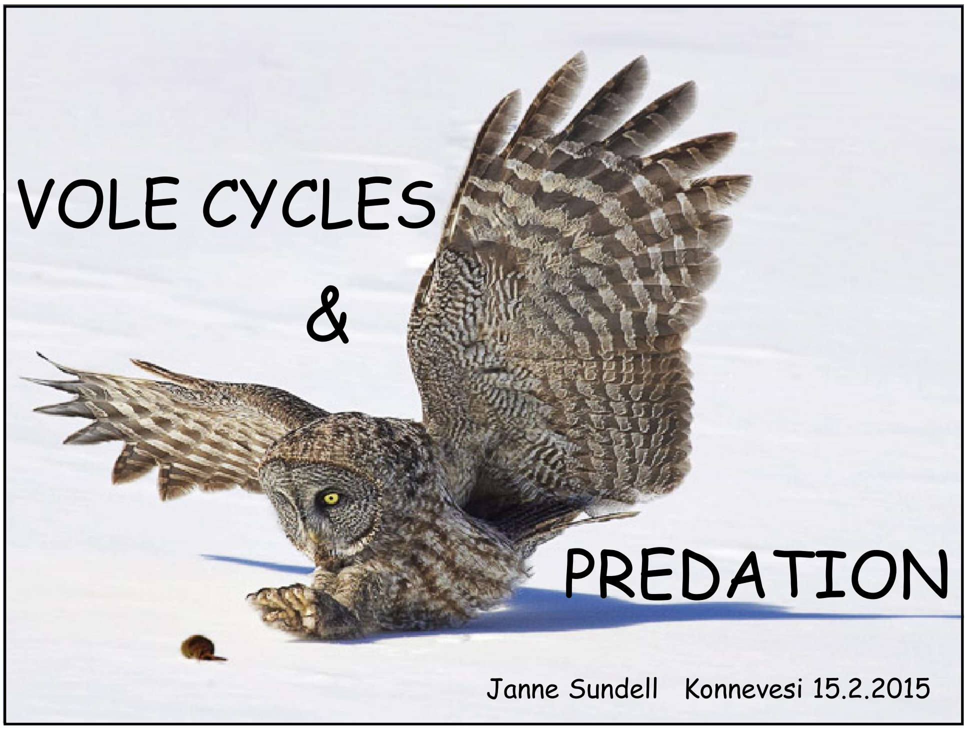
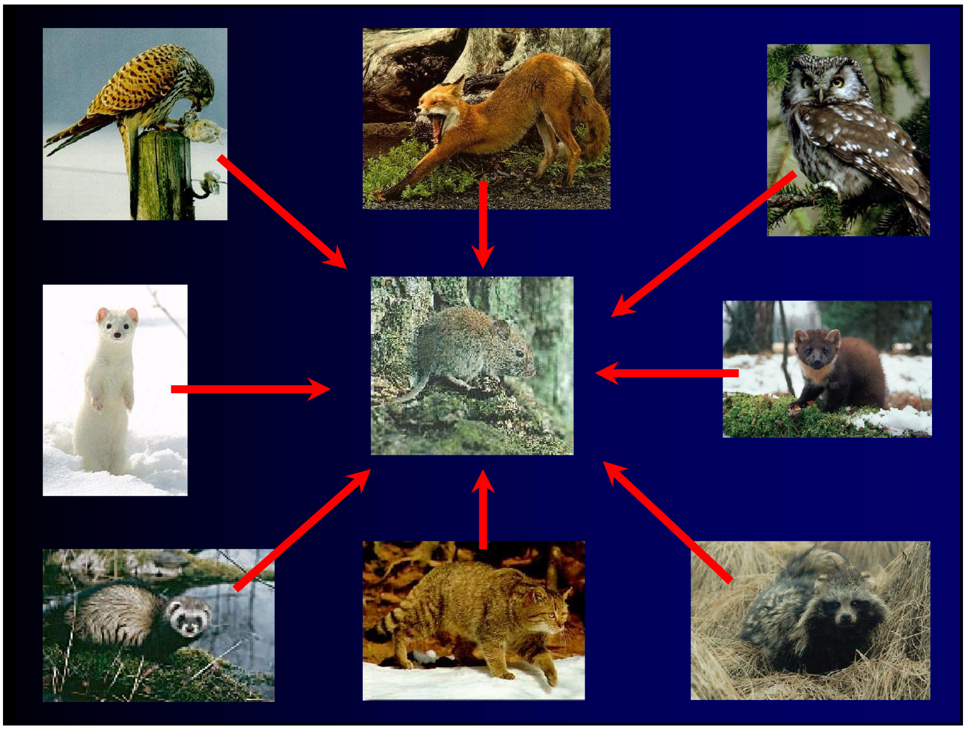


Hypotheses on cycles

- 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

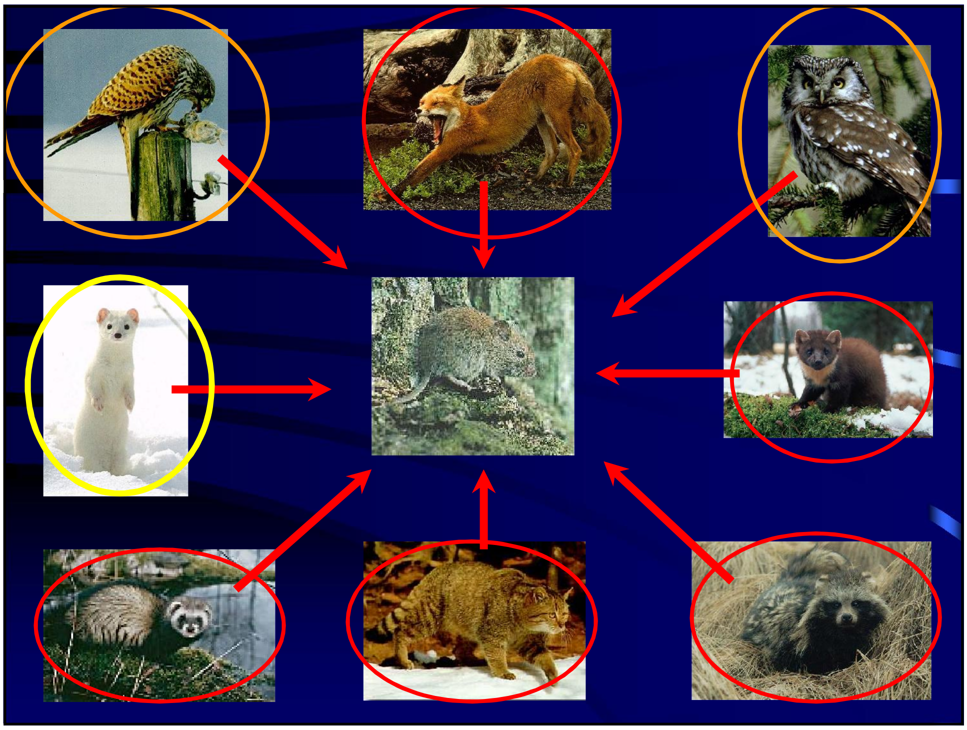
- It is long known that predator numbers fluctuate along with their prey
- Are they just follow their prey numbers or do they have any effect on the dynamics of their prey?

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

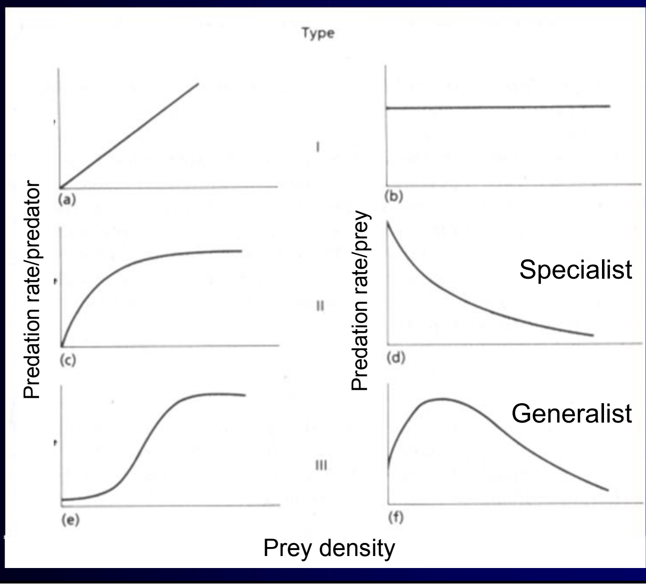
Functional response

- 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

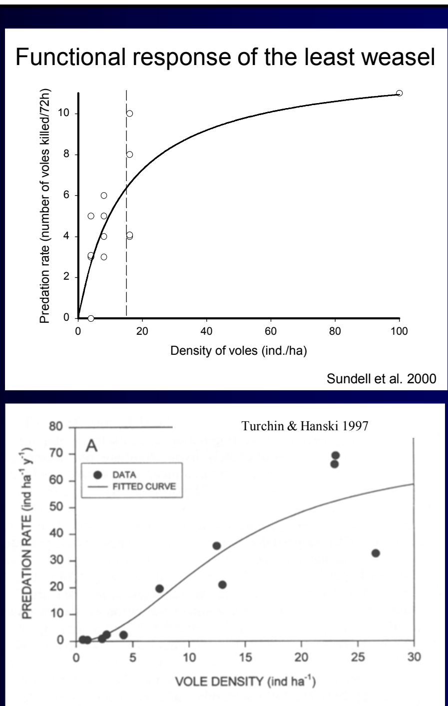
Functional response

- 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



Type
I
II
III
(a)
(b)
(c)
(d)
(e)
(f)
Predation rate/predator
Predation rate/prey
Specialist
Generalist
Prey density



Functional response of the least weasel
Predation rate (number of voles killed/72h)
Density of voles (ind./ha)
Sundell et al. 2000
Turchin & Hanski 1997
A
DATA
FITTED CURVE
PREDATION RATE (ind ha⁻¹ y⁻¹)
VOLE DENSITY (ind ha⁻¹)

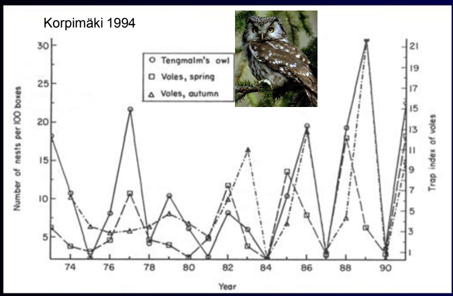
Numerical response

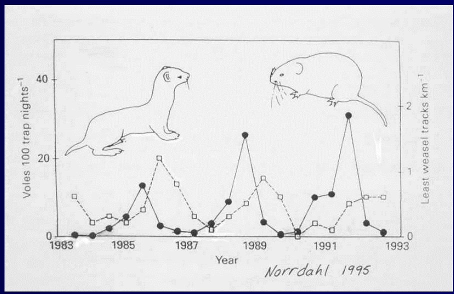
- How number of predators changes with number of prey.
- Including natality, mortality, immigration and emigration.

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

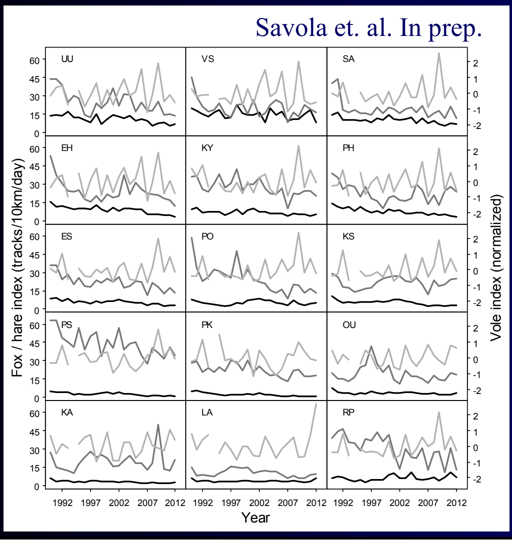




Nomadic specialist

Resident specialist

Numerical response



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

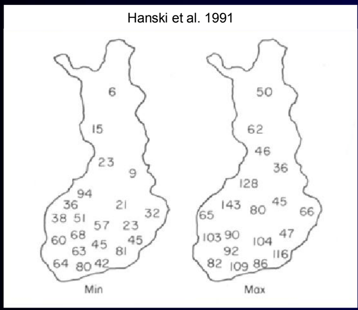
  ⇒destabilising effect, cyclic dynamics

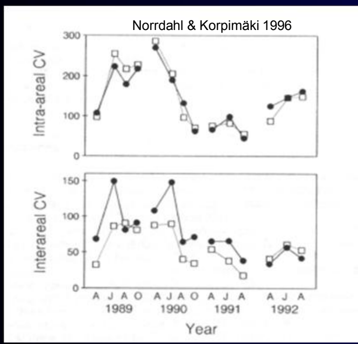
Role of generalist and nomadic avian predators

- 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

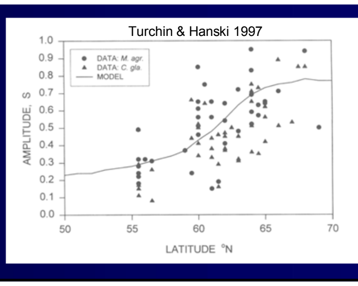
- Stabilising effect on dynamics: shortening the cycle length and decreasing the amplitude (geographical gradient).
- Synchronising spatial dynamics (avian predators).





Species	56° Revinge	59° Grimsö	68-69° North
Specialist mammalian predators			
Least weasel *Mustela nivalis*	?	?	up to 20
Stoat *Mustela erminea*	0·8–1·4	?	0·5–2·0
Specialist bird predators			
Short-eared owl *Asio flammeus*	–	–	<0·1
Long-eared owl *Asio otus*	0·2–1·3	0·0–0·3	–
Hawk owl *Surnia ulula*	–	<0·1	0·1–0·2
Tengmalm's owl *Aegolius funereus*	–	0·0–0·6	<0·1
Kestrel *Falco tinnunculus*	0·1–1·3	<0·1	<0·1
Long-tailed skua *S. longicaudus*	–	–	0·1–0·6
Generalist predators			
Red fox *Vulpes vulpes*	0·9–2·0	0·4	<0·1
Badger *Meles meles*	0·8–0·9	0·4	–
Domestic cat *Felis catus*	1·8–2·5	0·2–0·4	–
Polecat *Mustela putorius*	0·6–1·4	–	–
Pine marten *Martes martes*	–	0·4	0·1
Common buzzard *Buteo buteo*	1·5–2·5	0·2	–
Rough-legged buzzard *B. lagopus*	–	–	0·1–0·4
Tawny owl *Strix aluco*	0·7–1·4	<0·1	–
Corvids			
Raven *Corvus corax*	–	<0·1	?
Hooded crow *Corvus corone*	14	0·2	?
Jay *Garrulus glandarius*	–	4·0	?
Siberian jay *Perisoreus infaustus*	–	–	0·1–0·5
Pooled density of specialist bird predators and generalist predators	6·6–13·3	1·9–3·0	0·3–1·5

Hanski et al. 1991

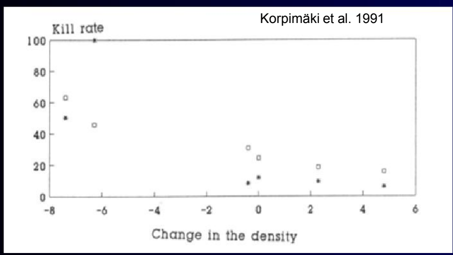


Evidence for predation hypothesis

- 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.

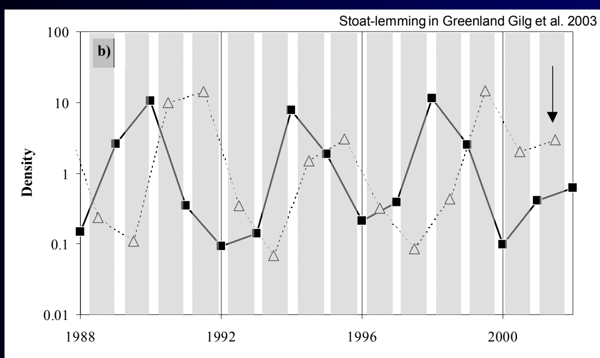


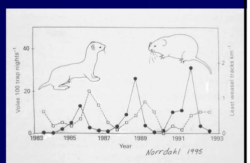
year	1992			1994		
phase	decrease			increase		
	all	killed	disapp.	all	killed	disapp.
sibling vole						
site 1	12	7 (5)	4	6	1 (1)	0
site 2	—	—	—	2	0	0
site 3	4	4 (4)	0	2	1 (1)	0
site 4	6	2 (2)	2	—	—	—
field vole						
site 1	1	1 (1)	0	5	2 (2)	2
site 2	7	3 (2)	2	1	1 (0)	0
site 3	6	3 (3)	1	5	2 (1)	0
site 4	1	1 (1)	0	—	—	—
	37	21 (18)		21	7 (5)	

Norrdahl & Korpimäki 1995

Observations

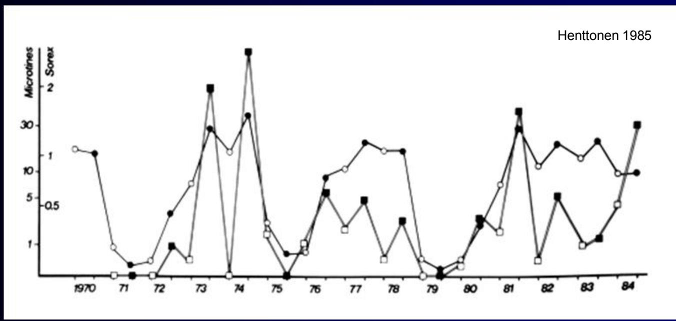
- Time lag in mustelid's numerical response.





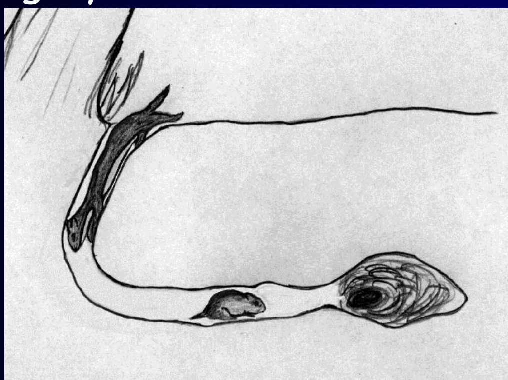
Observations

- Synchronous dynamics of small mammals having different diets.

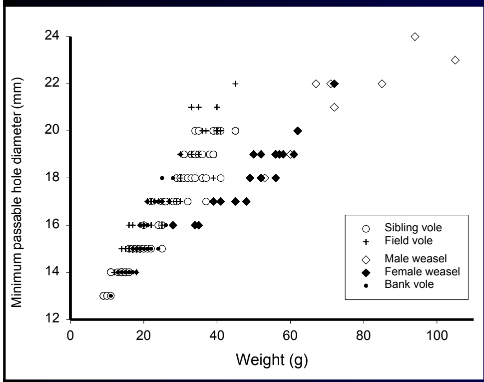


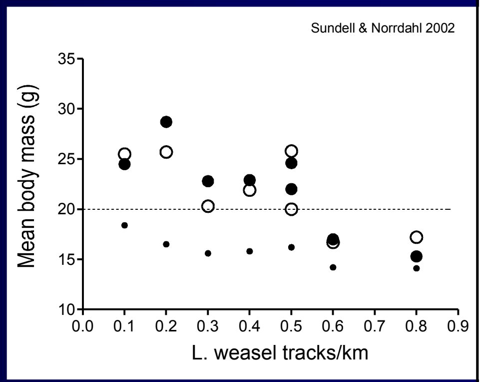
Observations

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



Observations





Evidence for predation hypothesis

- Observational evidence
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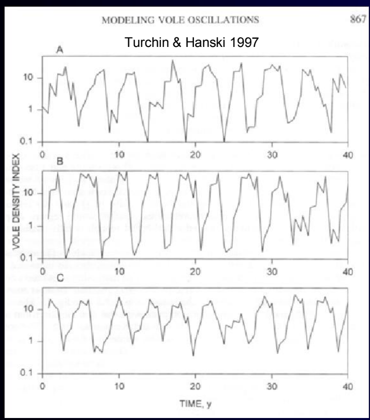
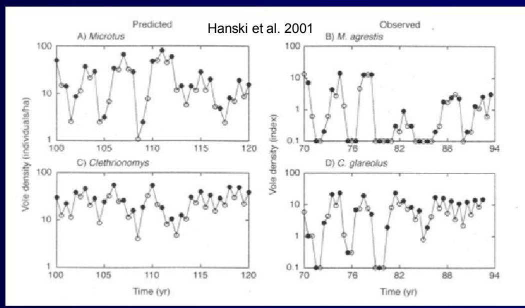
- Experimental evidence

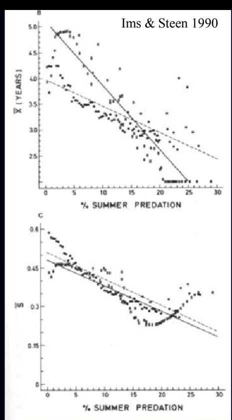
Vole-weasel models

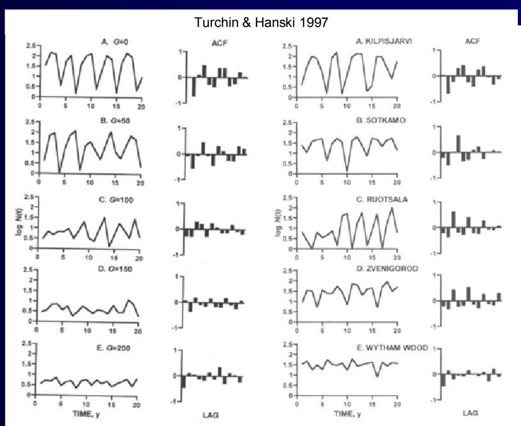




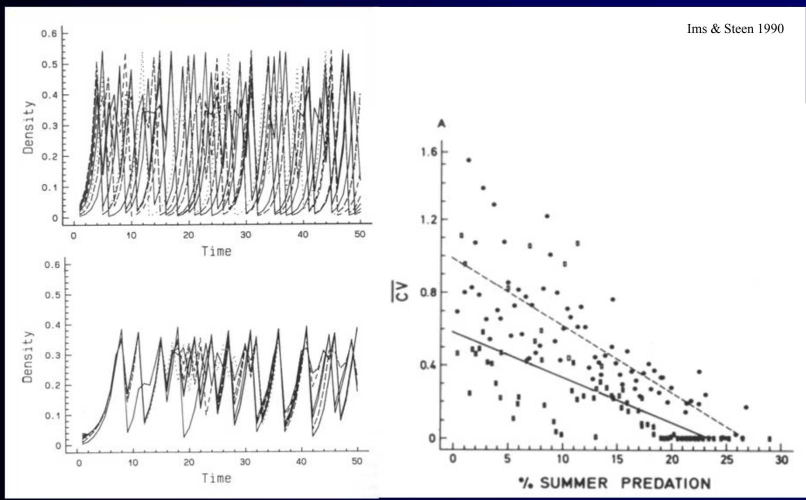
‘Gradient’ models

predicted observed





Synchrony models



Evidence for predation hypothesis

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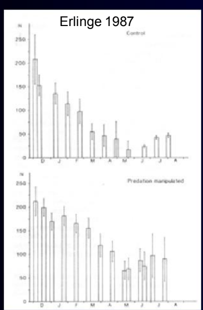
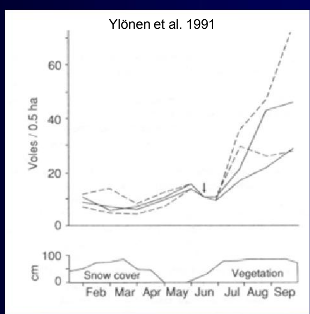
- Experimental evidence

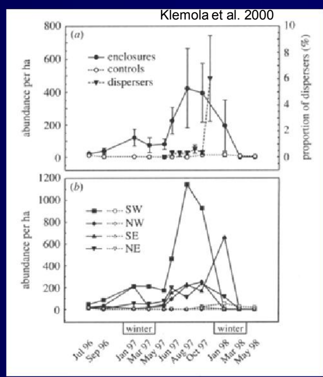
Experiments on predation

- 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

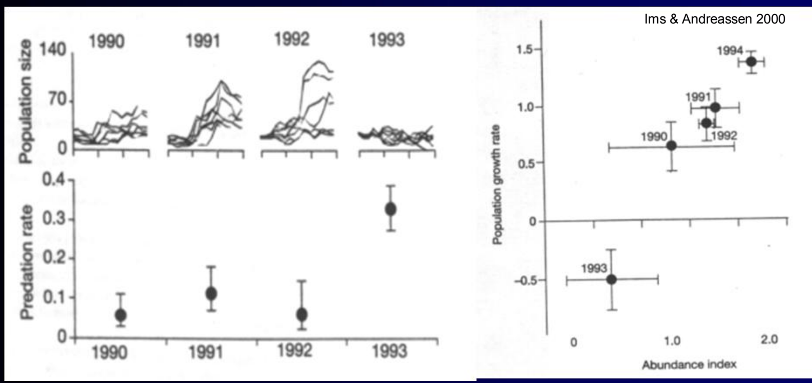
Exclosure experiments





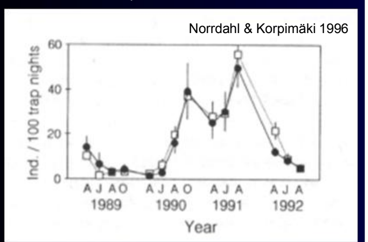


Exclosure experiments

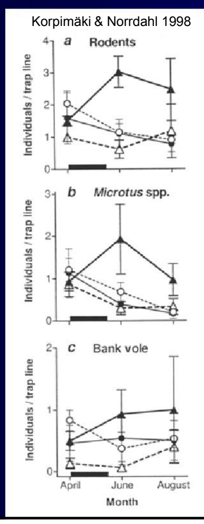


Removal experiments

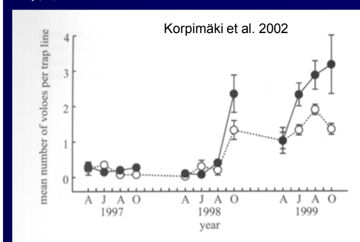
Avian predators



Avian predators and/or mustelids

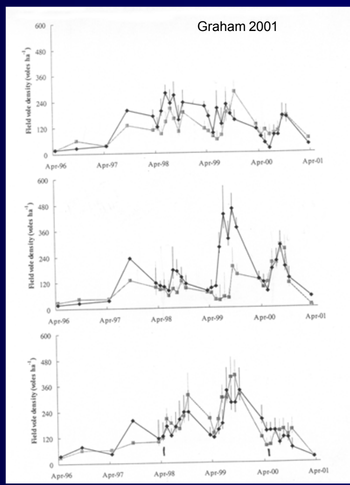


Avian predators and mustelids

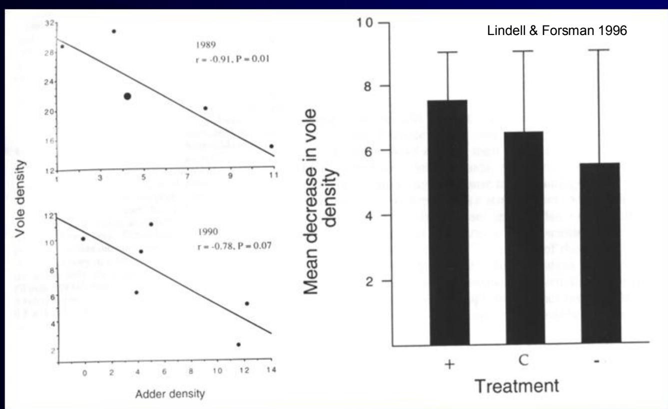


Removal experiments

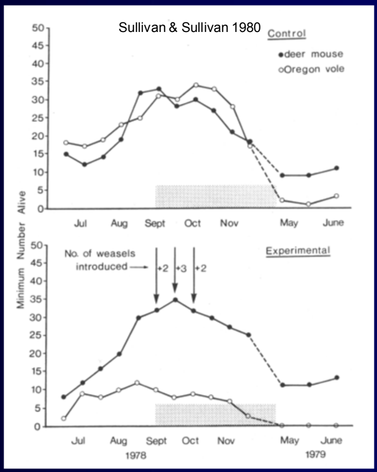
Reduction of common weasels



Introduction experiments

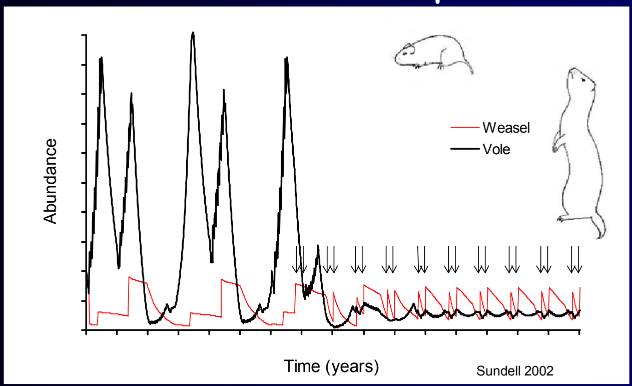


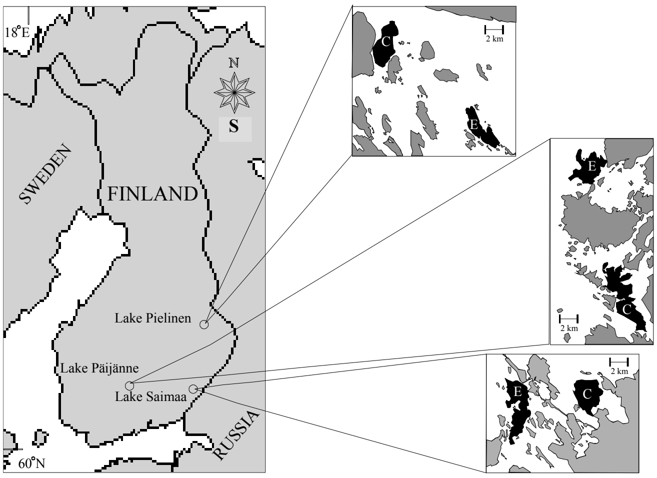
Introduction experiments



Introduction experiments

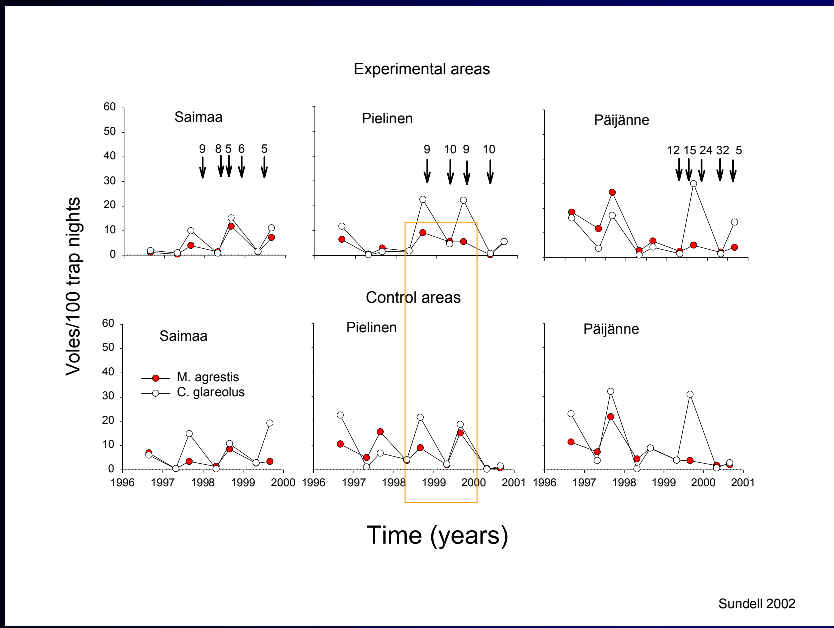
- Idea: eliminating natural time delay in weasel's numerical response





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 phyisiological responses
- What slows down the population growth of voles so that predators can catch them and cause decline?
- Can predators do it with indirect effets?

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 consequencies 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?