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
- \( \Delta t \) = time interval
- \( \Delta N / \Delta t \) = 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 \( r=0.1/\text{year} \)
  – \( N_1=1100 \)
  – \( N_2=1210 \)
  – etc
Continuous time model

• Now model specifies \( \frac{dN}{dt} \)
  – Like \( \Delta N/\Delta t \) but with infinitesimal time increments
  – \( \frac{dN}{dt} \)=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
  
  \[ \frac{dN}{dt} = rN \]

  – \( r \) 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
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? $\frac{dN}{dt}=?$
Logistic model of population growth

- $dN/dt = rN(1-N/K)$
  - $r =$ relative growth rate
  - $K =$ carrying capacity
$N_0 = 0.1 \quad r = 0.6 \quad K = 5$
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:
  \( A(t) = \text{number of individuals of prey at time } t \)
  (or just write A)
  
  \( L(t) = \text{number of individuals of predator at time } t \) (or just write L)
Model for prey

- Prey have logistic growth, plus mortality due to predation
- $\frac{dA}{dt} = rA(1 - A/K) - PRL$
- Form for $PR = \text{rate of predation/predator}$?
- Predation proportional to $A$
- $PR = aA$
L=0

L=2  a=0.1
Model for predator

- Rate of increase depends on rate of predation
- Mortality is proportional to $L$
- $\frac{dL}{dt} = bA*L - m*L$
few prey

many prey
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
(both in thousands)

Number of lynx
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?

Describe system
Ladybeetle adults overwinter in margins, eat prey there in spring

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

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?
  – 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

- $\text{Legg} = \text{density of ladybeetle eggs (number/m}^2\text{)}$
- $\text{LL1,\ldots,LL4} = \text{density of ladybeetle larvae stages L1,\ldots,nL4}$
- $\text{LPupa} = \text{density of pupae}$
- $\text{Ladult} = \text{density of adults}$
Ladybeetle development stages

• http://www.youtube.com/watch?v=6zrDGu2DIRU
Prey dynamics
• New model for prey populations.
  – \( \Delta A/\Delta t = r*A*(1-A/K) - \Sigma PR_i*Li \) (PRi=ai*A)
  – (Use discrete time intervals \( \Delta t = 10 \) 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
Predator model

- Egg stage
  - $\Delta L_{egg}/\Delta t = (\text{eggs laid/day})*L_{adult}$
    - megg*$L_{egg}$
    - (fraction eggs hatched per day)*$L_{egg}$

- For other stages $i=L1, L2, L3, L4, \text{pupa, adult}$
  - $\Delta L_i/\Delta t = (\text{fraction leaving stage } i-1 \text{ per day})*L(i-1)$
    - mi*$L_i$
    - (fraction leaving stage $i$ per day)*$L_i$
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/\Delta t = (1/development time)* \Delta t
- 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)

- \(1/9 \times 0.0069\) of population present at start of first period leaves during period
- \(1/6 \times 0.0069\) of population present at start of second period leaves during that period.
Fecundity

- Fecundity depends on predation rate.

![Graph showing the relationship between total prey eaten by adult and eggs laid per female. The x-axis represents total prey eaten by adult up to the start of egg lay, ranging from 0 to 500, and the y-axis represents eggs laid per female, ranging from 0 to 300. The graph shows a linear increase in eggs laid per female as the total prey eaten by the adult increases.](image-url)
More detailed predation function
• Rate of predation/predator was
  \[ RP = a \cdot A(t) \cdot L(t) \]
  – as prey increases, rate of predation increases. Without limit
  – Is that reasonable?
Ladybeetle eating aphid


- 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

- \( T = T_s + Th \)
  - \( T_s = \) search time, \( Th = \) handling time
- The number of prey found per predator per unit time is \( sr*A*T_s \)
- The handling time for those prey is \( ht*sr*A*T_s \)
- \( T = T_s(1 + ht*sr*A) \)
- $T = T_s (1 + h_t * s_r * A)$
- $T_s / T = 1 / (1 + h_t * s_r * A)$
- $P_R = s_r * A * 1 / (1 + h_t * s_r * A)$

**Correction factor**
Some real values

- At 20°
- Search rate sr cm²/day.
  - Value=51.9cm²/day (= 0.00519m²/day)
- At 2000aphids/m²
  - 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.
Ladybeetle adults overwinter in margins, eat prey there.

Around June, ladybeetles disperse to wheat field, lay eggs. That generation eats aphids.
• Model of field geometry?
• Divide the area studied (400m x 400m) into 10m x 10m blocks.
Complete model

- $40 \times 40 = 1600$ 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

\[
\frac{\Delta L_{\text{adult}(c)}}{\Delta t} = -m_i \cdot L_{\text{adult}(c)} - \text{(fraction emigrating per day)} \cdot L_{\text{adult}(c)} + \sum \text{(fraction moving from } c' \text{ to } c \text{ per day)} \cdot L_{\text{adult}(c')}
\]
Qualitative model for emigration

- Residence time proportional to aphid density
- Fraction emigrating per unit time?
  - Fraction emigrating = $1/(\text{residence time})$
Quantitative model for emigration

- Residence time $= r_c \times A$
- Numerical example
  - $A=2000\text{aphids/m}^2$
  - $R_c=0.002\ \text{days/(aphid/m}^2\)$
  - Residence time $= 4\ \text{days}$
  - Fraction that emigrate in 10 minute period?
  - $(1/4) \times 0.0069$ 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

Number that cover distance $d$
• 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/m²
– Initial aphid density in margins
  • 0, 1n 2, 5 or 10 aphids/m²
– 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
  – Intermediate 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