)

- 1/9*0.0069 of population present at start of first period leaves during period
- 1/6*0.0069 of population present at start of second period leaves during that period.

Fecundity

- Fecundity depends on predation rate.



More detailed predation function

- Rate of predation/predator was RP=a*A(t)*L(t)
  - as prey increases, rate of predation increases. Without limit
  - Is that reasonable?

Ladybeetle eating aphid

- http://video.aol.com/video-detail/ladybugs-eating-aphids-ladybug-larvae-and-ladybug-adult-chowing/2410493093

- What limits predation rate?

Qualitative model

- In a given time, part of time is spent searching and part is spent handling prey.
- Handling time is proportional to number of prey handled.

Functional response model

- T=Ts+Th
  - Ts=search time, Th =handling time
- The number of prey found per predator per unit time is sr*A*Ts
- The handling time for those prey is ht*sr*A*Ts
- T=Ts(1+ht*sr*A)

- $T = T_s(1+ht*sr*A)$
- $T_s/T = 1/(1+ht*sr*A)$

- $PR = sr*A*\underbrace{1/(1+ht*sr*A)}_{\text{Correction factor}}$

Some real values

- At 20°
- Search rate sr cm^2/day.
  - Value=51.9cm^2/day (= 0.00519m^2/day)
- At 2000aphids/m^2
  - Prey found in time Ts is sr*A(t)*Ts
    =10.4 aphids/day of searching.

- Handling time, for an adult at 20°
  - 0.0049 days = 7 minutes
- $PR=10.4/(1+10.4*0.0049)=9.9$
- Correction factor is 0.95.
- Is it worthwhile?
  - This is a major question in modeling.
  - Is all extra detail good? If not, why not?

Spatial organization

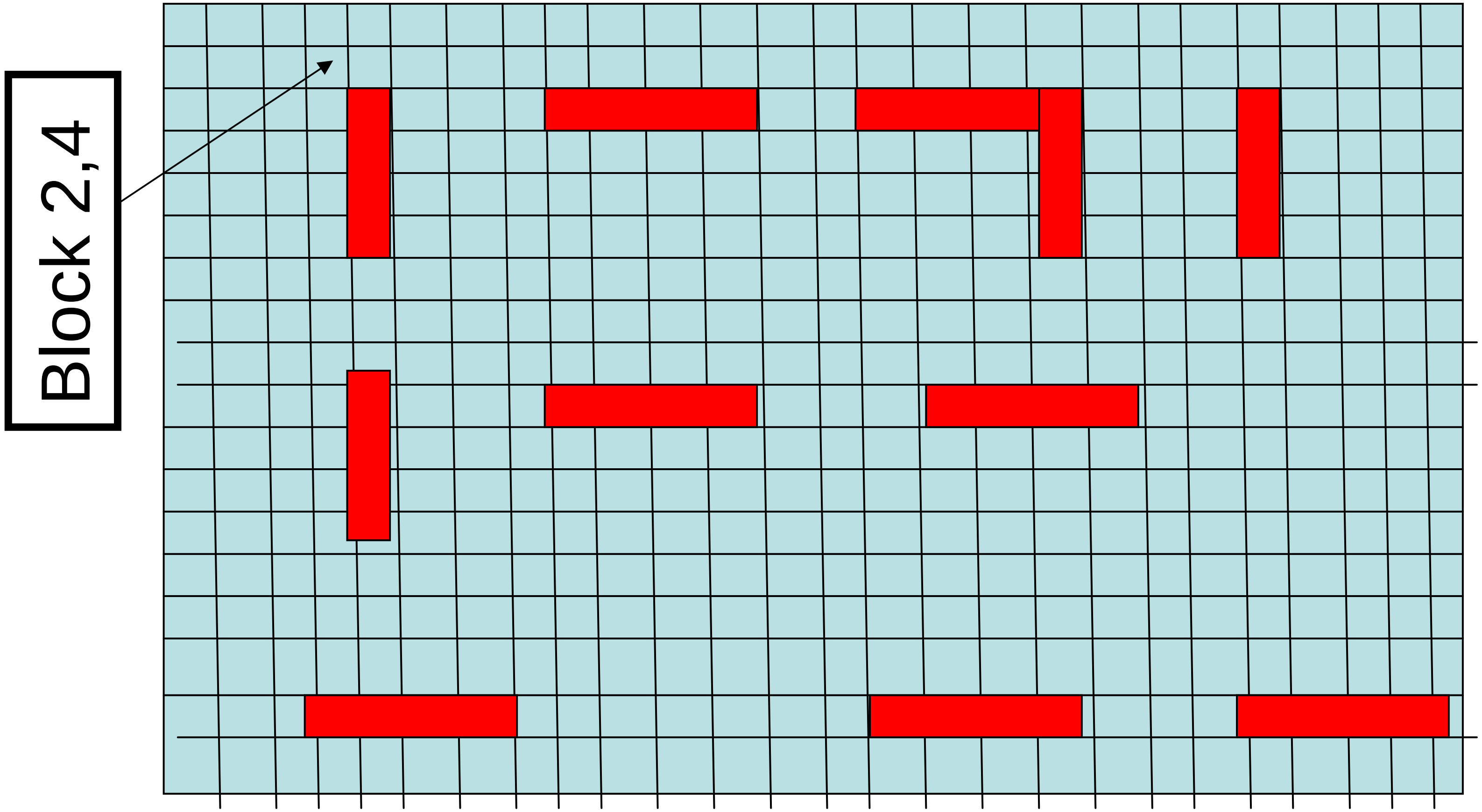
- The move of ladybeetles from margins to wheat is essential.
- So we need to model the spatial organization and movement of ladybeetles.

Around June, ladybeetles disperse to wheat field, lay eggs. That generation eats aphids

Ladybeetle adults overwinter in margins, eat prey there

- Model of field geometry?

- Divide the area studied (400m x 400m) into 10m x10m blocks.



90% wheat, 10% margins

Complete model

- 40*40 = 1600 cells
- In each cell, 1 prey population and 7 stages of predator
- Overall 14400 state variables

Qualitative model

- Aphids, ladybeetle eggs, larvae, pupae
  - Same as before
- Ladybeetle adults, cell c

ΔLadult(c)/Δt=

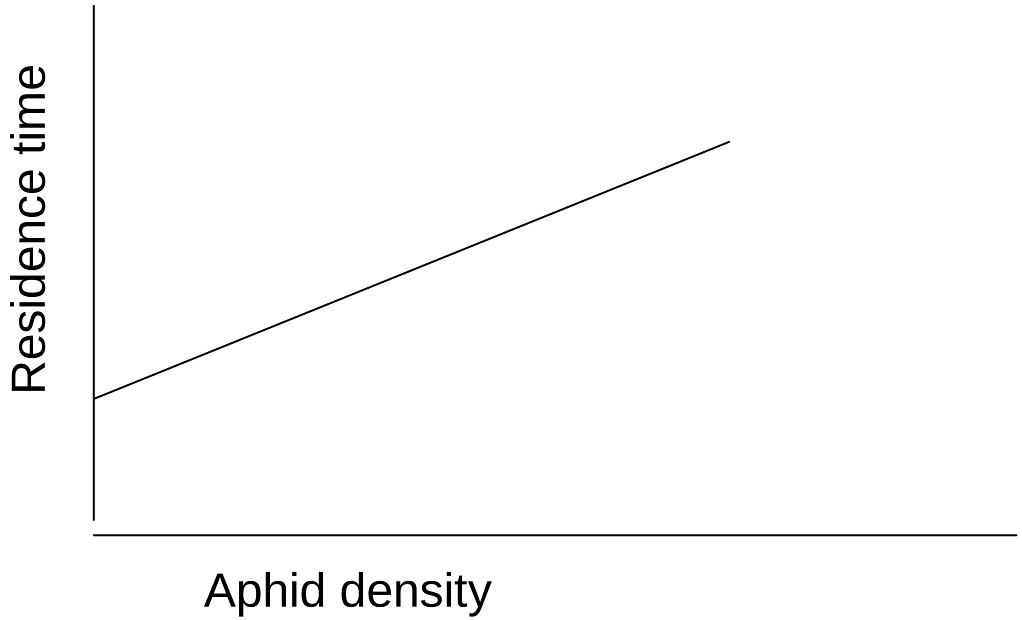
-mi*Ladult(c)

-(fraction emigrating per day)*Ladult(c)

+Σ(fraction moving from c’ to c per day)*Ladult(c’)

Qualitative model for emigration

- Residence time proportional to aphid density
- Fraction emigrating per unit time?
  - Fraction emigrating = 1/(residence time)

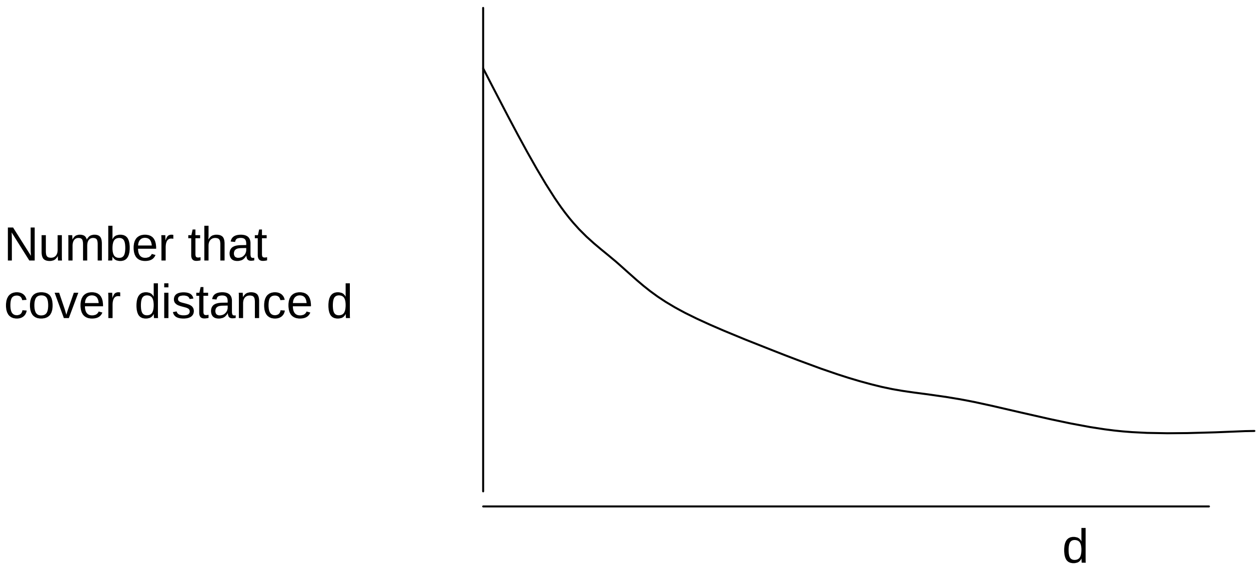


Quantitative model for emigration

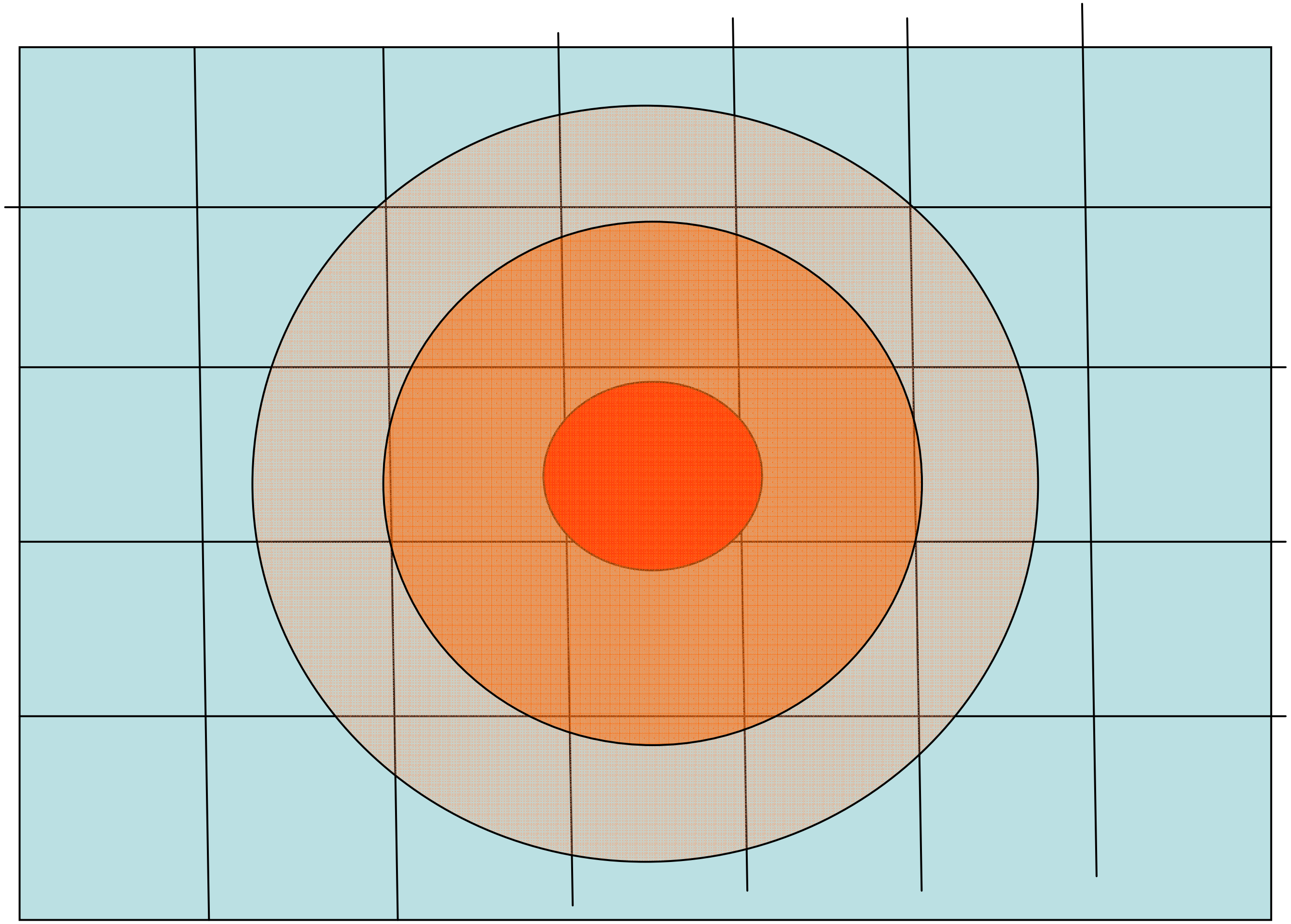
- Residence time= rc*A
- Numerical example
  - A=2000aphids/m^2
  - Rc=0.002 days/(aphid/m^2)
  - Residence time=4 days
  - Fraction that emigrate in 10 minute period?
  - (1/4) *0.0069 of population present at start of period leaves during period

Qualitative model for immigration

- Emigrating ladybeetles have no preferred direction
- Number that cover distance d declines with distance



- For each starting cell, calculate number that leave then partition among other cells according to distance.



What about ladybeetles that leave simulated area?

Parameters

- Relative growth rates, mortality rates, development times etc at various temperatures.
- Where do parameters come from?
  - Literature.
  - Some are from controlled conditions
  - Others are from field (e.g. mortality rates)
  - How accurate are parameters?

Explanatory variables

- Temperature
- Geometry
- Initial population in each cell

Calculations

- Lots of calculations
  - 10 minute time step
  - At each step, calculate migration between all 1600 cells = 2.6 million combinations

Evaluating the model

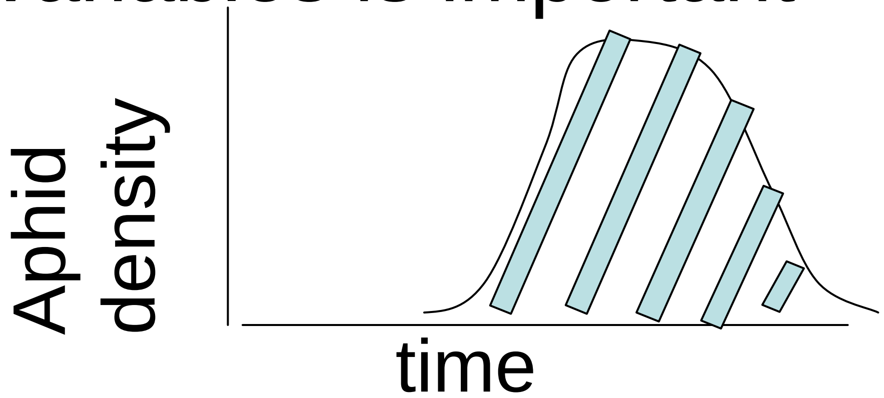
- In this case, no experimental data
- How would you evaluate this model?
- Check that results seem qualitatively reasonable
  - In particular, do adults move from margins to wheat as expected?

Scenario studies

- Field geometry fixed
  - 90% wheat, 10% margins
- Fixed constant temperature
  - 20° (but explore other temperatures)
- Initial ladybeetle density in filed margins fixed
  - $10/m^2$
- Initial aphid density in margins
  - 0, 1n 2, 5 or 10 aphids/m^2
- Date of colonization of wheat by pest aphids
  - Day of year 120, 130, 140, 150
- Choice of scenarios is important

Results

- The model calculates values of all state variables (there are 12,800) at each time.
- Need summary variables
- Here look at integral of pest aphid density over time. (« cumulative aphids »)
- Choice of output variables is important



Conclusions

- Early infestation of wheat
  - Ladybeetles are effective (reduce cumulative aphids by 52%).
  - But very little effect of aphid density in margins
- Late infestation
  - Cumulative aphids is small in any case.
  - Ladybeetles reduce that by 19% with added aphids in field margins, 17% without.
  - But perhaps problem next year
- Intermediate infestation
  - Intermedaite value of cumulative aphids.
  - Value reduced by 40% with added aphids in margin, 14% without.
  - Also, more overwintering ladybeetles with added aphids.

Role of model?

- Organize thinking about system
  - Identify essential aspects (dispersion)
  - Identify important factors (effect of date of wheat infestation)
  - Give precise definition of objectives (integral of aphids)
- Better understanding about system
  - What to look for in field results (date of wheat infestation, fecundity, dispersal dynamics)
- Propose strategies to be tested
  - Reduce number of strategies (give approximate numbers of added prey, geometry,…)
- Decision tool?
  - Calculate optimal number of added prey?
  - Probably not sufficiently accurate for each situation.

THE END