Hypotheses on cycles

• Many different hypotheses to explain the phenomenon
  - Abiotic factors: weather, sun spots
  - Intrinsic biotic factors: changes in quality of individuals during the cycle, density induced stress
  - Extrinsic biotic factors: food quality/quantity, parasites, diseases and predation
  - Multifactorial hypothesis
Outline

• A brief history of predation effects
• Role of predation
• Predation hypothesis
• Supporting evidence for predation hypothesis: observations, modelling, experiments
• Alternative prey hypothesis
• Indirect effects of predation
Hypotheses on cycles

Olaus Magnus 1555

A brief history of predation

- It is long known that predator numbers fluctuate along with their prey
- Are they just follow their prey numbers or do they have any effect on the dynamics of their prey?
A brief history of predation

• For long it was assumed that predator cycles are consequence of prey cycles
• Predators concentrate on ‘unimportant’ part of the population; sick and old ind.
• At most predators can only accelerate the decline and deepen the low phase
• Until late 1970’s when the roles of different predators was re-evaluated (Erlinge & Andersson 1977)

Predator types

• Generalists
• Specialist
  - Resident
  - Nomadic
• Different kinds of strategies
Role of predation

- Different kinds of predators have different effects on prey population dynamics.
- Predators differ in their total response.
- Total response = functional response + numerical response
Functional response

- How the predation rate of predator changes with prey density.
- Includes many aspects of hunting behaviour.
  - Prey choice or vulnerability of prey
  - Changes in hunting habitat

Functional response

- Different kinds of f-responses have different kinds of effects on prey population dynamics.
  - type I, no effect
  - type II, typical for specialist predator, destabilising effect
  - type III, typical for generalist predator, stabilising effect at low prey densities
F-types

- Specialist
- Generalist

Predation rate/predator

Prey density

Functional response of the least weasel

Turchin & Hanski 1997

Sundell et al. 2000

Density of voles (ind./ha)

Predation rate (number of voles killed/72h)
Numerical response

• How number of predators changes with number of prey.
• Including natality, mortality, immigration and emigration.

Numerical response

• Different kinds of responses have different kinds of consequences on population stability
  - **Rapid response** to changes in prey population numbers (nomadic predators) - increases stability
  - **Time lag** in numerical response (resident specialist predators) - decreases stability and may lead to cyclic dynamics
  - **Generalist predators response** mainly functionally
Numerical response

Nomadic specialist  Resident specialist

Savola et. al. In prep.

Light grey: voles
Dark grey: hares
Black: foxes

Generalist
Predation hypothesis I

- The multiannual oscillations in northern Europe are due to delayed mortality imposed on the vole populations by small mustelids, particularly the least weasel.
- The interaction between voles and their mustelid predators is the cause of population cycles.

Predation hypothesis II

- Generalist mammalian predators and many avian predators (nomadic) have a stabilising effect on small mammal dynamics, which explains the decreasing cycle amplitude and length of small mammal oscillations from north to south in Fennoscandia.
The least weasel, *Mustela nivalis nivalis*

- Why the least weasel is thought to be important in shaping vole population dynamics?

## The least weasel, *Mustela nivalis nivalis*

- World’s smallest carnivore
  - Capable of hunting voles in their burrows and in subnivean space
  - High energy demand, surplus killing
  - Specialist predator of small mammals
  - Type II functional response
- Common and numerous
  - High reproductive capacity
- Time lag in numerical response
  - Destabilising effect, cyclic dynamics
Role of generalist and nomadic avian predators

- Role of generalist and nomadic avian predators on cyclic dynamics is similar.
- They react rapidly functionally (generalist) or numerically (avian predators) to changes in vole numbers.

Role of generalist and nomadic avian predators

- Stabilising effect on dynamics: shortening the cycle length and decreasing the amplitude (geographical gradient).
- Synchronising spatial dynamics (avian predators).
Evidence for predation hypothesis

- Observational evidence
- Theoretical evidence
  - Vole-weasel -models
  - Models on gradient in cycle length and amplitude
  - Models on spatial synchrony caused by avian predators
- Experimental evidence
Observations

• The most important mortality factor in declining vole populations is predation by small mustelids.

Korpimäki et al. 1991
Norrdahl & Korpimäki 1995

Observations

• Time lag in mustelid’s numerical response.

Stoat-lemming in Greenland Gilg et al. 2003
Observations

- Synchronous dynamics of small mammals having different diets.

Observations

- Chitty-effect: potential size selective killing by the least weasel.
16.2.2015

Observations

Evidence for predation hypothesis

- **Observational evidence**
- **Theoretical evidence**
  - Vole-weasel models
  - Models on gradient in cycle length and amplitude
  - Models on spatial synchrony caused by avian predators
- **Experimental evidence**
Vole-weasel models

'H Gradient' models

predicted  observed
Synchrony models

Evidence for predation hypothesis

- Observational evidence
- Theoretical evidence
  - Vole-weasel models
  - Models on gradient in cycle length and amplitude
  - Models on spatial synchrony caused by avian predators
- Experimental evidence
Experiments on predation

- **Exclosure experiments**
  - prey population fenced
  - entry of predators prevented
- **Removal experiments**
  - number of predators is reduced in unfenced area
- **Introduction experiments**
  - introductions to islands or other defined areas

Exclosure experiments

Erlinge 1987  
Ylönen et al. 1991  
Klemola et al. 2000
Exclosure experiments

Ims & Andreassen 2000

Removal experiments

Avian predators

and/or mustelids

Avian predators and

mustelids

Norrdahl & Korpimäki 1996

Korpimäki & Norrdahl 1998

Korpimäki et al. 2002
Removal experiments

Reduction of common weasels

Introduction experiments

Lindell & Forsman 1996
Introduction experiments

• Idea: eliminating natural time delay in weasel's numerical response
Introduction experiments

- Monitoring abundance of voles:
  - biannual snap-trappings: 30-45 SQ:s/island in forests, fields and clear-cuttings.
  - live-trappings in field vole habitats: 6/island, each ca. 0.25 ha, spring, summer and autumn for five days.
Alternative prey hypothesis

• Explains why some other prey species fluctuate in synchrony with voles
• (Generalist) predators change from voles, after their crash, to alternative prey species (f-response)
• Observations and experiments generally support this hypothesis
Alternative prey hypothesis

- Small game animal, hares and grouse species, numbers increase when voles are abundant and their reproductive output (juvenile survival) is worse in years of low vole abundance
- Foxes, martens and large avian predators, eagle owl, are important generalist in APH
- Low breeding success of cavity nesting small birds in low vole years - weasel?

Indirect effects predators

- Direct effects: killing by predation
- Indirect effects due to predation risk - behavioural and physiological responses
- What slows down the population growth of voles so that predators can catch them and cause decline?
- Can predators do it with indirect effects?
Indirect effects predators

• Stress - deteriorate reproduction, expose to diseases and harsh environmental conditions - increase of mortality
• Avoidance of predators voles reduce activity
  - Difficult to find mates -decrease repr.
  - Food intake worse -decrease repr. and increase mortality
• Change to safe but unproductive habitat
  - Same consequences as in reduced activity
• Delayed maturation and avoidance of mating
  - Repr. costly under predation risk

Indirect effects predators

• All these can slow down the population growth rate
• Predators are able ‘catch’ up the vole population
• Effects on population level?

• Alternative option: Synergistic predation hypothesis
  - All predators together can increase numerically and cause the decline of voles
Take home messages

- Predation hypothesis the most popular and plausible hypothesis to explain northern vole cycles
- Small mustelid can be the motor of the cyclic dynamics but need also other predators
- Role of indirect effects?
- Even if evidence is strong, the enigma of cycle is not solved

Something to think about

- Is the role of predators the same in everywhere?
- Is there universal explanation for cycles?
- Can there be many factors needed to explain cycles?