

ICTP-SAIIR. Jan 2015

*'The Wonderful World of
Macroparasites'*

Andy Dobson

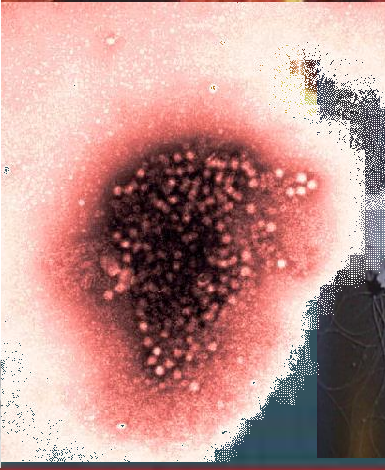
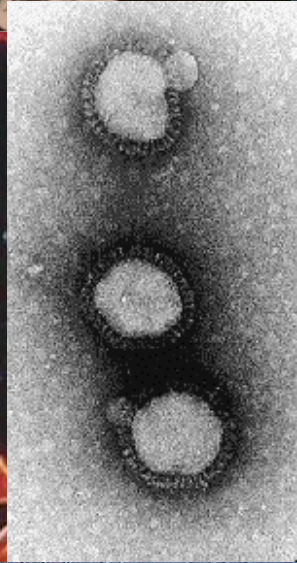
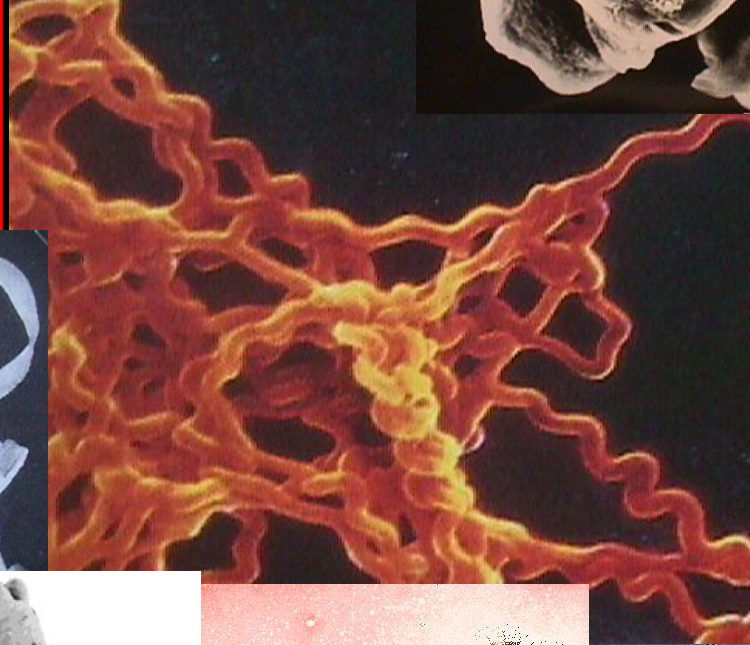
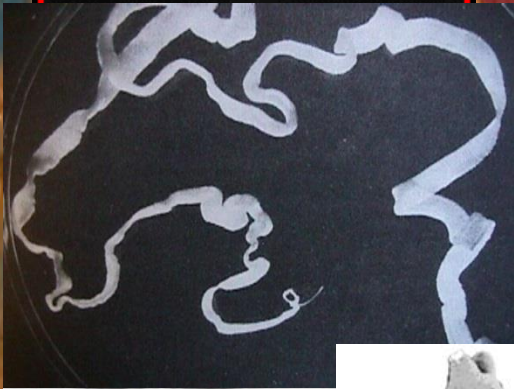
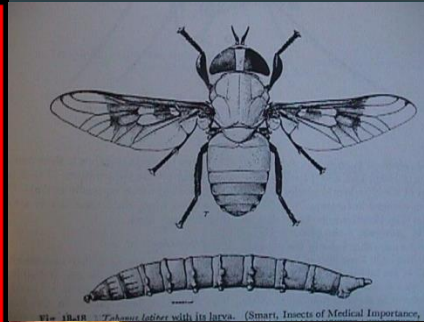
dobson@princeton.edu

Cymothoa exigua
in
rose spotted snapper

There are some really,
really cool
parasites
out
there



Parasitology



Happy Birthday...Chuck!!



CHARLES DARWIN



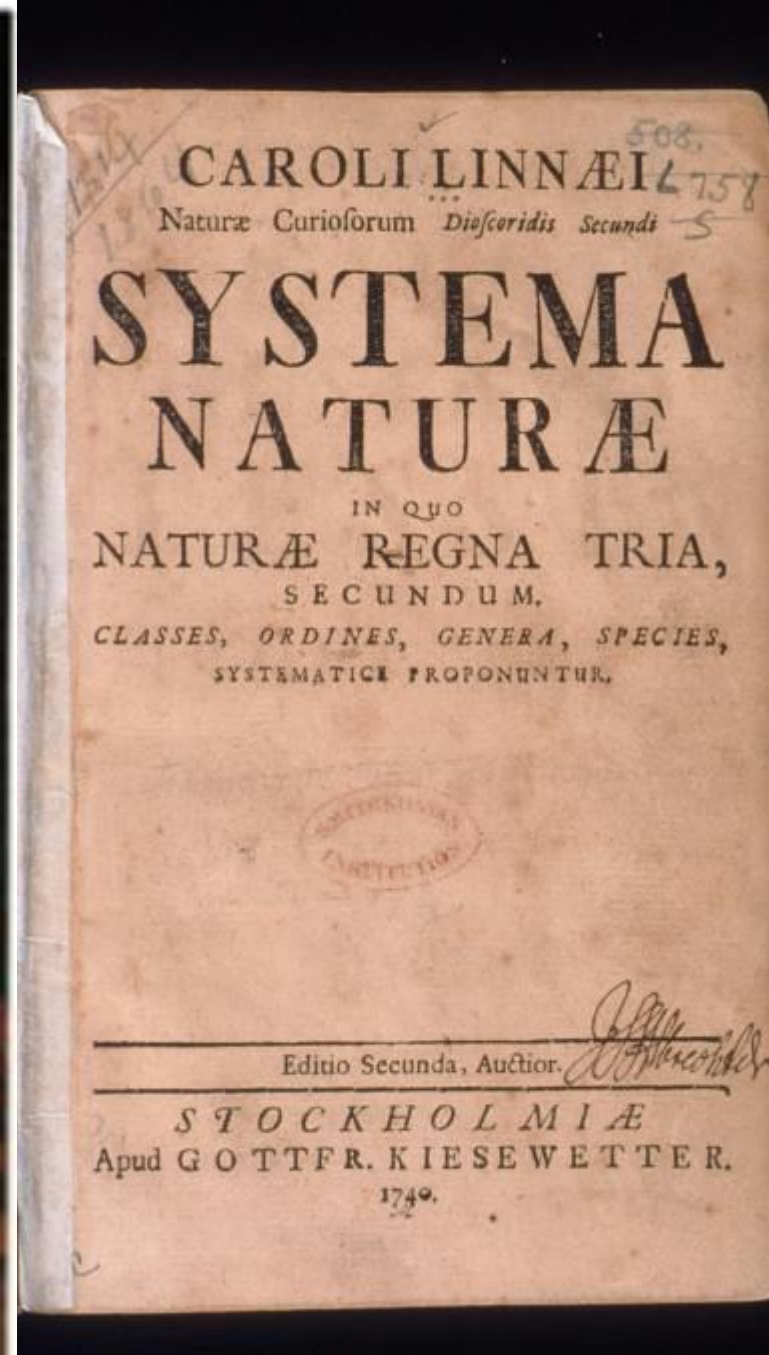
"Punch"
Dec 26, 1881.

Charles Robert Darwin.
Born, February 12, 1809. Died, April 19, 1882.
A strenuous power over Nature's plan.
Calm tracker of her steps, heri, watchful, wise;
Banner of the long Descent of Man,
And a most living witness of his rise;
Long live his life-work may the light be bright,
Yet leave him still a leading light of Thought.



Outline

- How many species are there?
- How many parasitic species are there?
- The population dynamics of one very special macroparasitic worm....
- Is there any good news?



REGNUM ANIMALE.

VI VERMES

Corporate Mafiosi in una parte del nostro sistema giudiziario.

Tedeschi	Il loro governo, secondo gli americani, è un governo di guerra.	Il loro governo, secondo gli americani, è un governo di guerra.
ITALIANI		
Roma	Il loro governo, secondo gli americani, è un governo di guerra.	Il loro governo, secondo gli americani, è un governo di guerra.
Laurea	Il loro governo, secondo gli americani, è un governo di guerra.	Il loro governo, secondo gli americani, è un governo di guerra.
Angelo	Il loro governo, secondo gli americani, è un governo di guerra.	Il loro governo, secondo gli americani, è un governo di guerra.

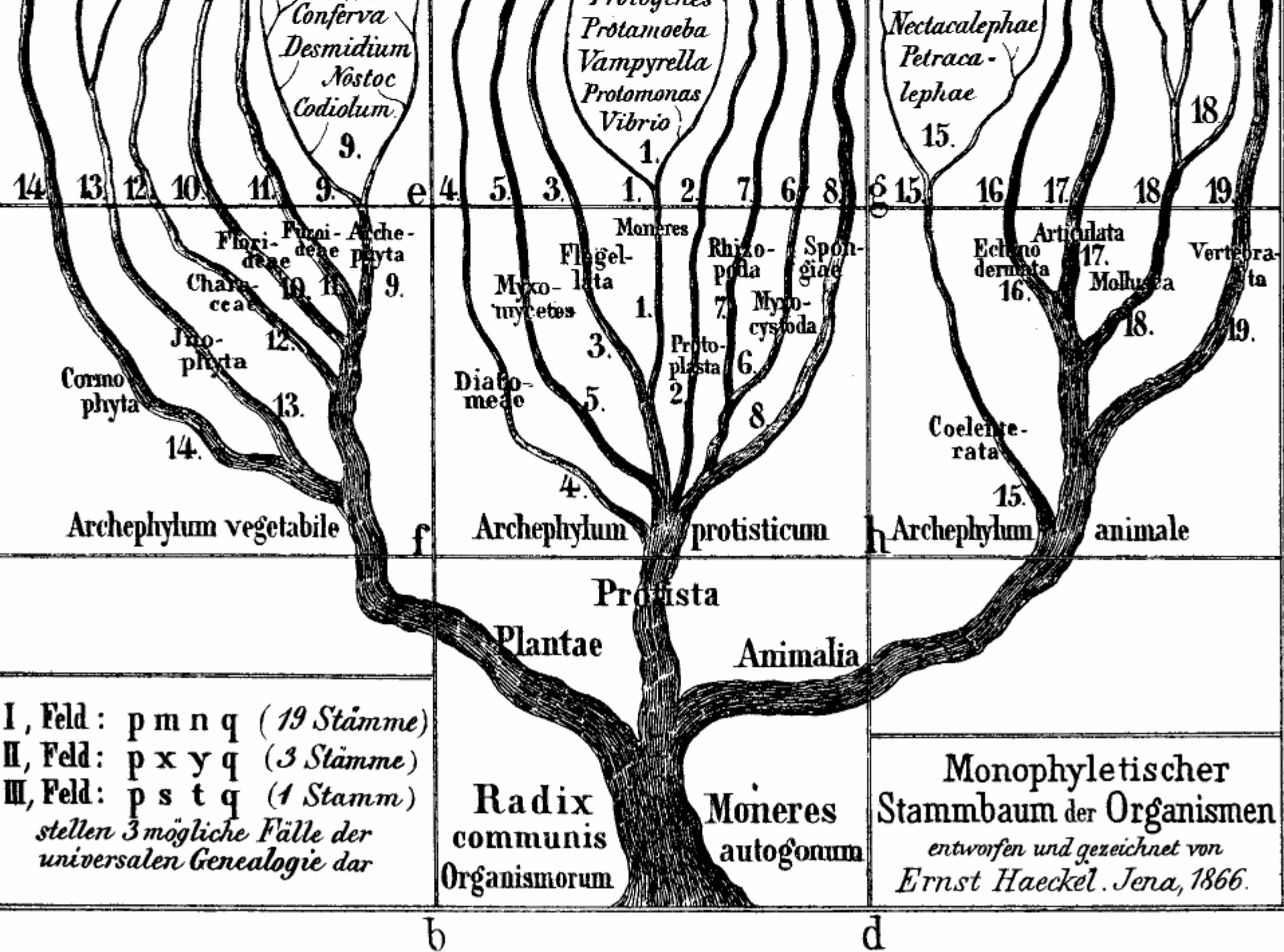
Ammonizione: Chi non conosce l'italiano non può leggere il Corriere. In tutti i casi il Corriere, che viene pubblicato in Italia, è un giornale di guerra, secondo gli americani, è un governo di guerra.

PARADOXA

Il loro governo, secondo gli americani, è un governo di guerra.

[illegible]

Order	Family	Genus	Species	Notes
Mammalia	Primates	Cercopithecidae	<i>Alouatta palliata</i> , <i>Macaca mulatta</i> , <i>Presbytis pardalis</i>	Old world monkeys
		Hominoidea	<i>Homo sapiens</i> , <i>Pongo pygmaeus</i> , <i>Gorilla gorilla</i>	Great apes
		Prosimii	<i>Loris oryx</i> , <i>Galago senegalensis</i> , <i>Leontideus rosalia</i>	Small primates
		Platyrrhini	<i>Alouatta palliata</i> , <i>Leontideus rosalia</i> , <i>Platyrrhinus latifrons</i>	New world monkeys
		Cynoidea	<i>Canis lupus</i> , <i>Ursus arctos</i> , <i>Vulpes vulpes</i>	Carnivores
		Carnivora	<i>Felis concolor</i> , <i>Canis lupus</i> , <i>Ursus arctos</i>	Carnivores
		Carnivora	<i>Felis concolor</i> , <i>Canis lupus</i> , <i>Ursus arctos</i>	Carnivores
		Carnivora	<i>Felis concolor</i> , <i>Canis lupus</i> , <i>Ursus arctos</i>	Carnivores
		Carnivora	<i>Felis concolor</i> , <i>Canis lupus</i> , <i>Ursus arctos</i>	Carnivores
		Carnivora	<i>Felis concolor</i> , <i>Canis lupus</i> , <i>Ursus arctos</i>	Carnivores
Mammalia	Rodentia	Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
Mammalia	Carnivora	Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
Mammalia	Carnivora	Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents
		Citellidae	<i>Citellus richardsoni</i> , <i>Peromyscus maniculatus</i>	Small rodents
		Sciuridae	<i>Sciurus hudsonicus</i> , <i>Uta stansburiana</i>	Small rodents



insight review articles

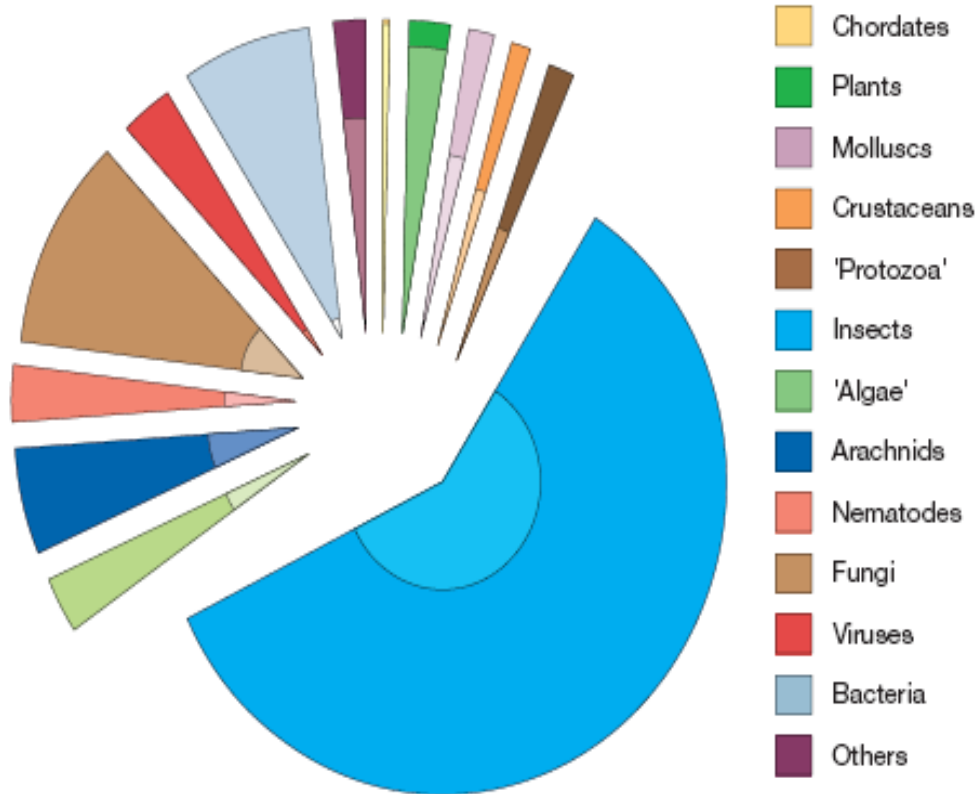
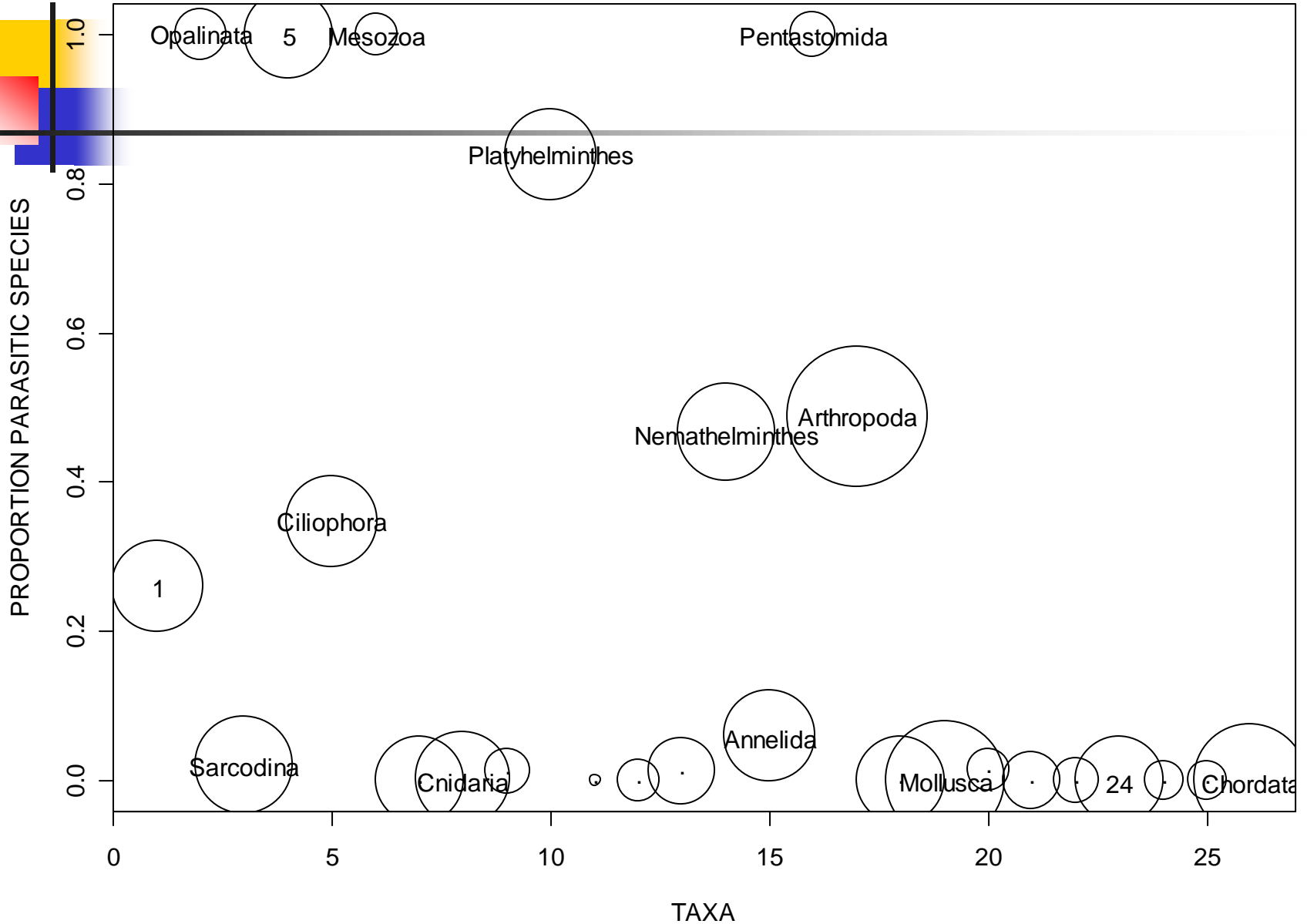


Figure 4 Species richness in major groups of organisms. The main 'pie' shows the species estimated to exist in each group; the hatched area within each slice shows the proportion that have been formally described. Data from ref. 7.

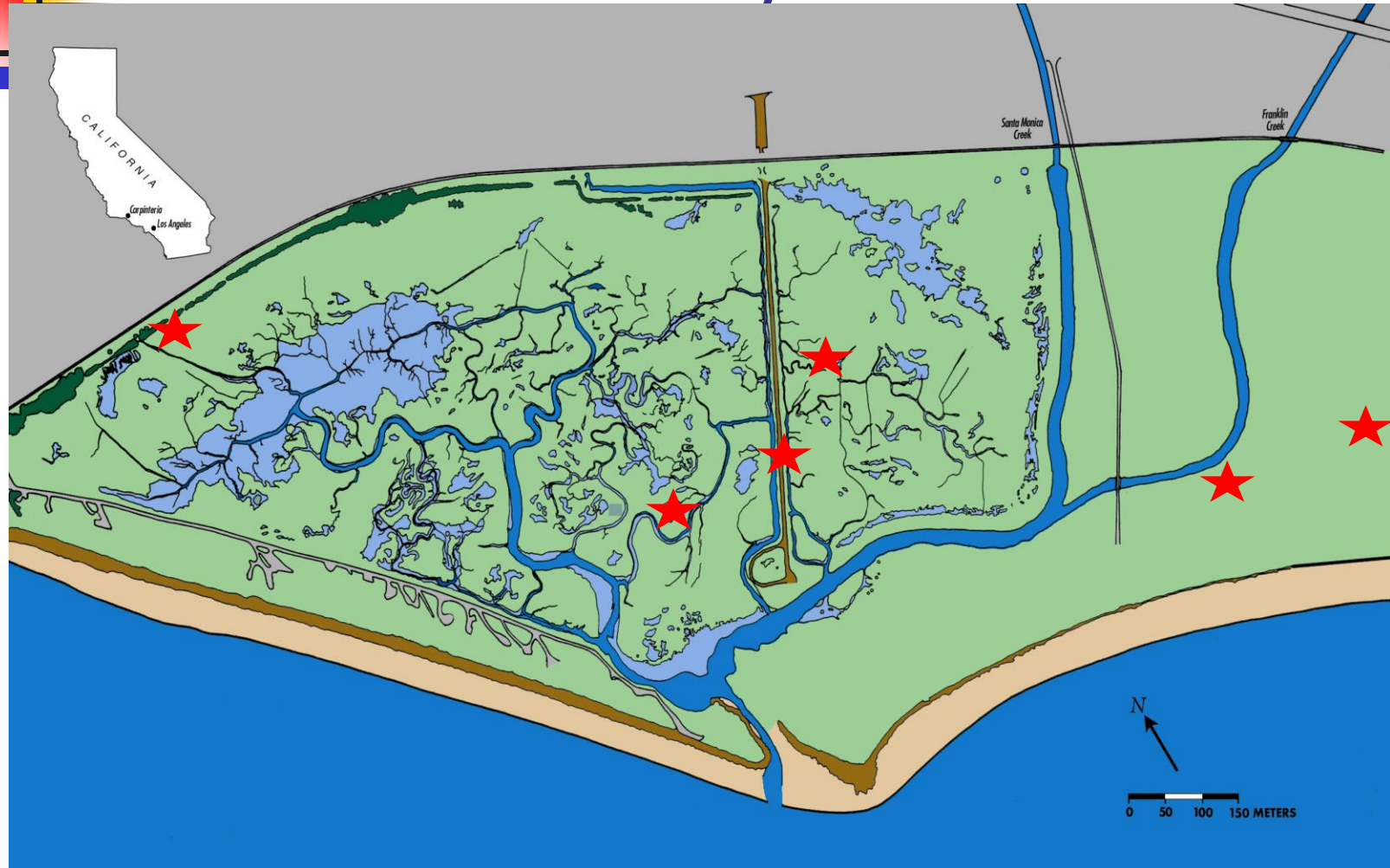
Getting the measure of Biodiversity
Andy Purvis and Andy Hector,
Nature 405, May 2000.

Phylogenetic distribution of parasitism



How much biodiversity is there in a tidal marsh??

Carpinteria Salt Marsh Santa Barbara County CA USA



(Work with Kevin Lafferty, Armand Kuris, and UCSB/NIH/NSF Saltmarsh Parasite Project



UCSB
Salt marsh
Parasite food-web
Team in action.





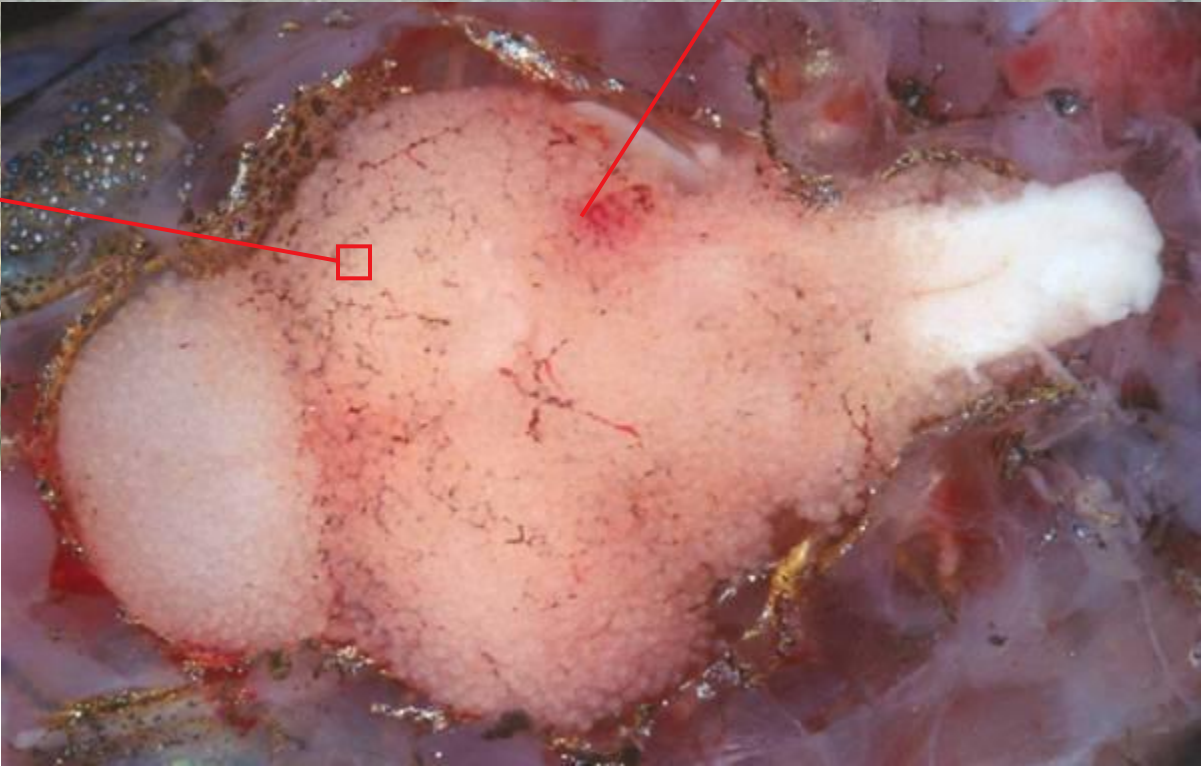
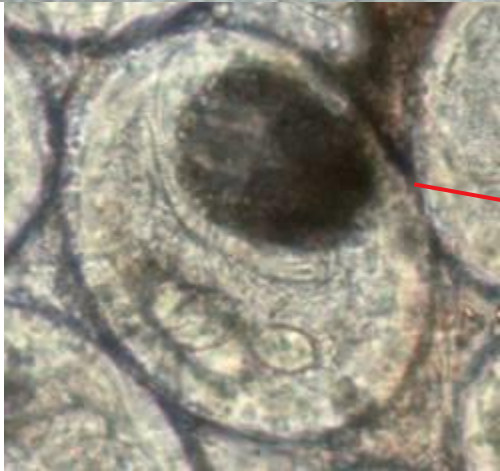
All trematodes identified to species



Digenean cercariae



Euhaplorchis californiensis metacercariae coat the killifish's brain



**Lafferty and Morris 1996,
Ecology 77:1390-1397**

What do food webs look like?

Tertiary consumers

Primary/secondary consumers

Primary producers

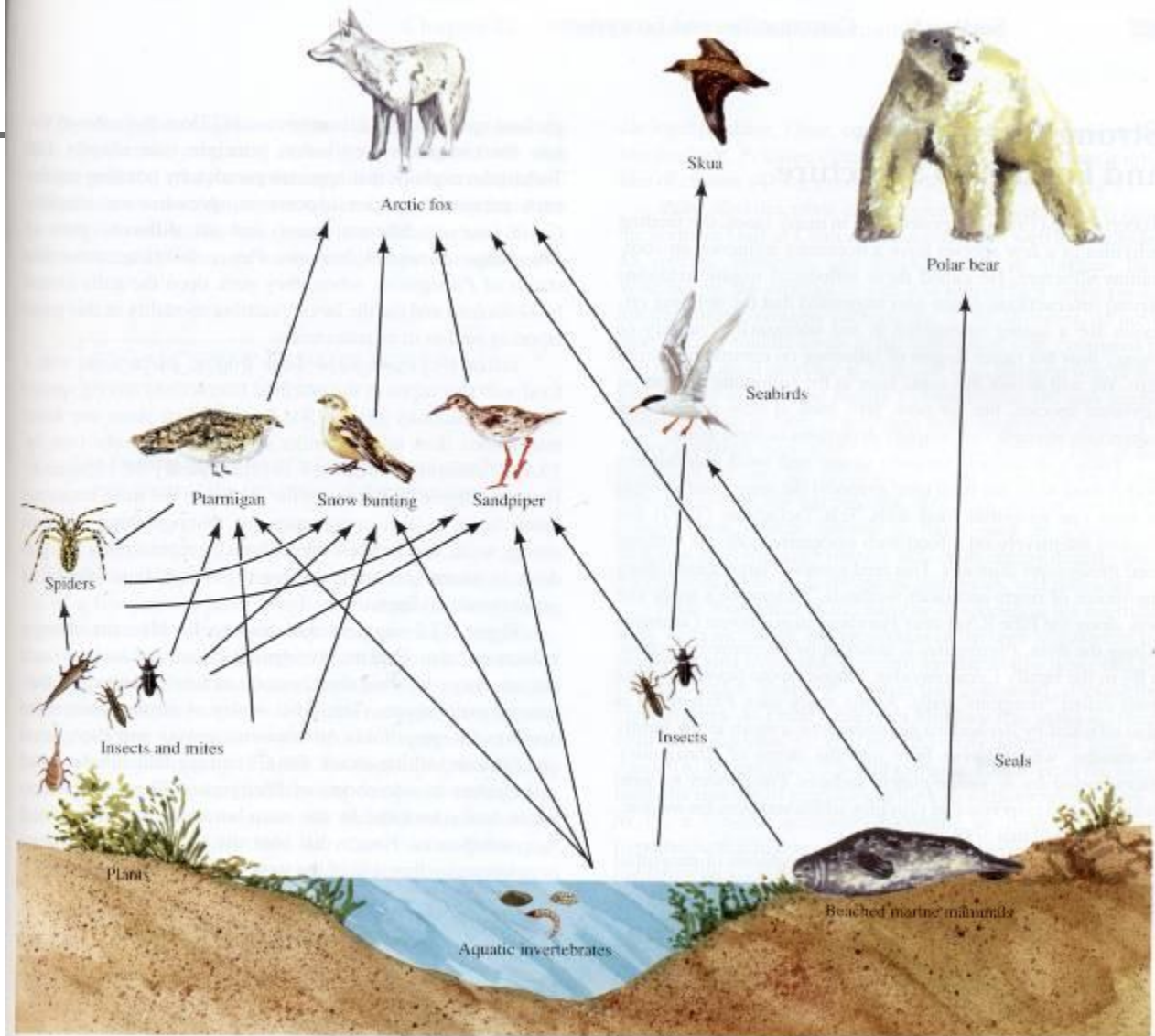
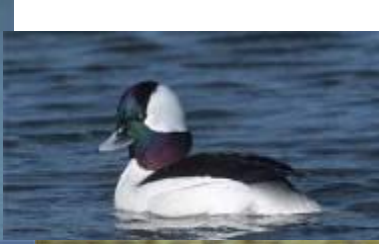
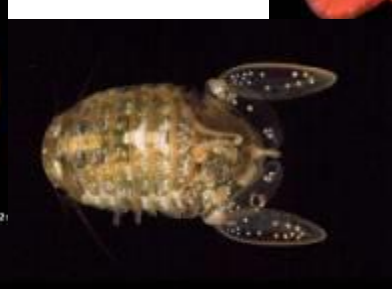
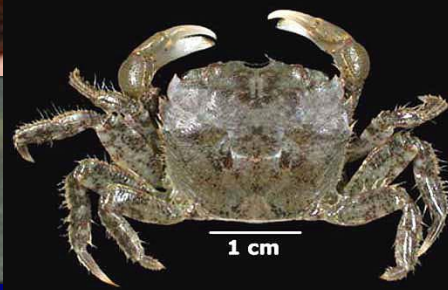


Figure 17.3 Simple food web of an Arctic island.



Peter LaTourrette





3 Coastal Wetlands



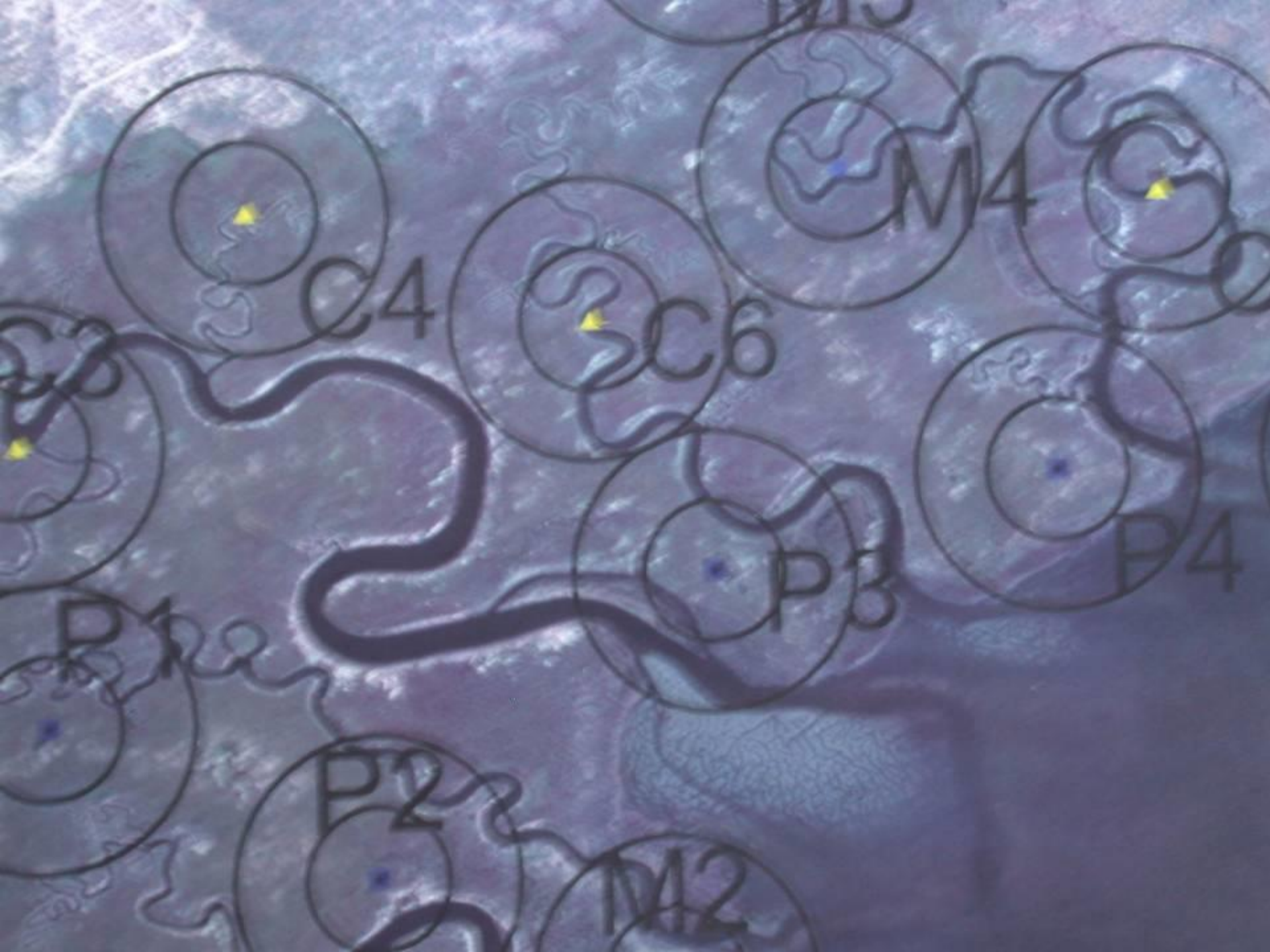
CSM – Carpinteria Salt Marsh



BSQ – Bahia San Quentin, Baja California



EPB – Estero de Punta Banda,
Baja California



Snail sampling at each site:

- 20 random quads
- Measure and count every snail

→ Density and Size-frequency distributions



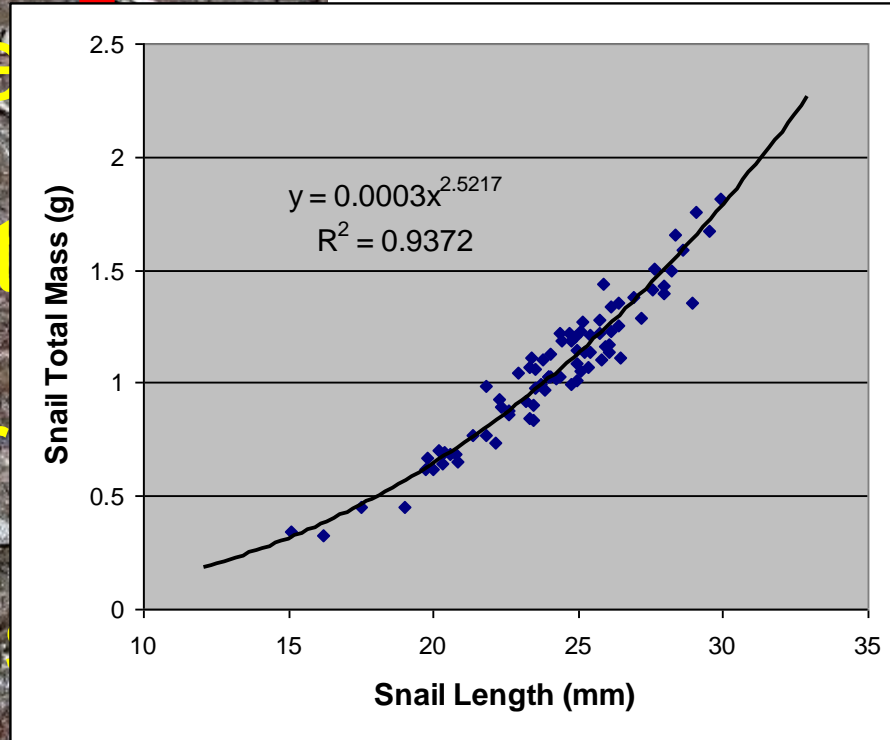
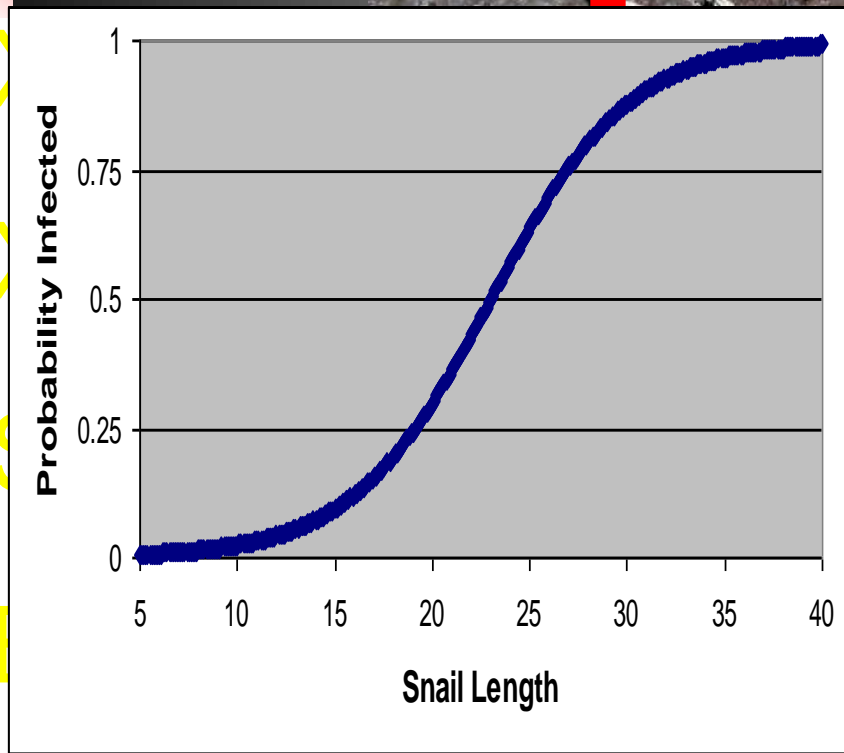
UCSB
Salt marsh
Parasite food-web
Team in action.



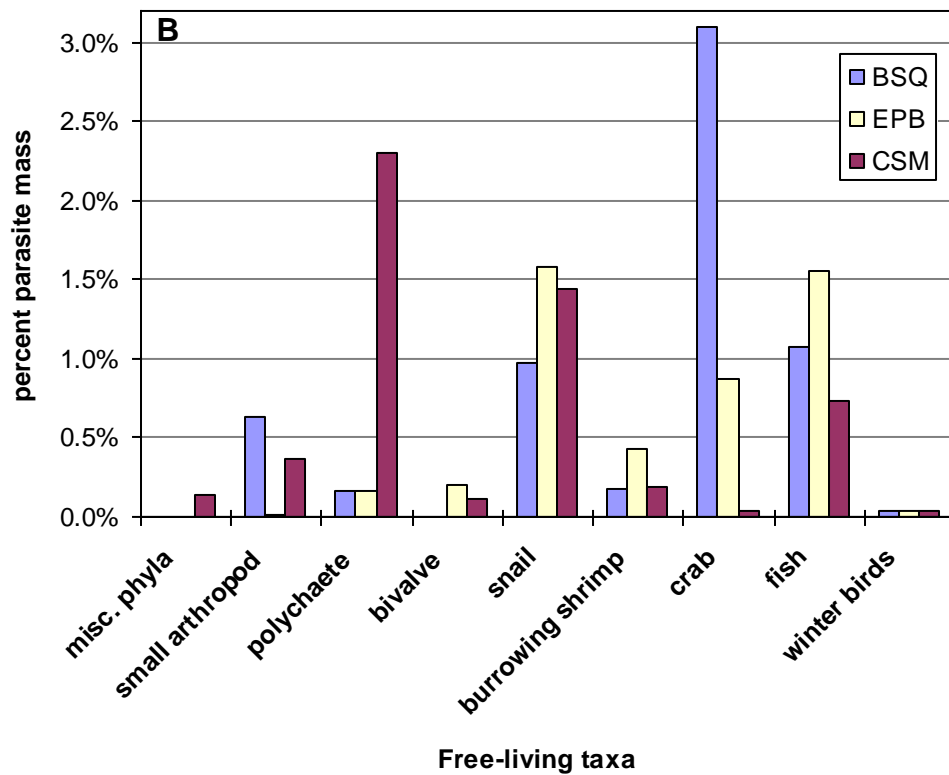
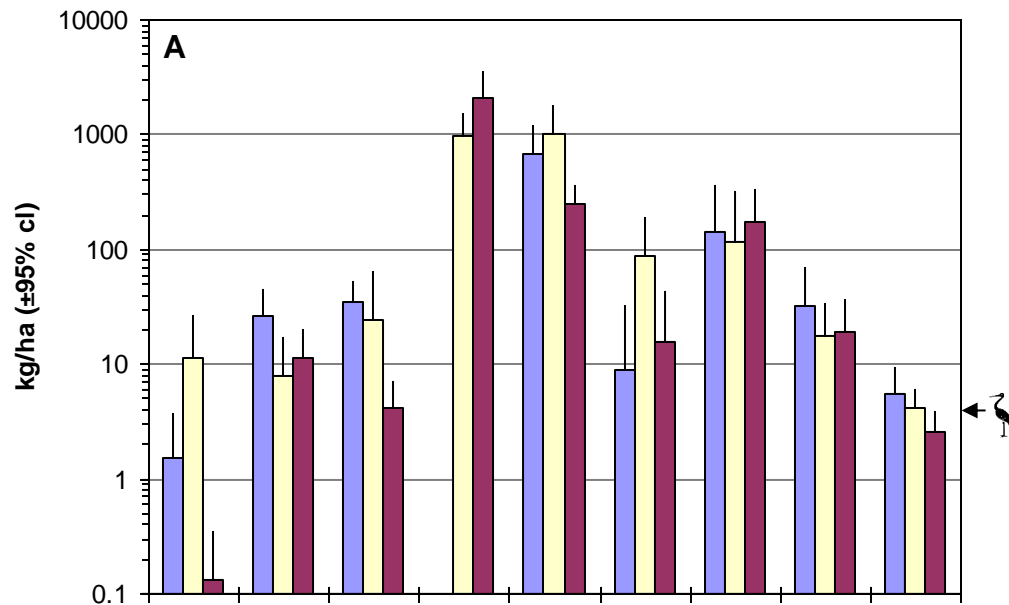
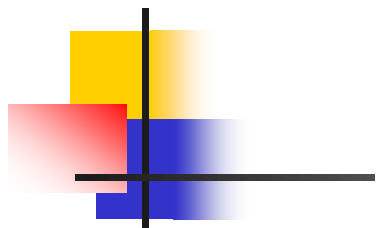


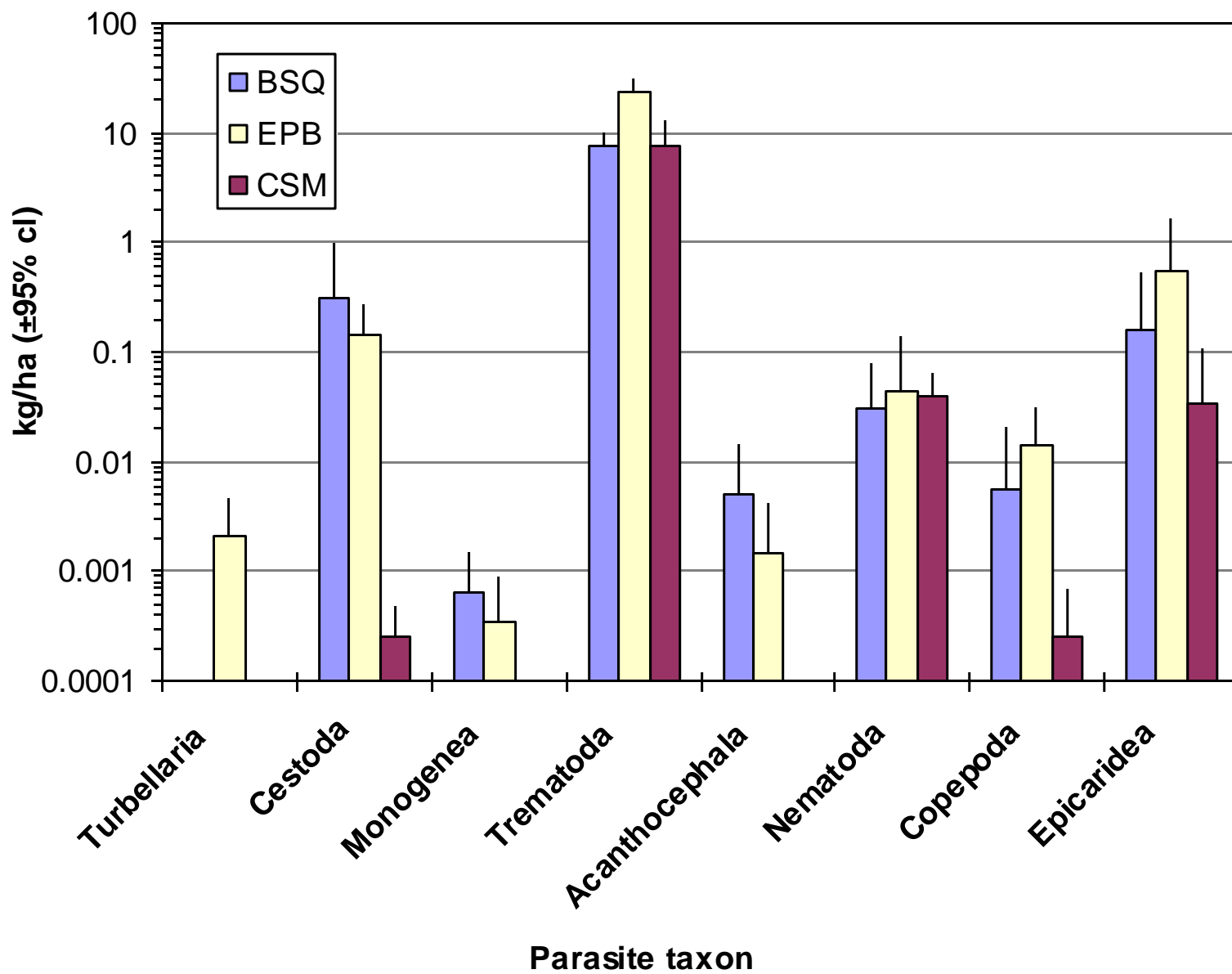
How to calculate biomass?

(individual snail length)

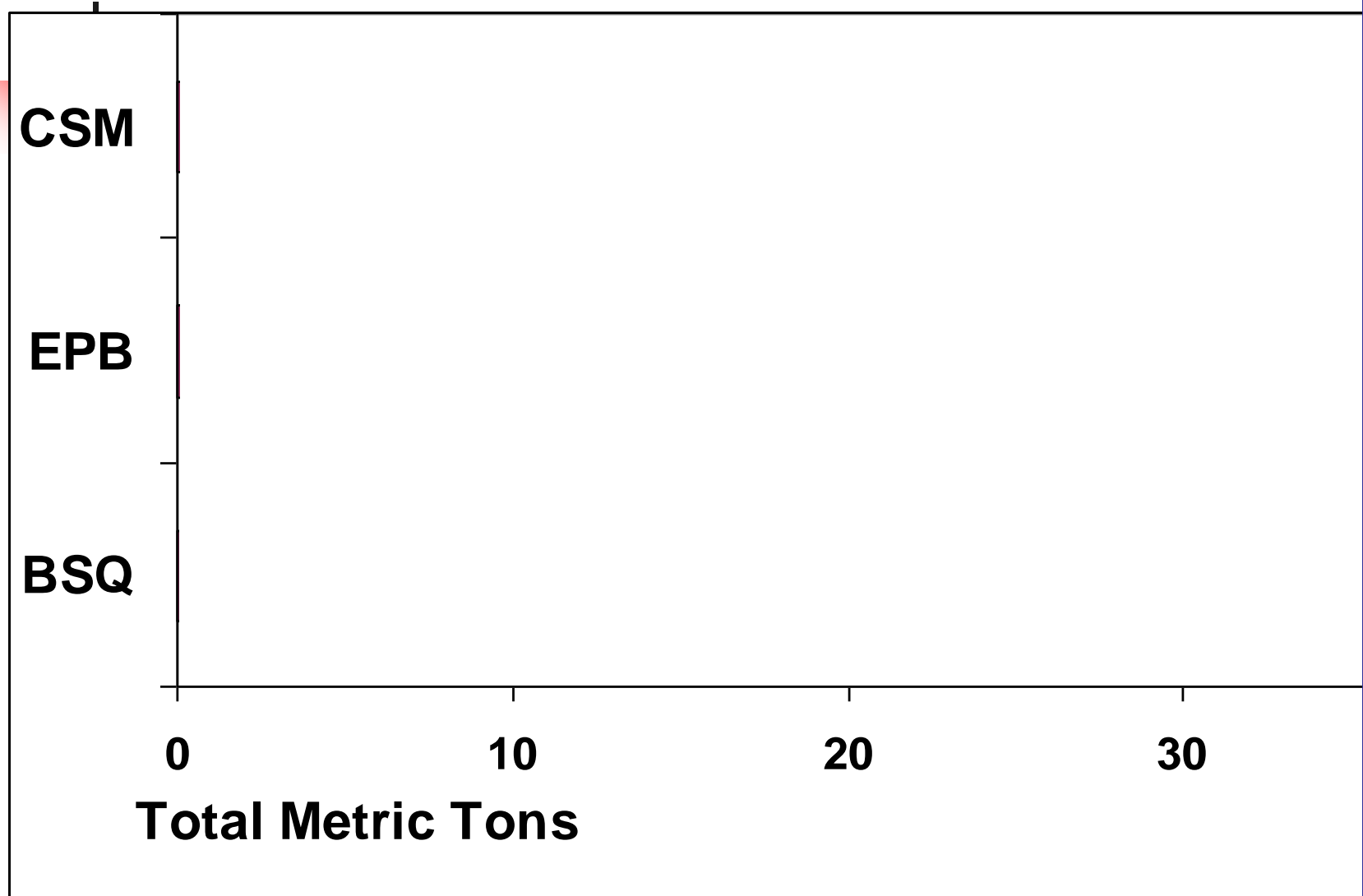


Determine mass density for each habitat type by averaging across sites

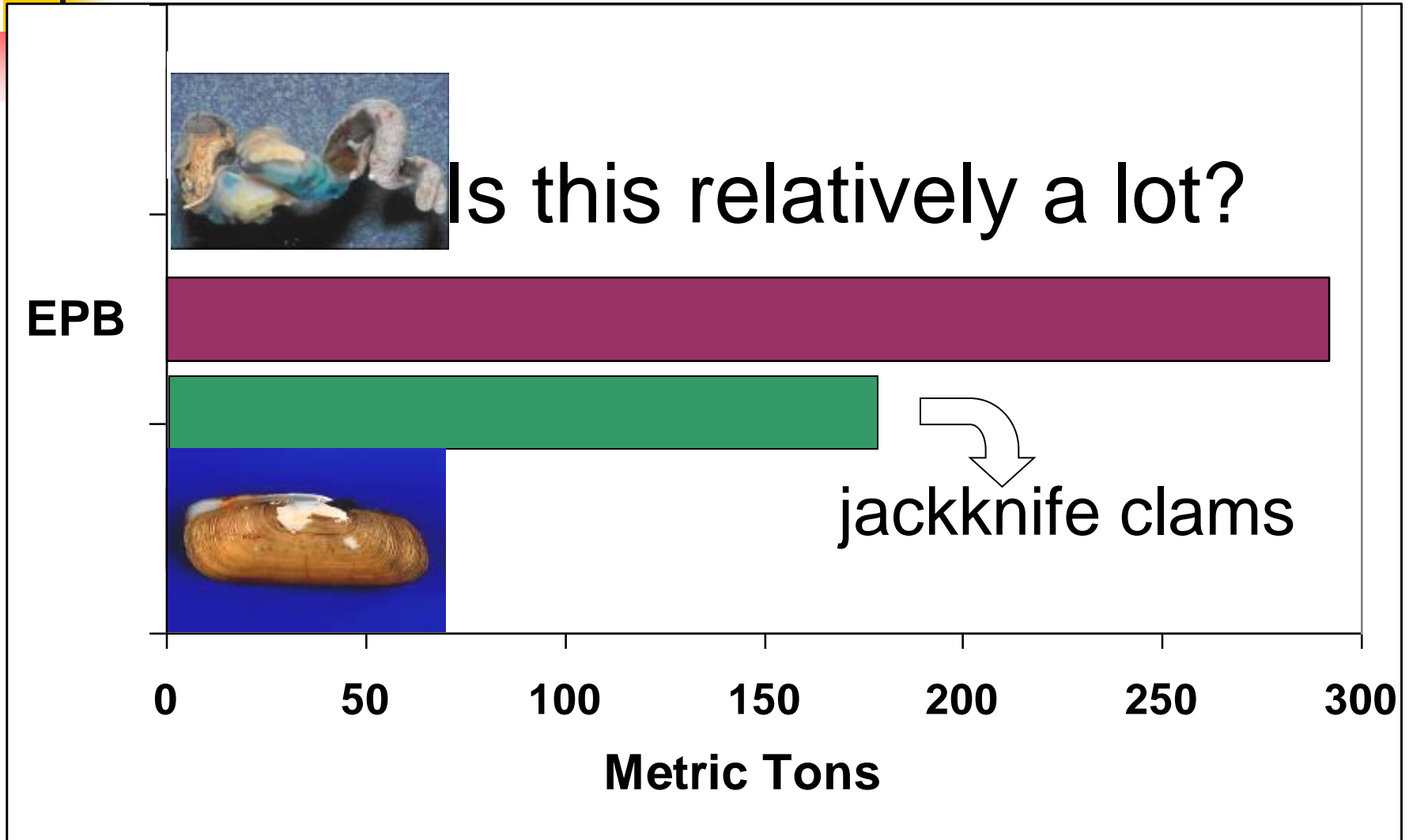


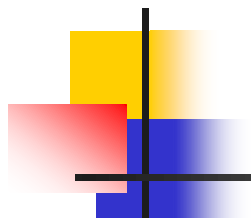


Total Parasite Snail Biomass



Total Parasite Snail Biomass





But, is that biomass a lot?

What's a metric ton?

Express in units we can all identify with

→ Convert biomass to numbers of people

The Armand Kuris

~75 kg



CSM 97 x



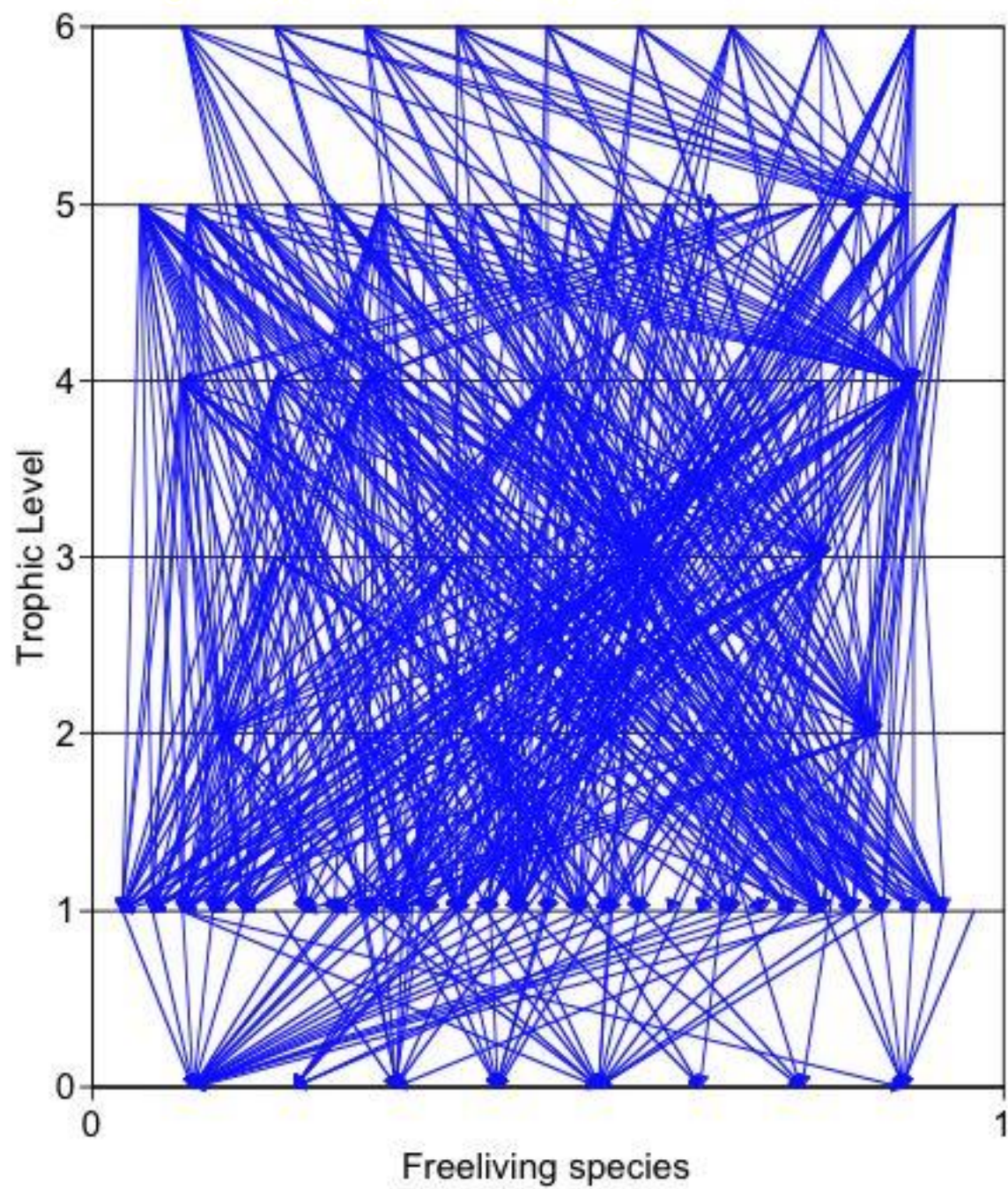
EPB 3,891 x

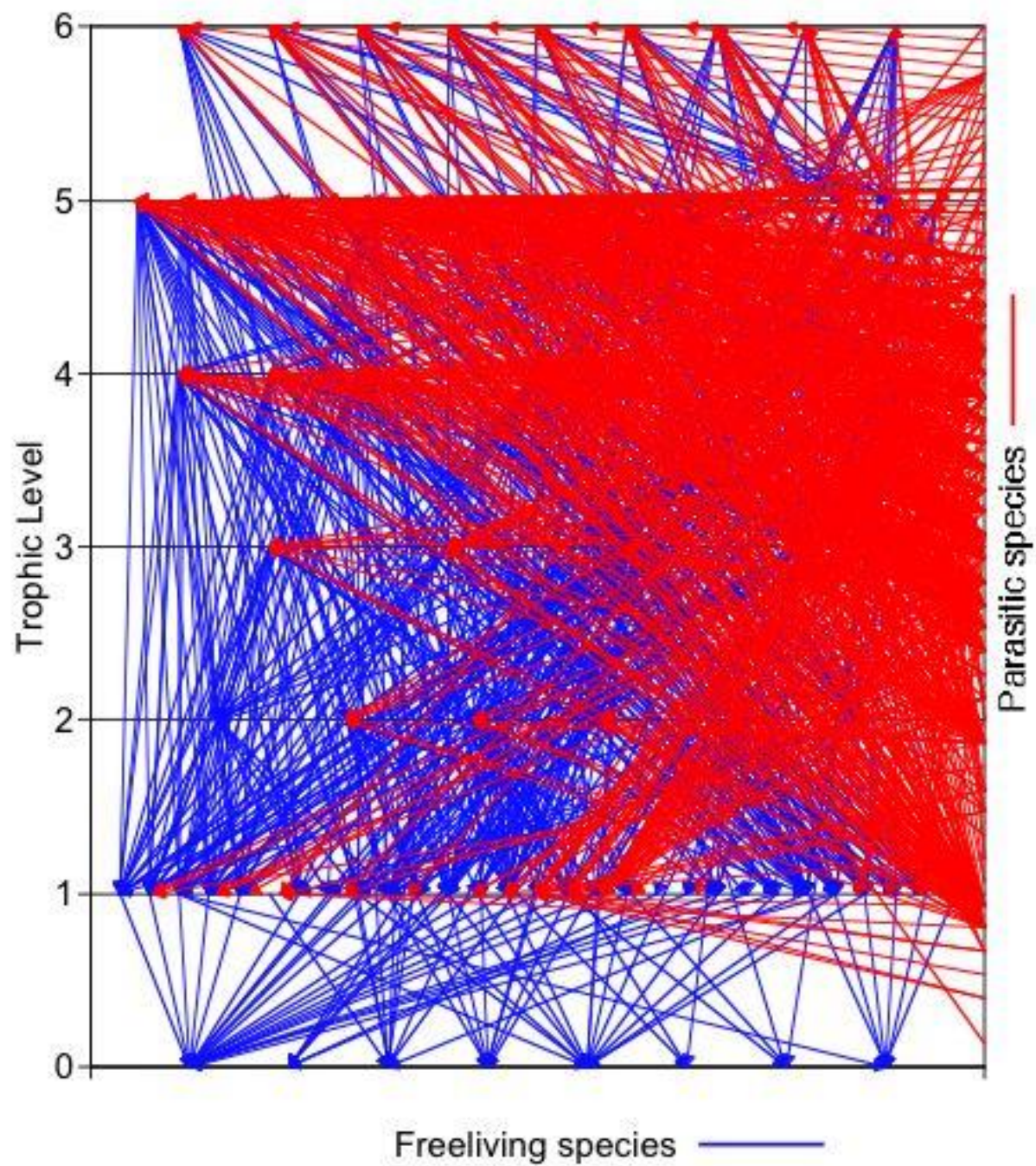


BSQ 373 x

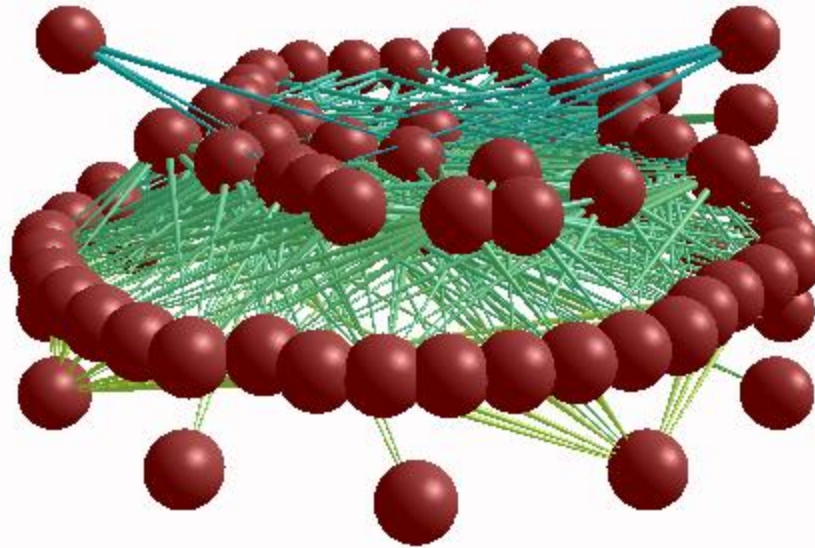
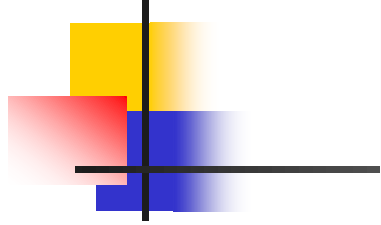




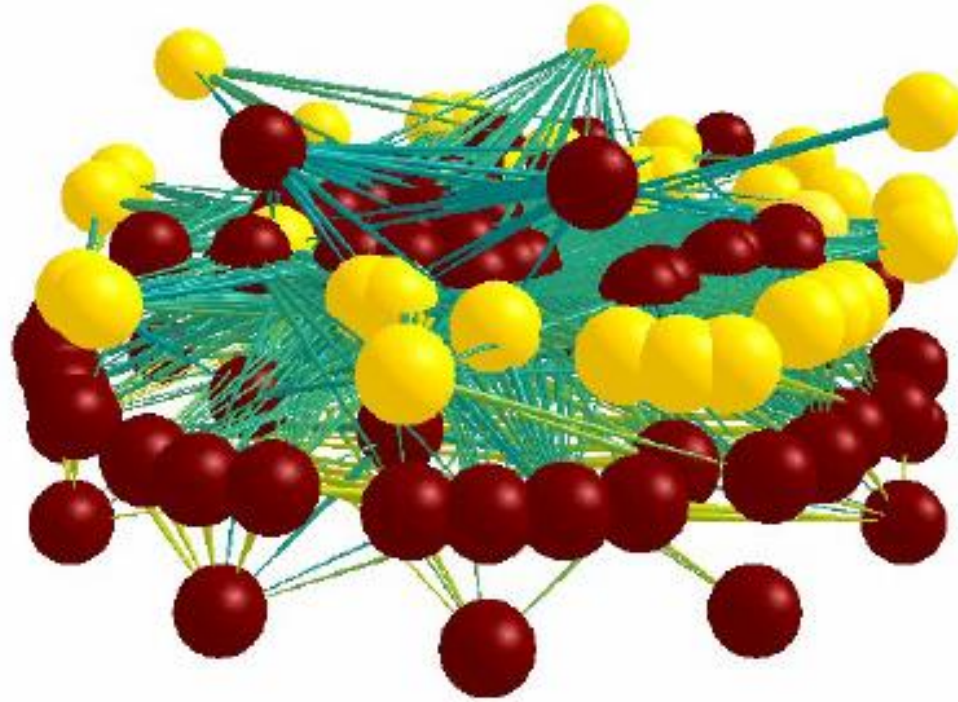
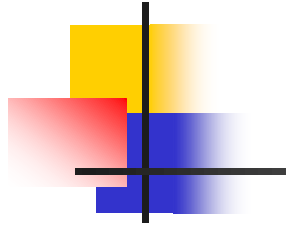




Carpinteria free-living species web

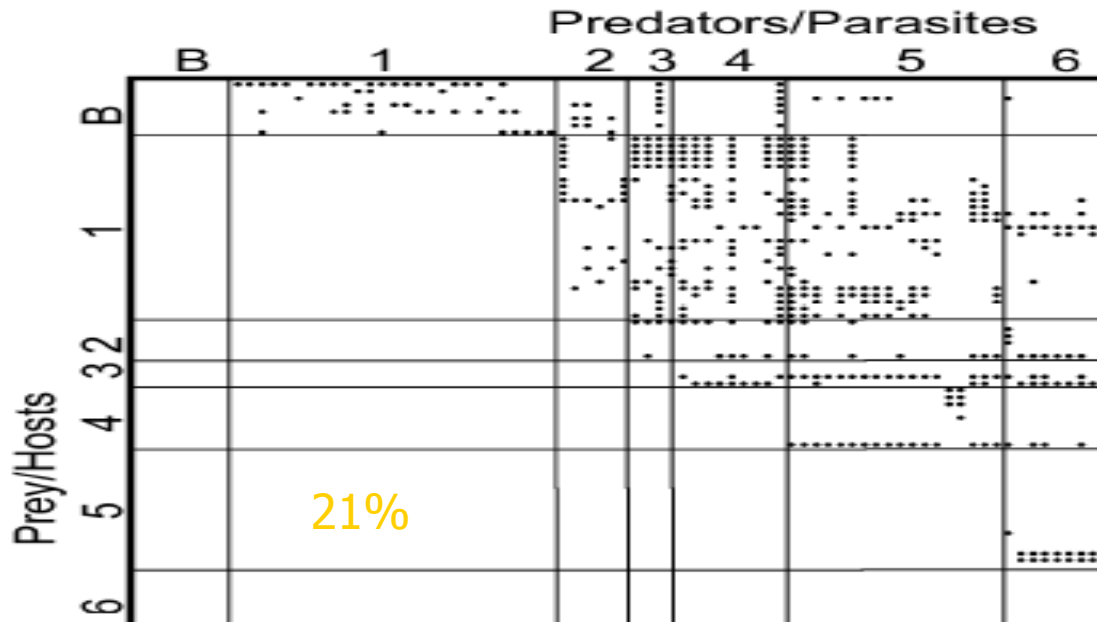


Carpinteria complete species web

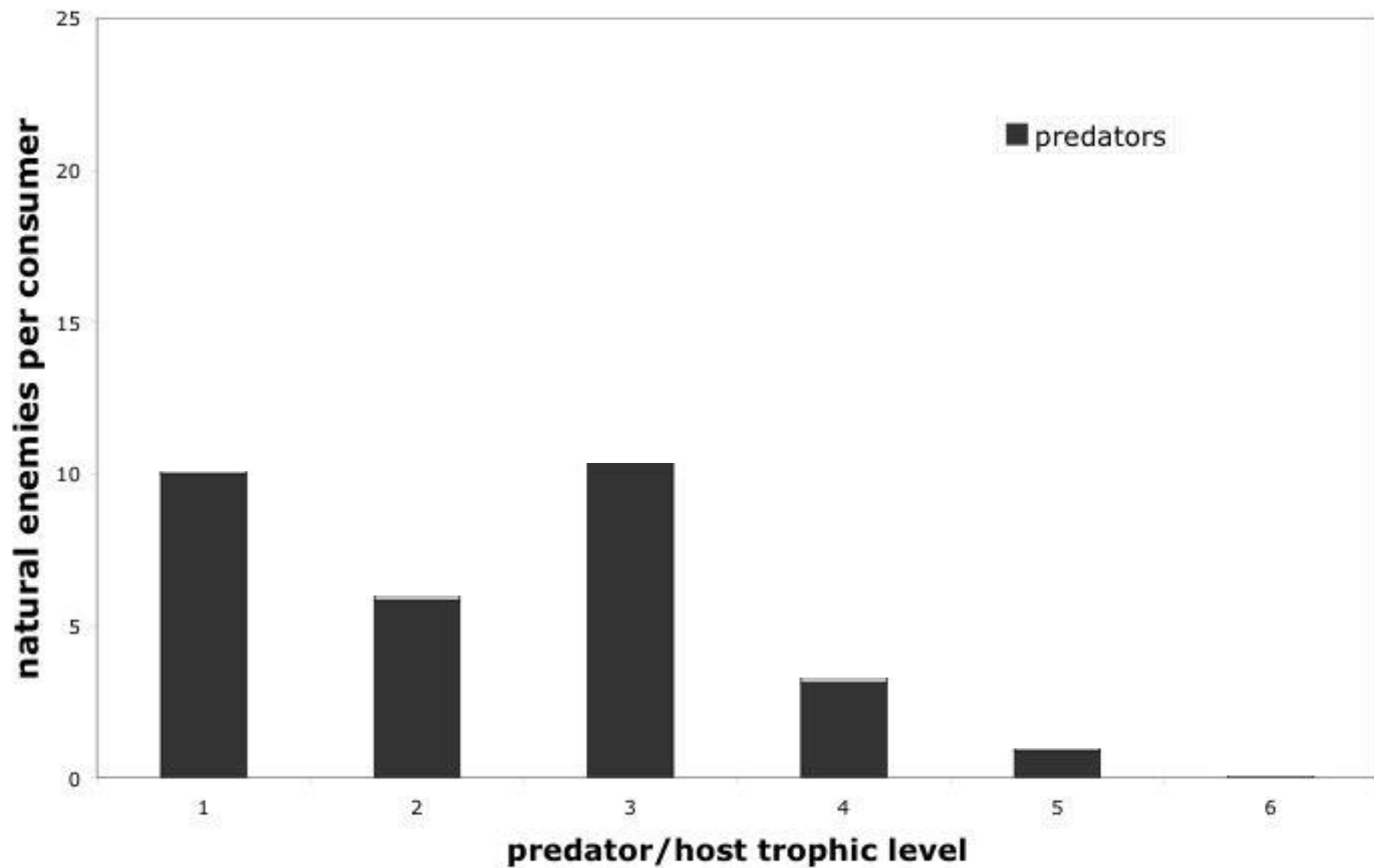


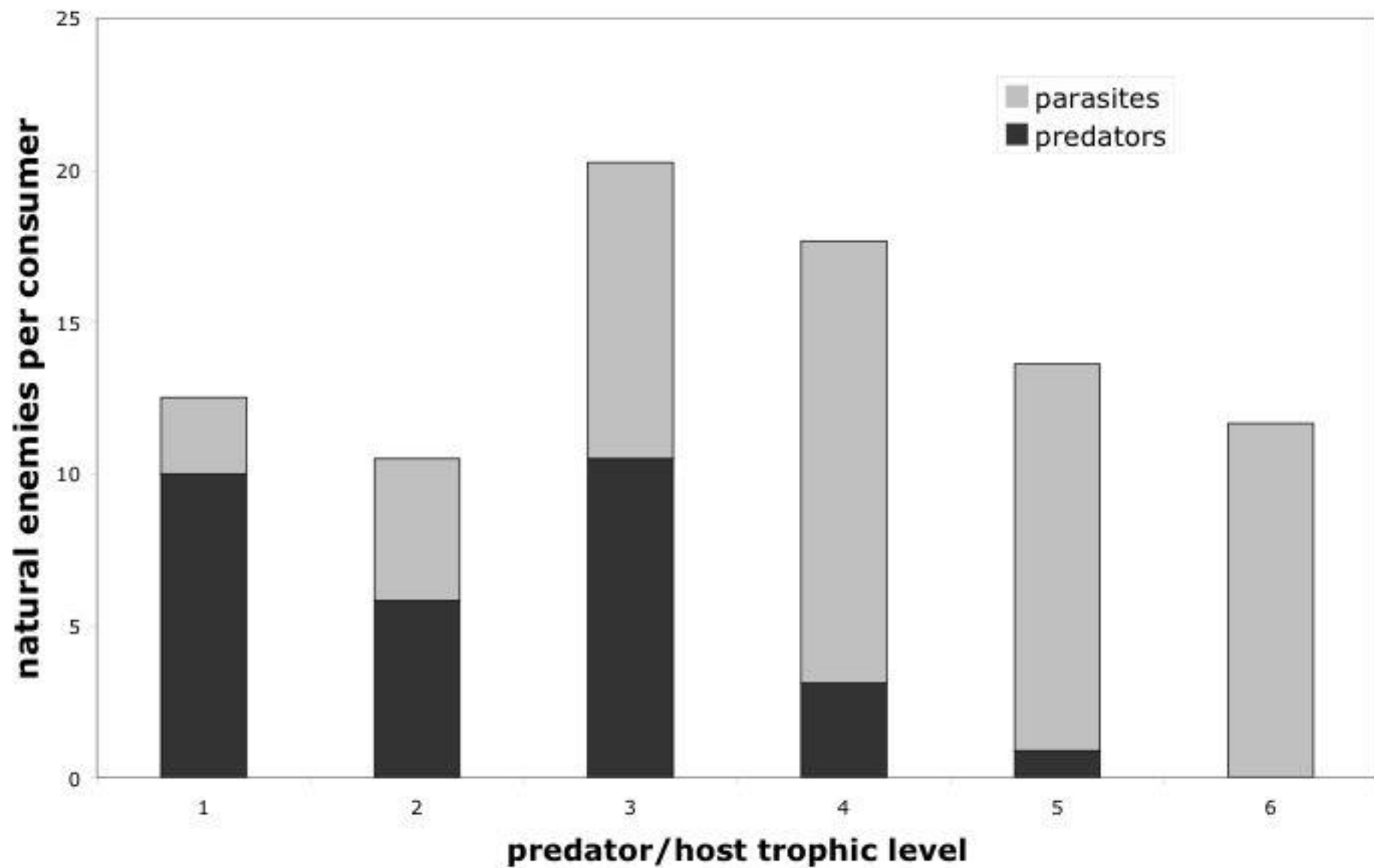
Yellow balls are parasitic species

Carpinteria Salt marsh food web



Species along the top consume those arranged along the left edge





Genomic analyses of sediment in almost the same salt marsh

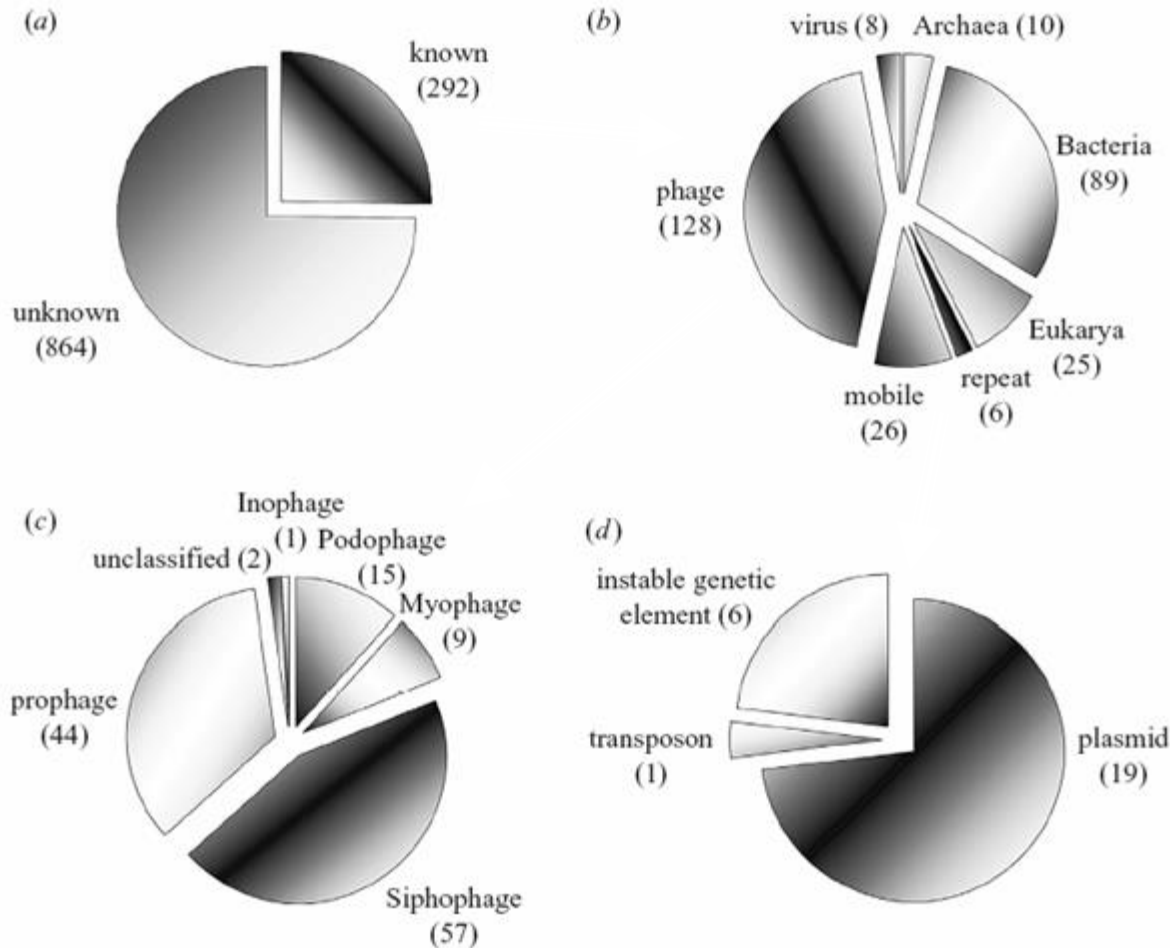


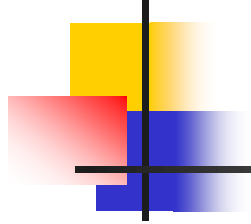
Figure 1. Genomic overview of the uncultured sediment viral community from Mission Bay, CA, USA, based on sequence similarities. (a) Number of sequences with a significant hit (E -value < 0.001) to GenBank. (b) Distribution of significant hits among the major classes of biological entity. (c) Families of phage represented in the sediment library. (d) Types of mobile element identified in the library.

Diversity and population structure of a near-shore marine-sediment viral community

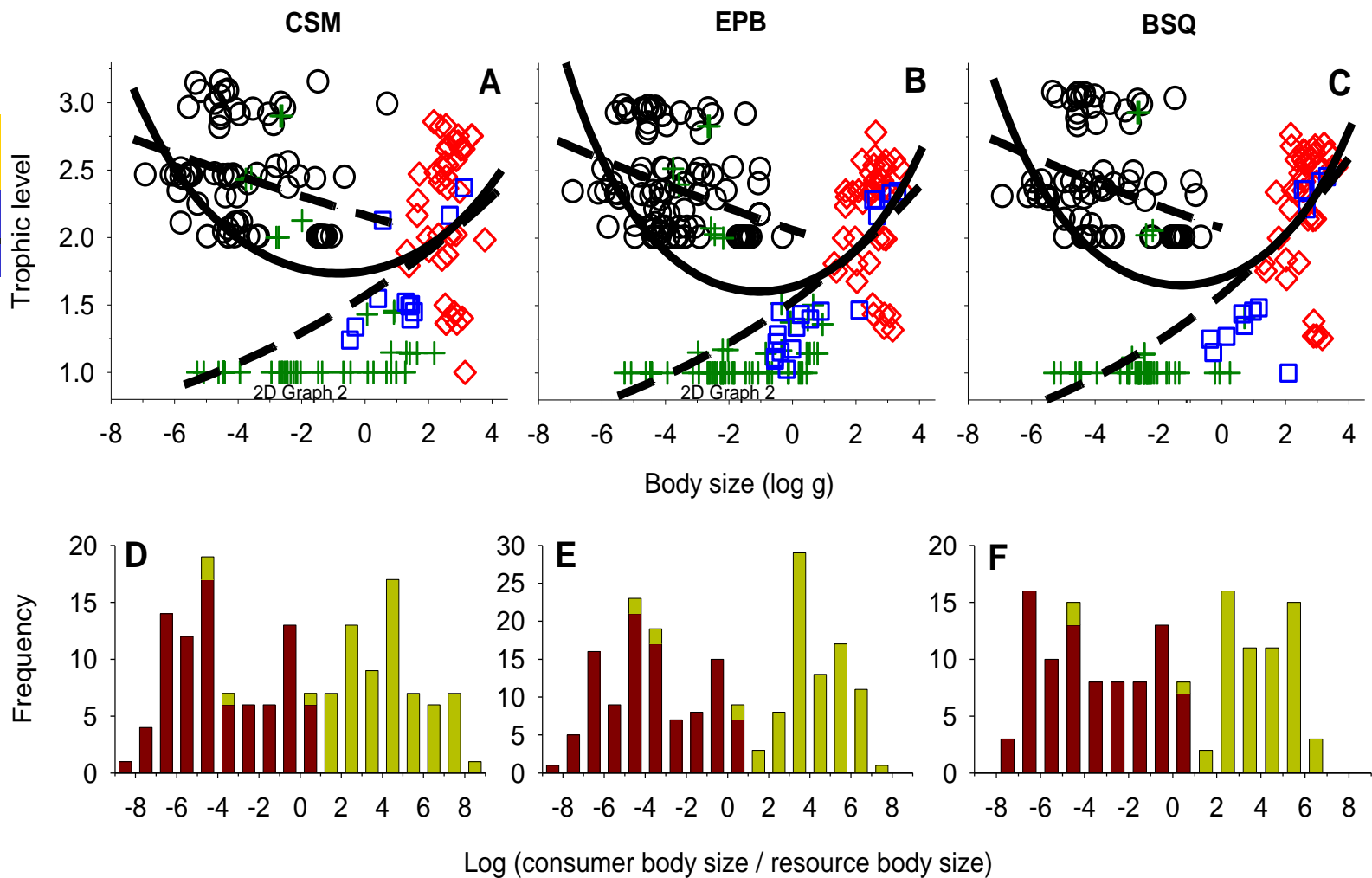
Proc. R. Soc. Lond. B (2004)

Mya Breitbart¹, Ben Felts², Scott Kelley¹, Joseph M. Mahaffy², James Nulton², Peter Salamon² and Forest Rohwer^{1,3*}

Creates a interesting set of huge questions



- How many species / taxa in marsh in total?
- What determines pattern of abundance?
- How do they all coexist?
- Questions that go back to MacArthur, May, and constant discussion in EEB & ESA to this day....



■ **Fig. 2. Variation in trophic level with body size and in consumer-resource body-size ratios for parasitic and free-living species in three estuarine food webs.**

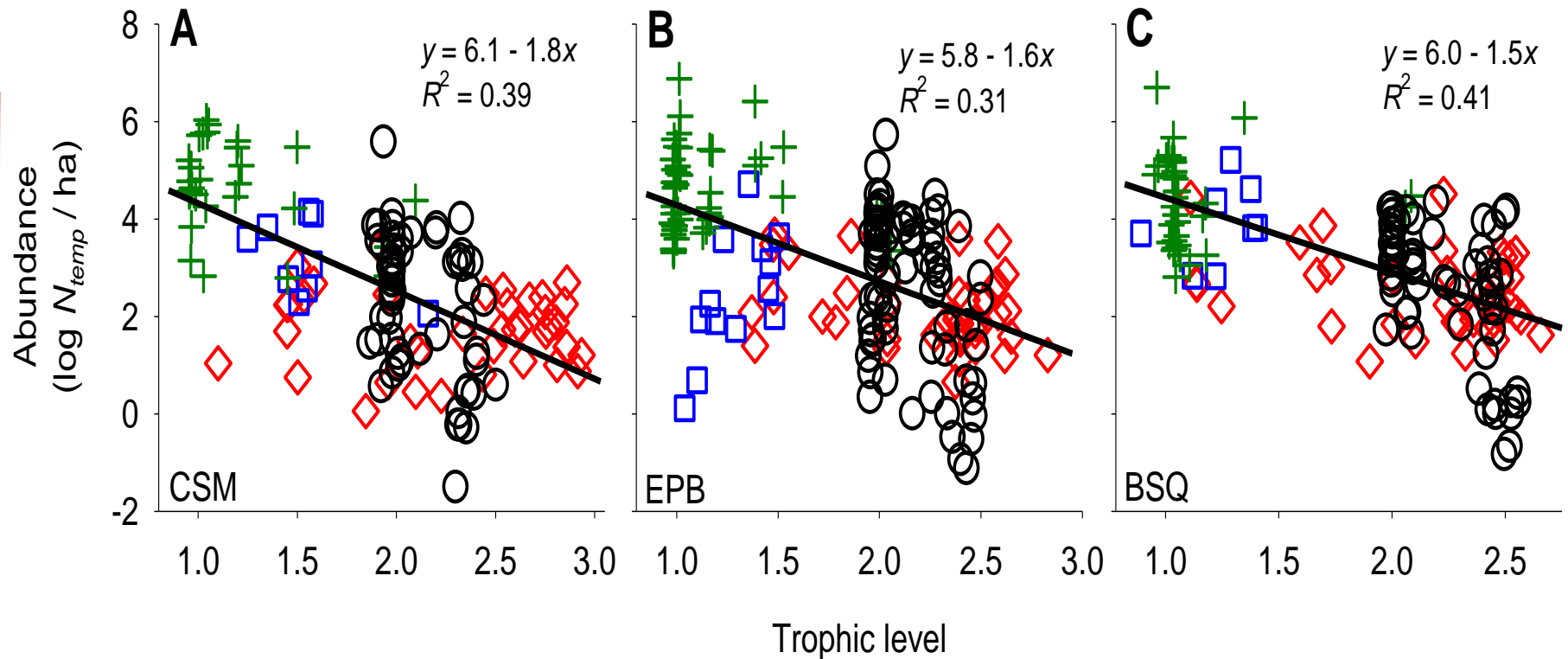


Fig 3. Abundance as a function of trophic-level for parasites and free-living species in three estuaries. (A-C)

Log₁₀ temperature-corrected abundance decreases with trophic level using a GLM (Tables S3, S4) to control for body size (holding constant the mean log₁₀ body size in each estuary, CSM: -0.83, EPB: -1.13, BSQ: -1.23). The anti-log of the slope provides an estimate of λ , the overall trophic transfer efficiency (TTE) in each ecosystem. Symbol key: parasite (○), invertebrate (+), fish (□), bird (◇).

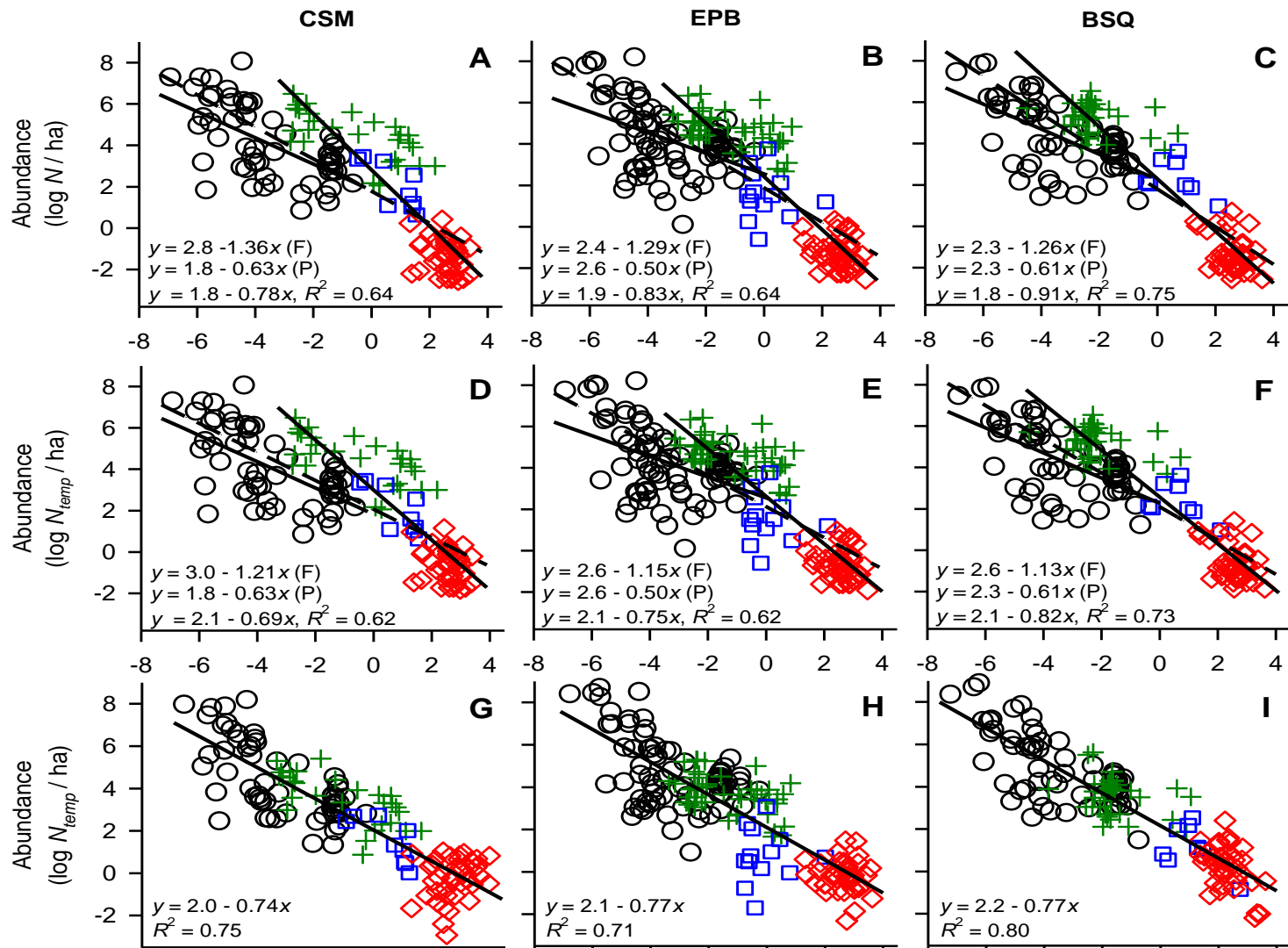


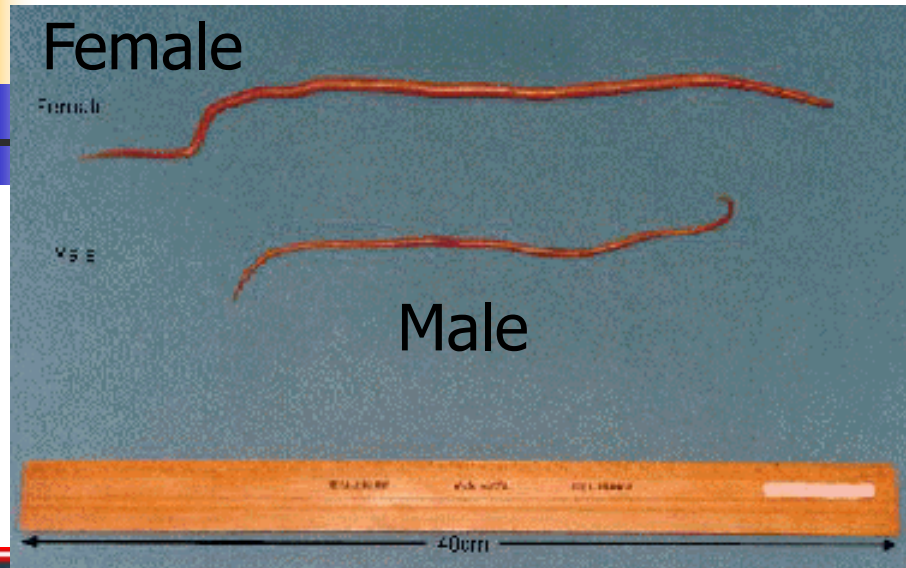
Fig 1. Abundance as a function of body-size, plotted on logarithmic axes, for parasites and free-living species in three estuaries.



Hookworms sink their teeth into the intestinal walls of more than a billion people every day to drink their fill of blood (500x magnification).

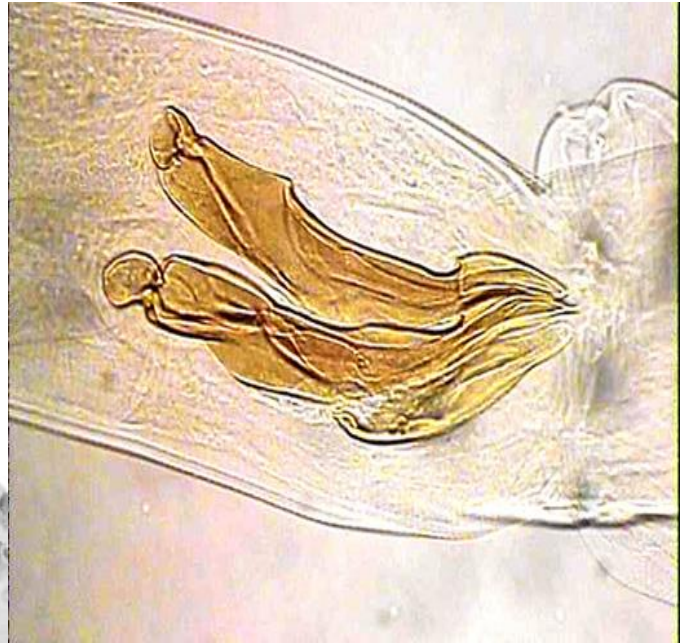
Do Parasites Rule the World?

Ascaris lumbricoides



Immunity is more subtle and transient....

Complex body structures that produce by-products.
Inhabit a variety of tissues and organs, internal and external
! Charismatic at all scales !





Parasitic helminths

- Nematodes – simple and complex life cycles
- Cestodes – always complex, sequential vertebrate & invertebrate hosts
- Trematodes – always complex, always a snail for asexual, then vertebrate, sometimes a second invertebrate
- Acanthocephalans – always complex, arthropod and vertebrate

Global Burden of Intestinal Nematode Infections



- How many people are infected globally?
- What impact does this have on them?
- How much has the situation changed in last 50 years?

M.-S. Chan (1997) *Parasitology Today*, 13, 438-443



This Wormy World....

Stoll, 1947 & Chan 1997

■ 1947

- Humans – 2.2×10^9
- 29% urban
- *Ascaris* 30%
- 644 million cases
- *T.trichura* 16%
- 355 million
- Hookworm 21%
- 457 million

■ 1997

- 5.6×10^9
- 45% urban
- 24%
- 1273 million cases
- 17%
- 902 million cases
- 24%
- 1277 million cases

The Worm gets the Bird.
Trichostrongylus tenuis and
red grouse

Andy Dobson and Peter Hudson

Parasite Ecology meets
Downton Abbey....!



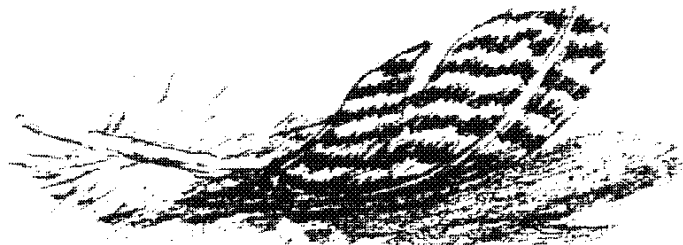
Dobson (Jnr) and Hudson (Snr)

Grouse Parasite Interactions

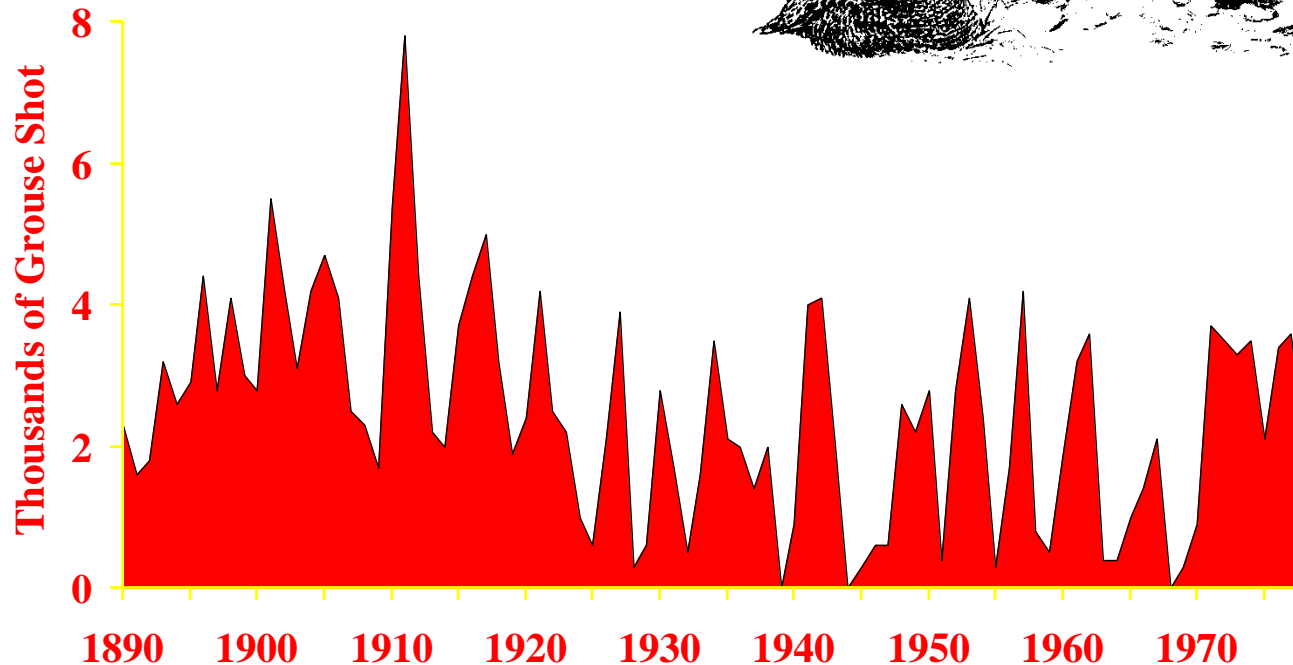
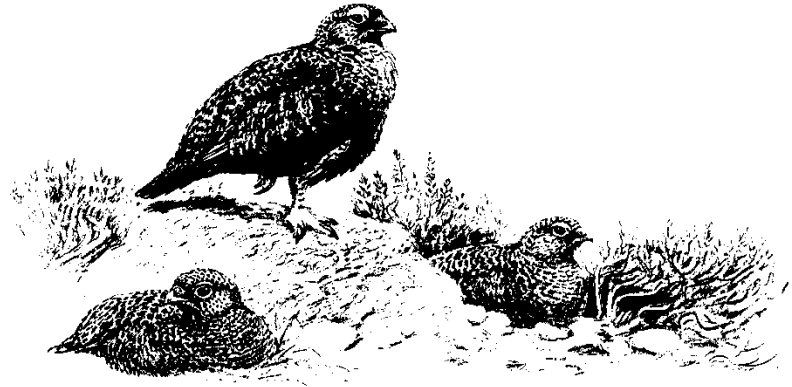
What are the consequences for population & community?

1. Individual level productivity
2. Population level dynamics
3. Community level interactions

Understanding ~ Monitoring Experiments & models



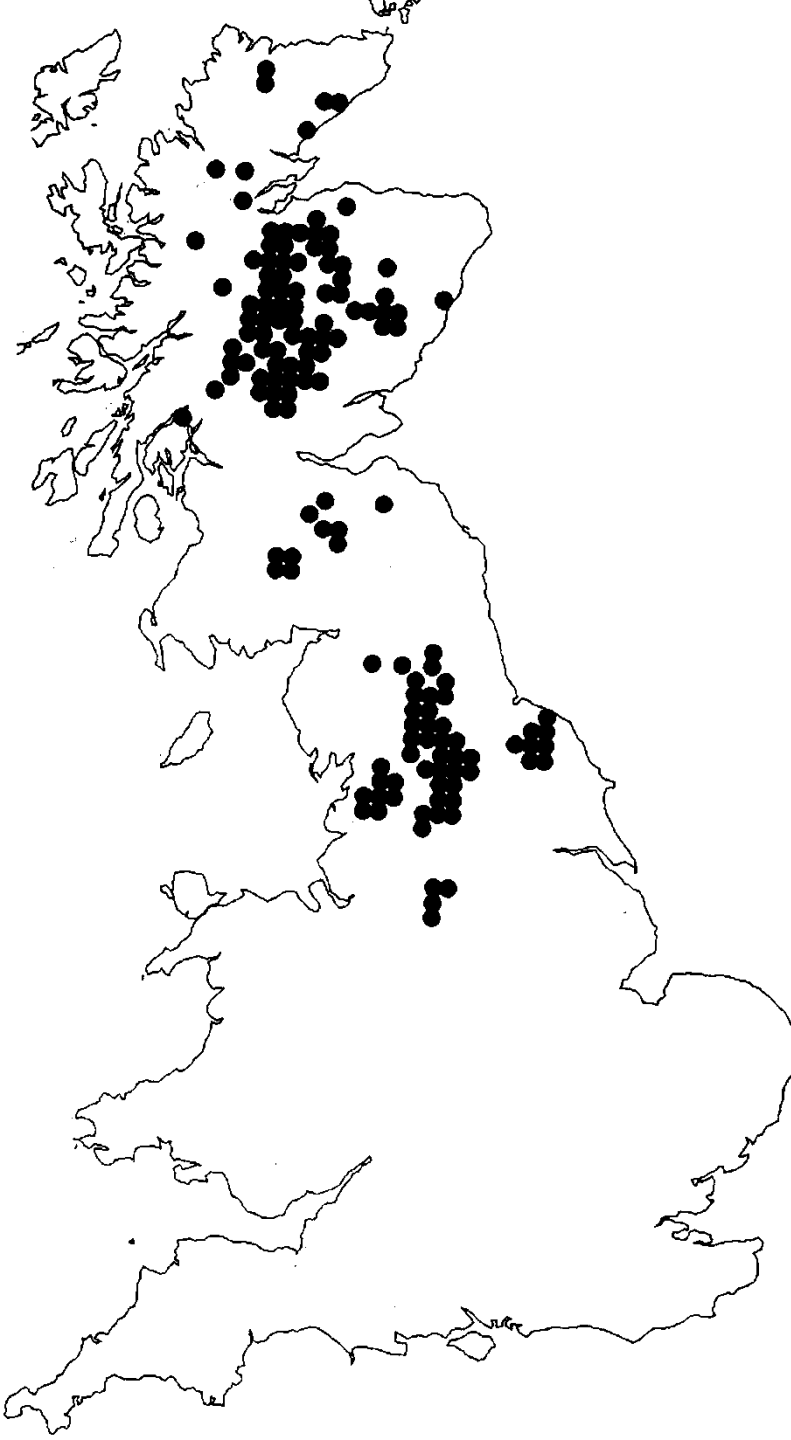
2. Grouse Demography



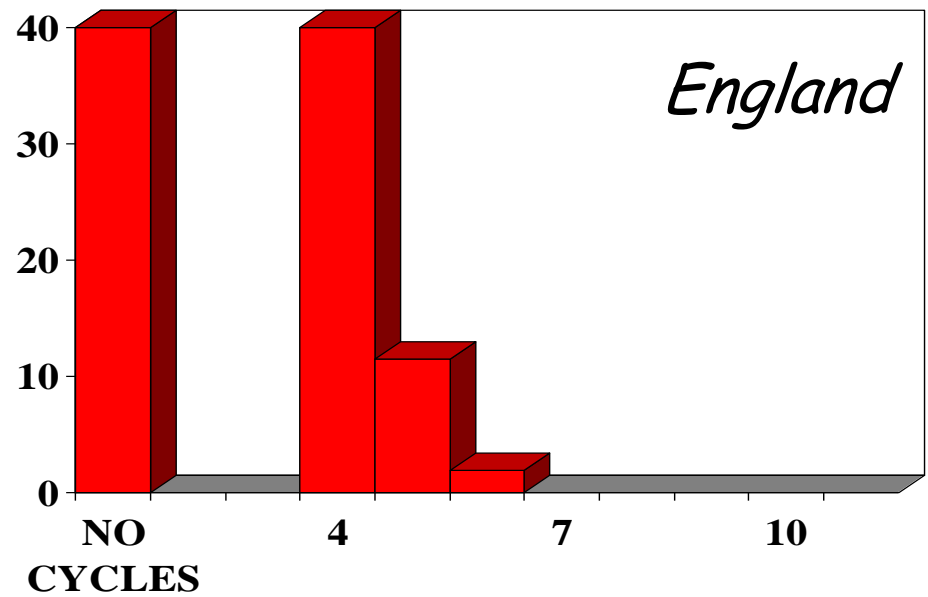
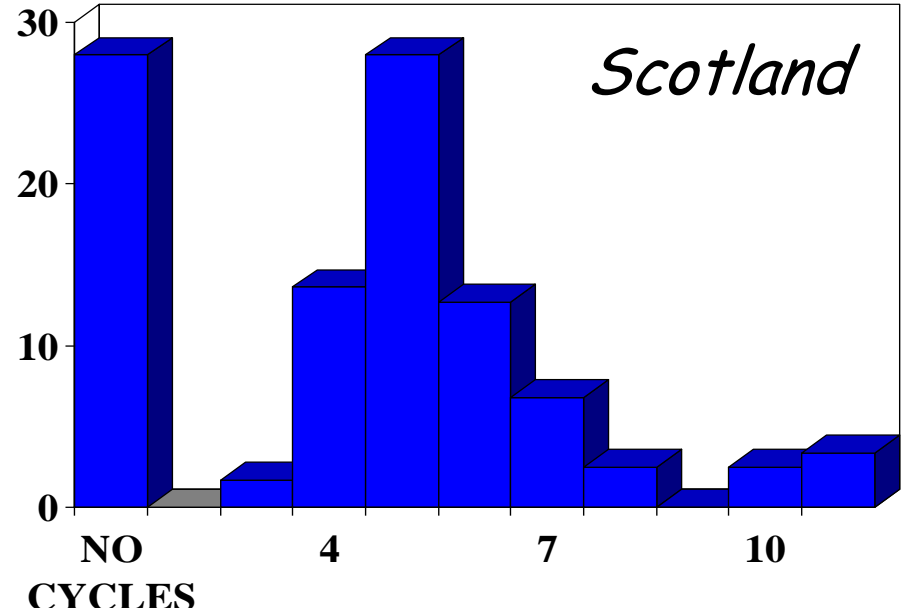
Earlier grouse workers....



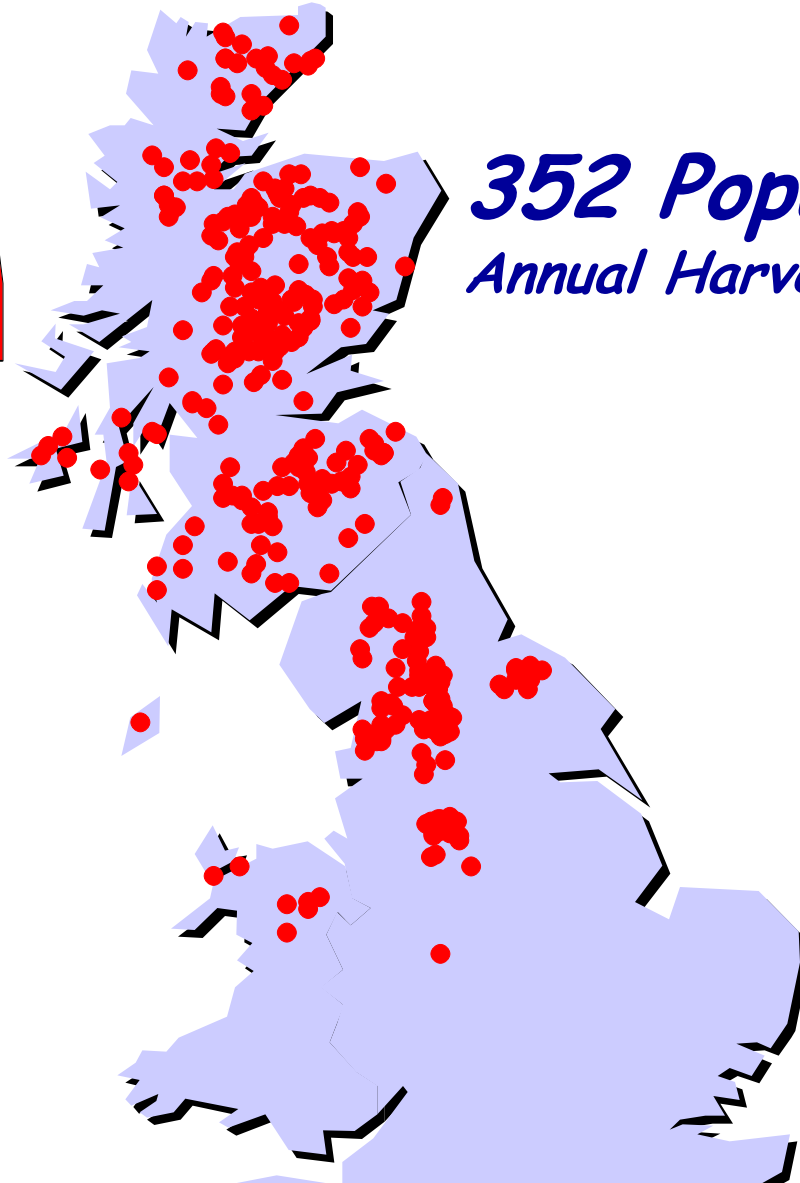
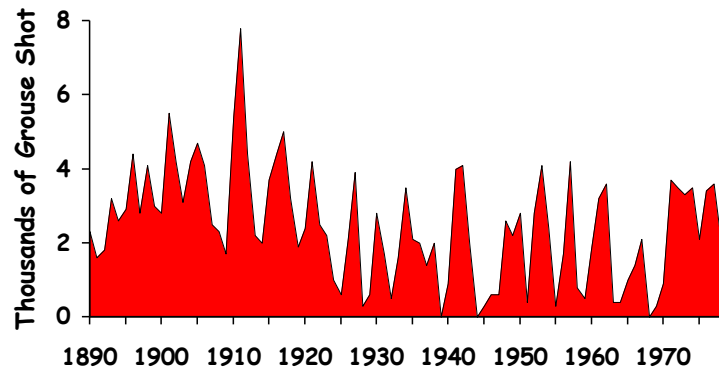
Hunting Records - **England** & **Scotland**



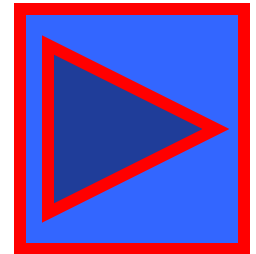
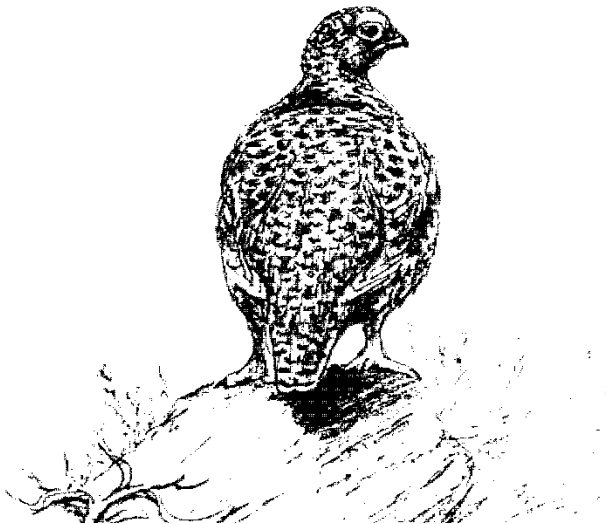
Spatial Variation in Cycle Period



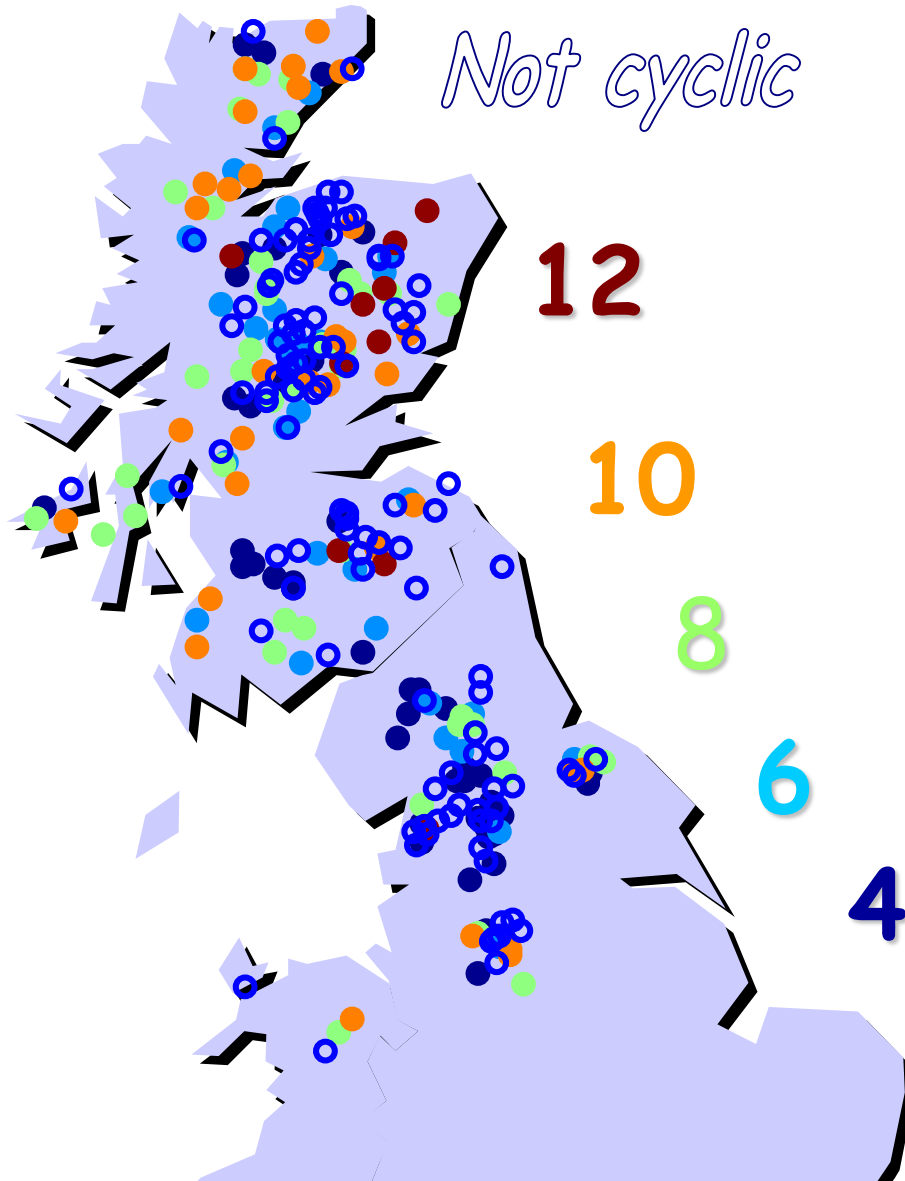
Harvested Red Grouse Populations



352 Populations
Annual Harvesting Data



Harvested Red Grouse Populations



Not cyclic

12

10

8

6

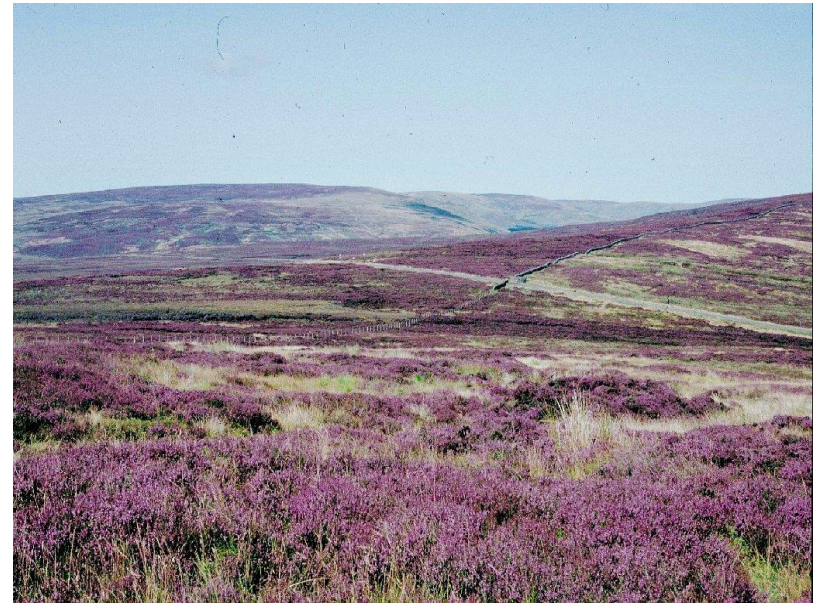
4

57% cyclic
21% weakly cyclic
22% not cyclic

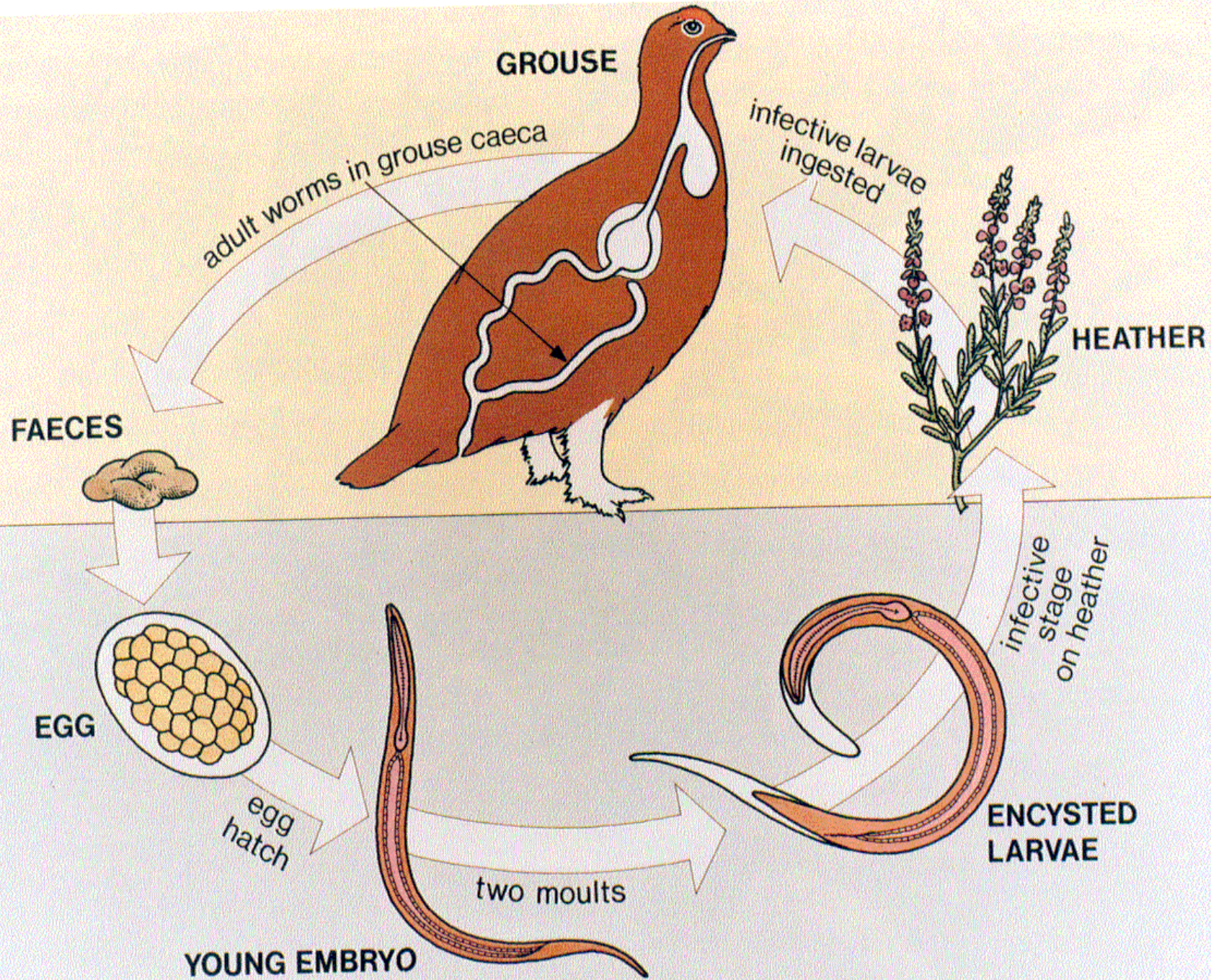
Do Parasites influence Host Dynamics?

Red grouse and *Trichostrongylus tenuis*

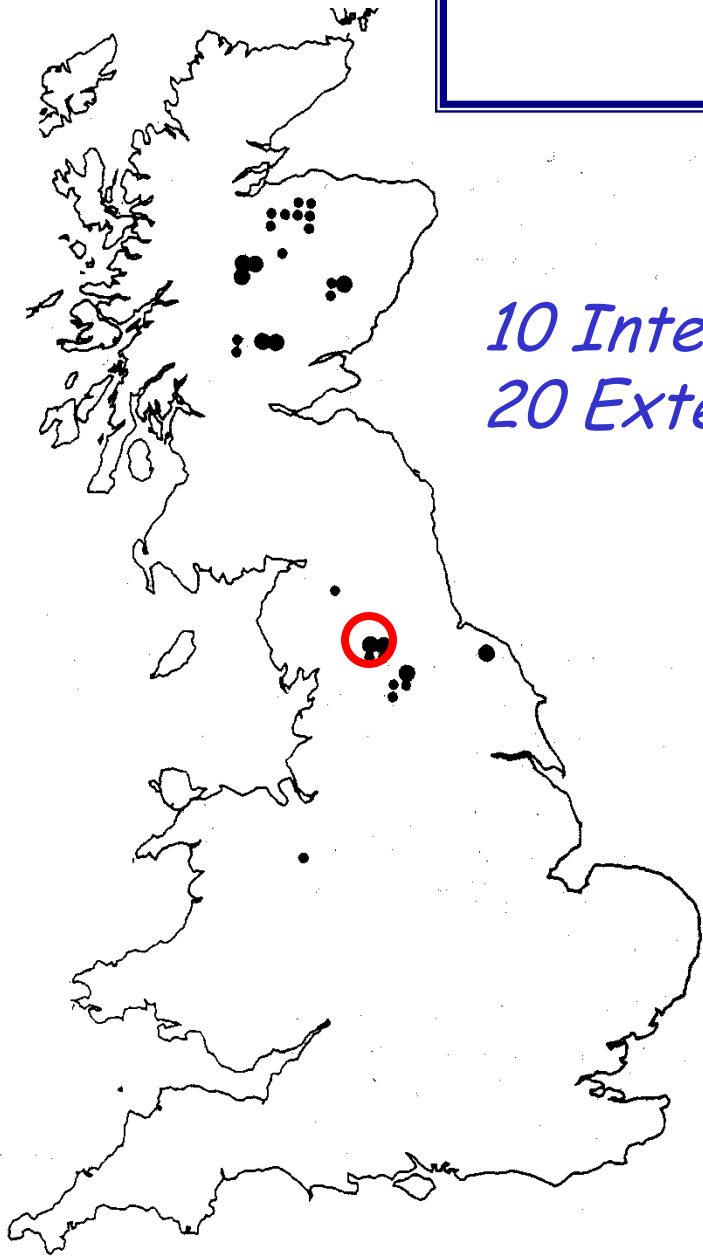
Red Grouse



Trichostrongylus tenuis



Demography ~ 20 years



10 Intensive
20 Extensive

Spring: Breeding density

Clutch size

Hatching success

Chick survival

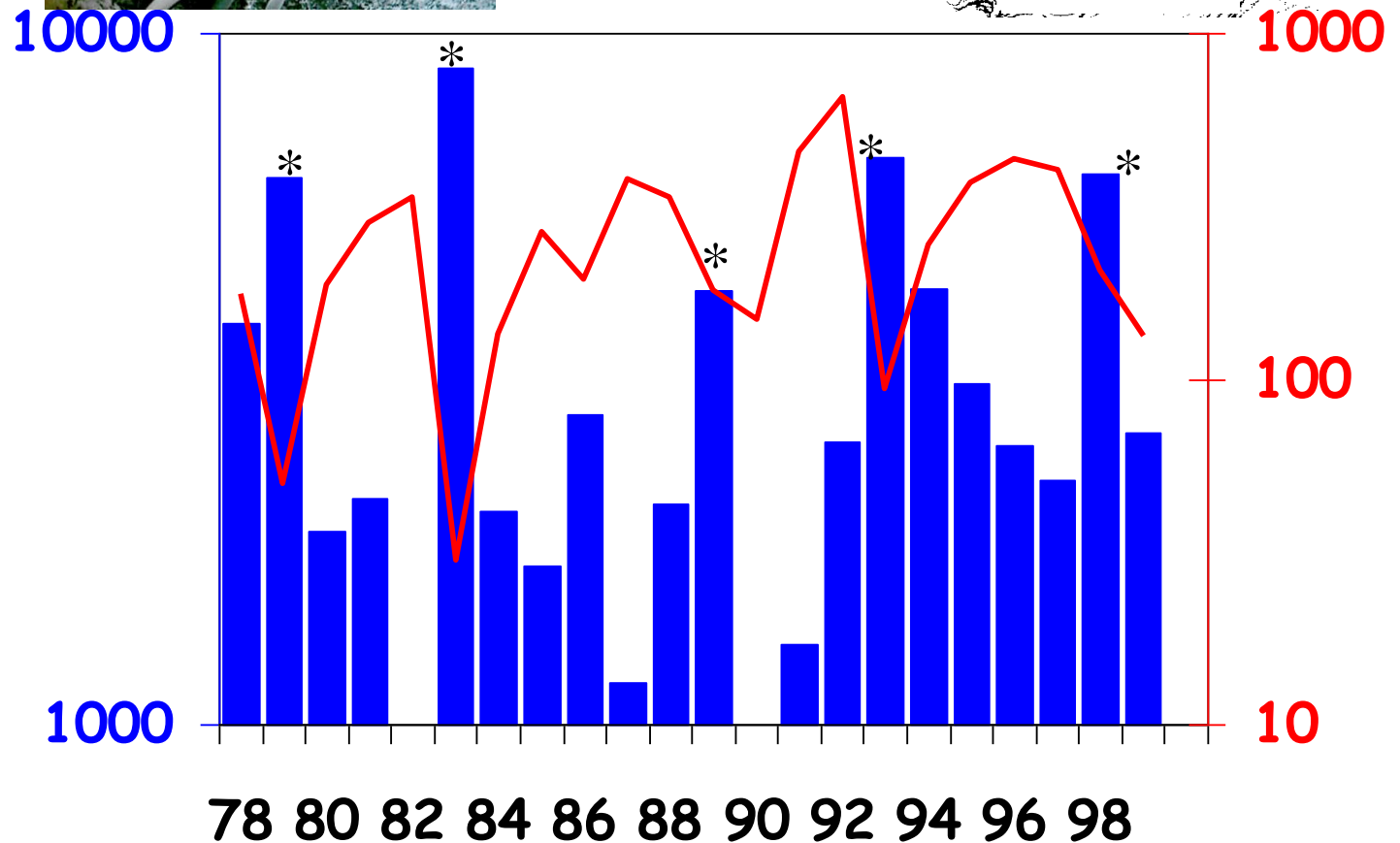
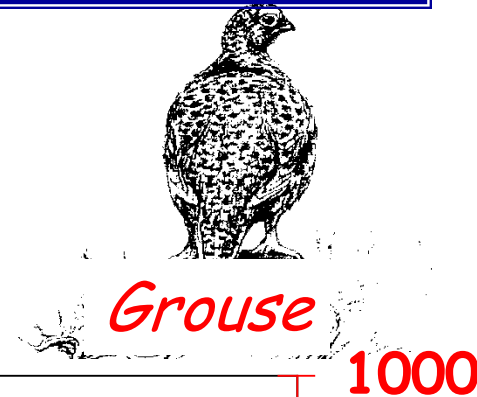
July: Breeding Production

August: Numbers shot

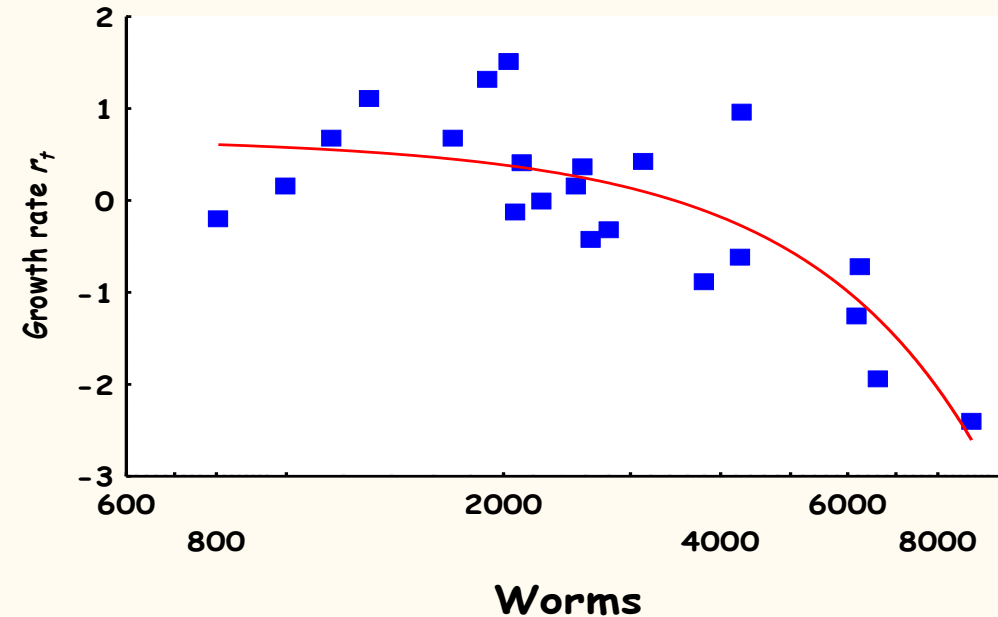
Winter: Corpses



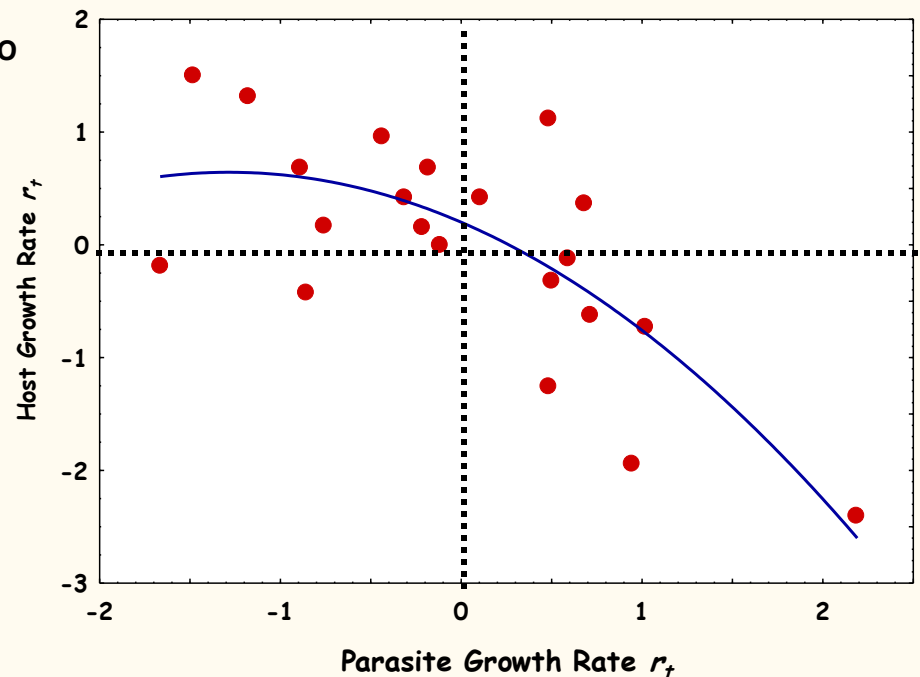
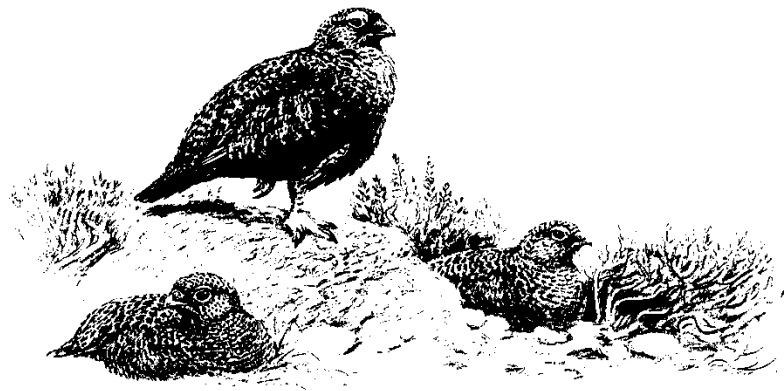
Intensive Study Area



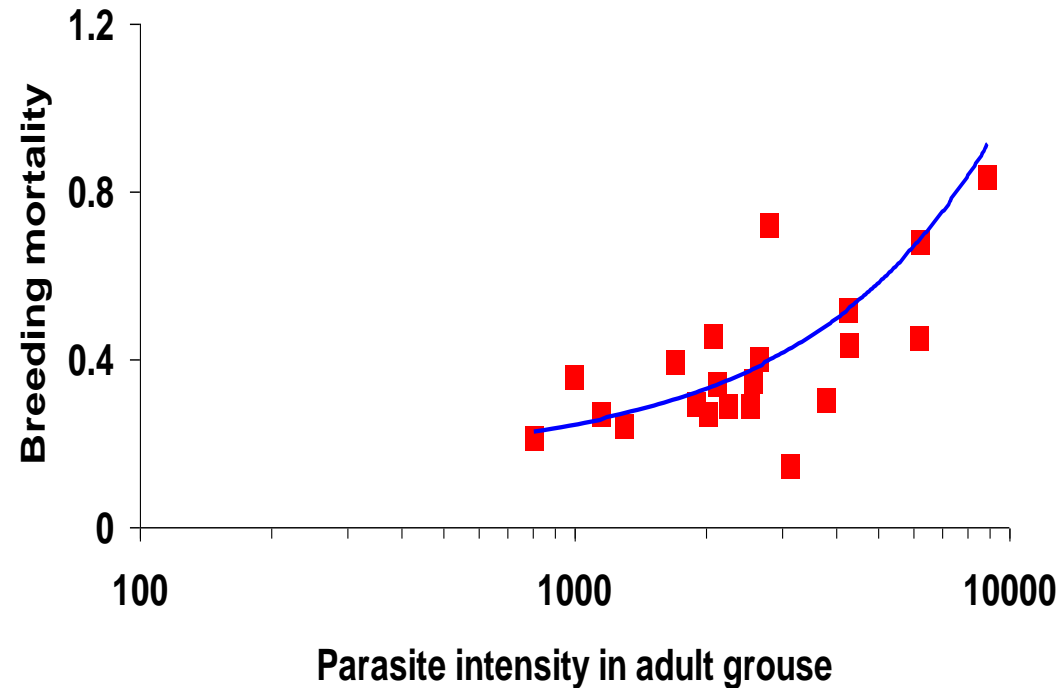
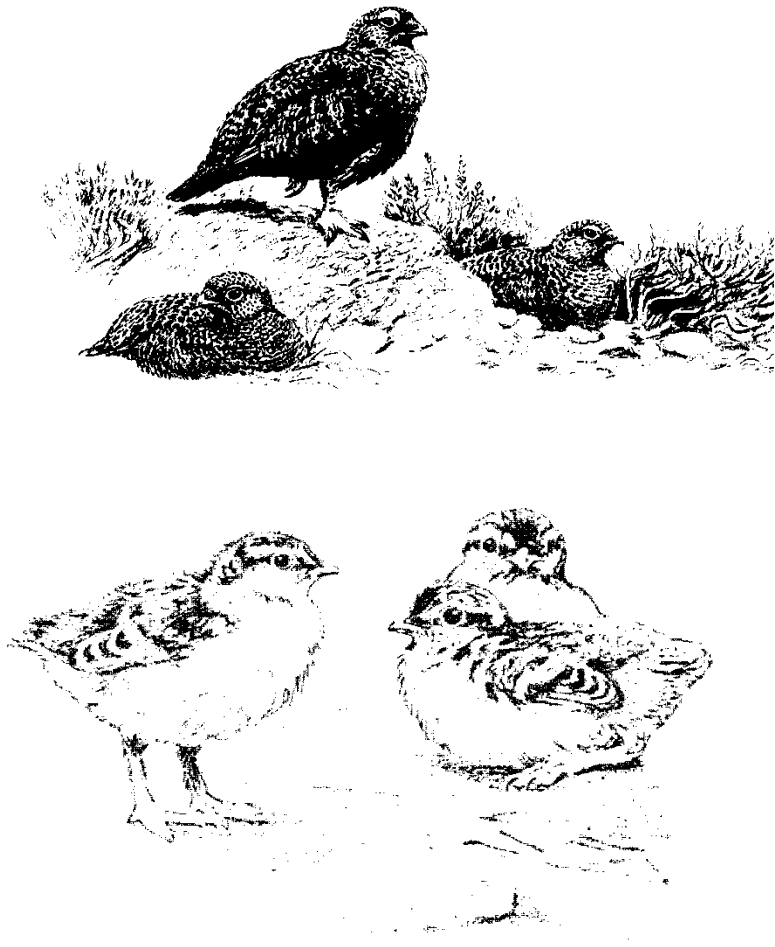
Grouse & Worms: Demographic Data



*Parasite Associated
Reduction in Growth Rate*



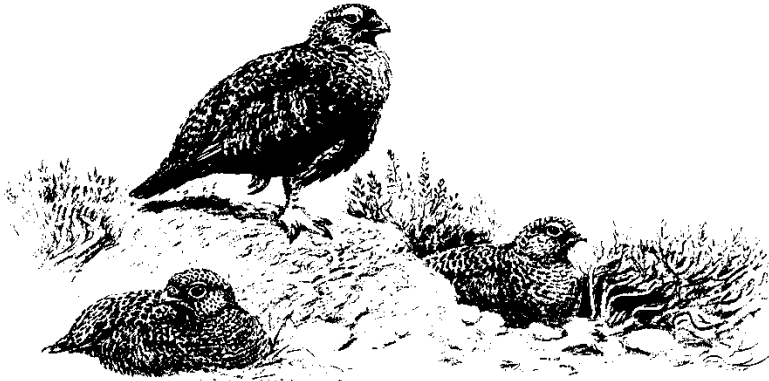
Grouse & Worms: Demographic Data



Do Parasites influence Host Dynamics?

Destabilising Features at individual level

Red Grouse



Trichostrongylus tenuis

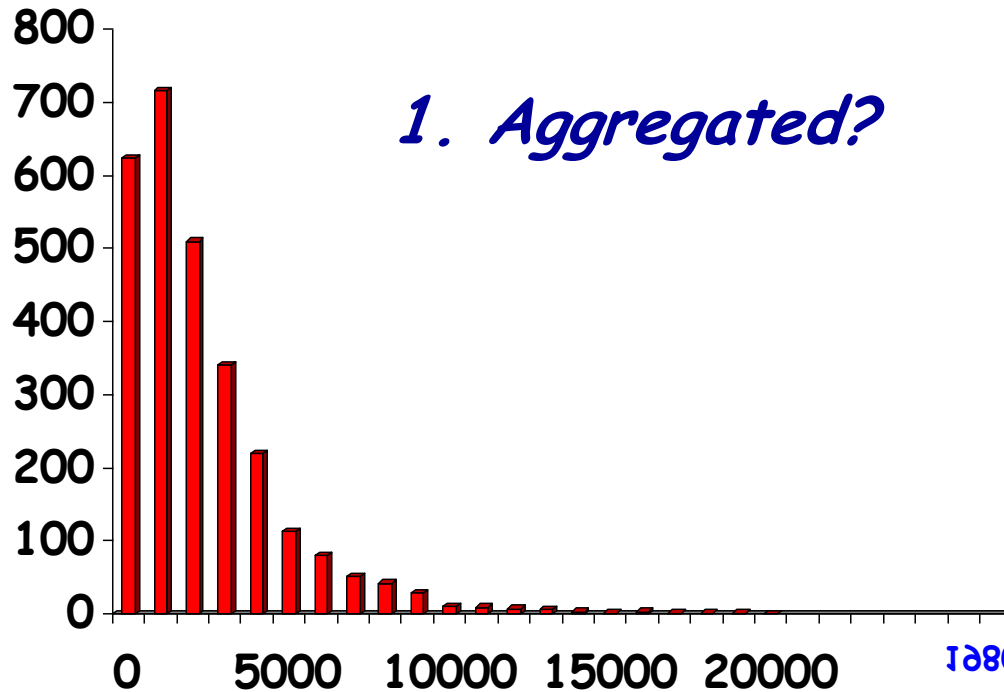


Destabilizing Features:

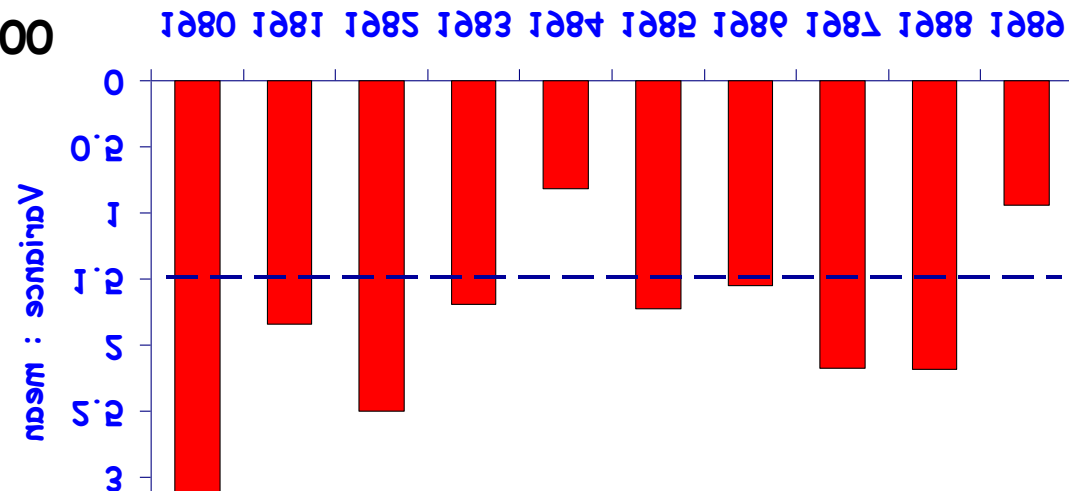
1. Regular distribution $\kappa \rightarrow \infty$
2. Parasite induced reduction in host fecundity $\delta < \alpha$
3. Time delays in life cycle

1. Individual Level Productivity

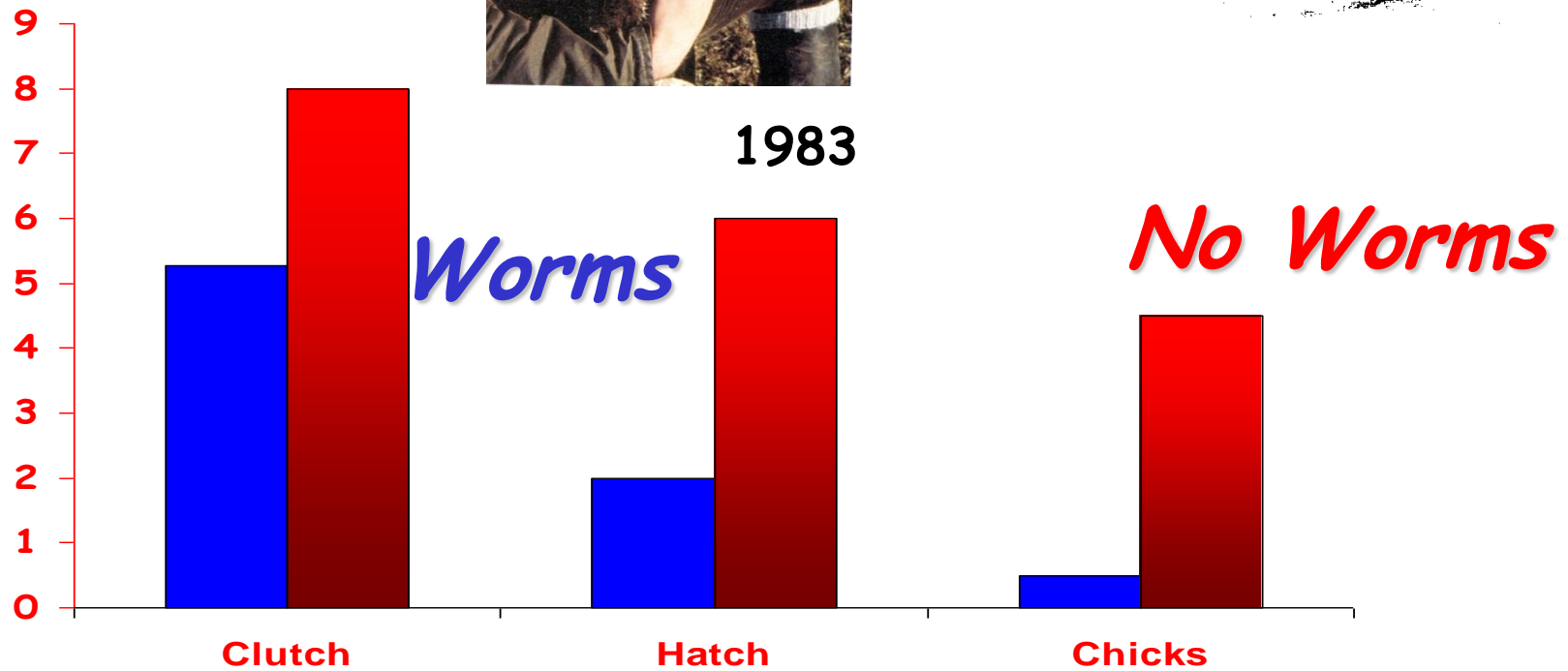
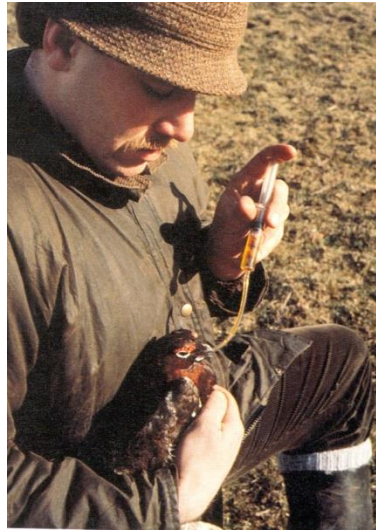
Grouse parasite frequency distributions



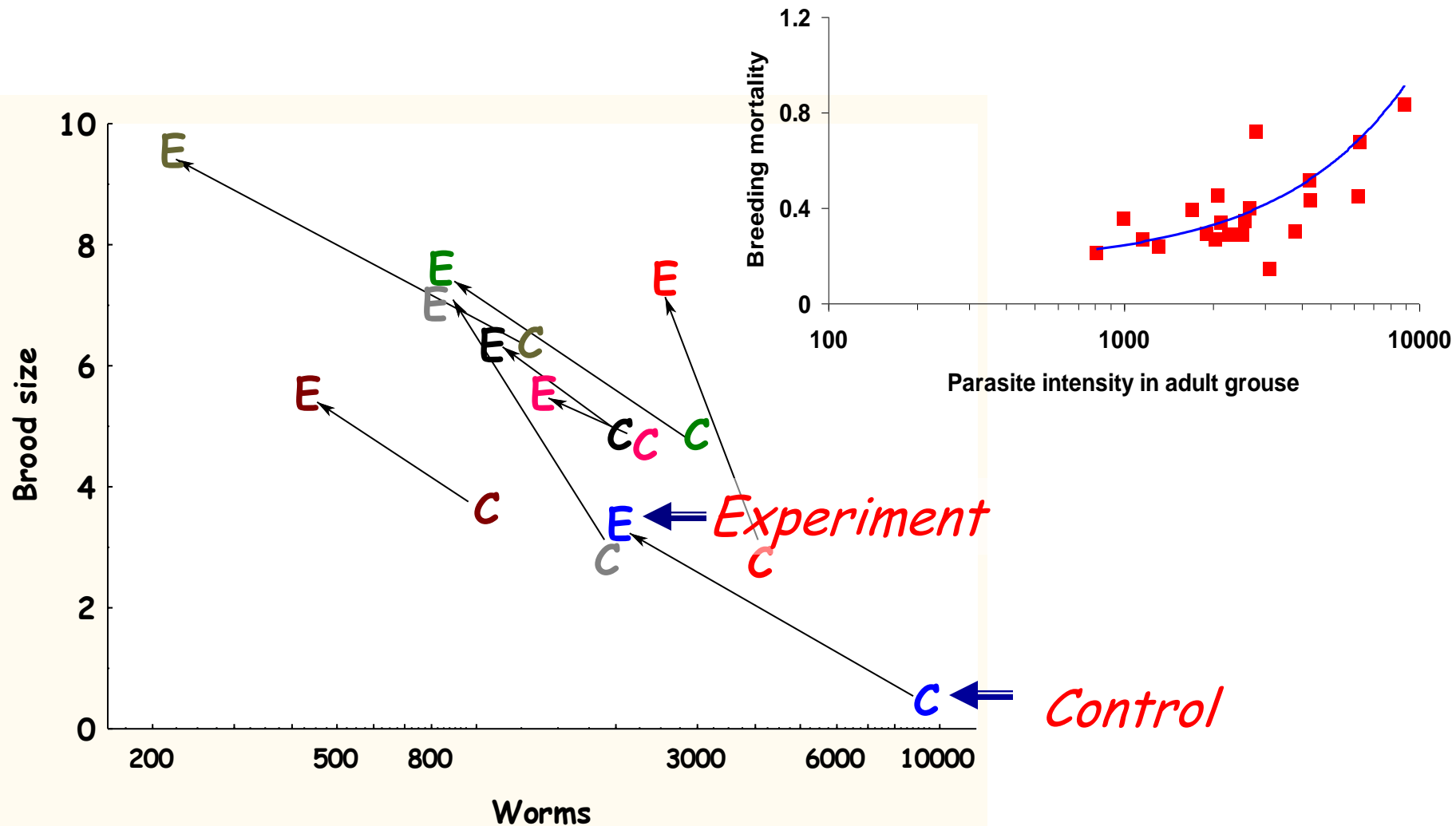
2. No...Close to Random



2b. Parasite induced reduction in host fecundity

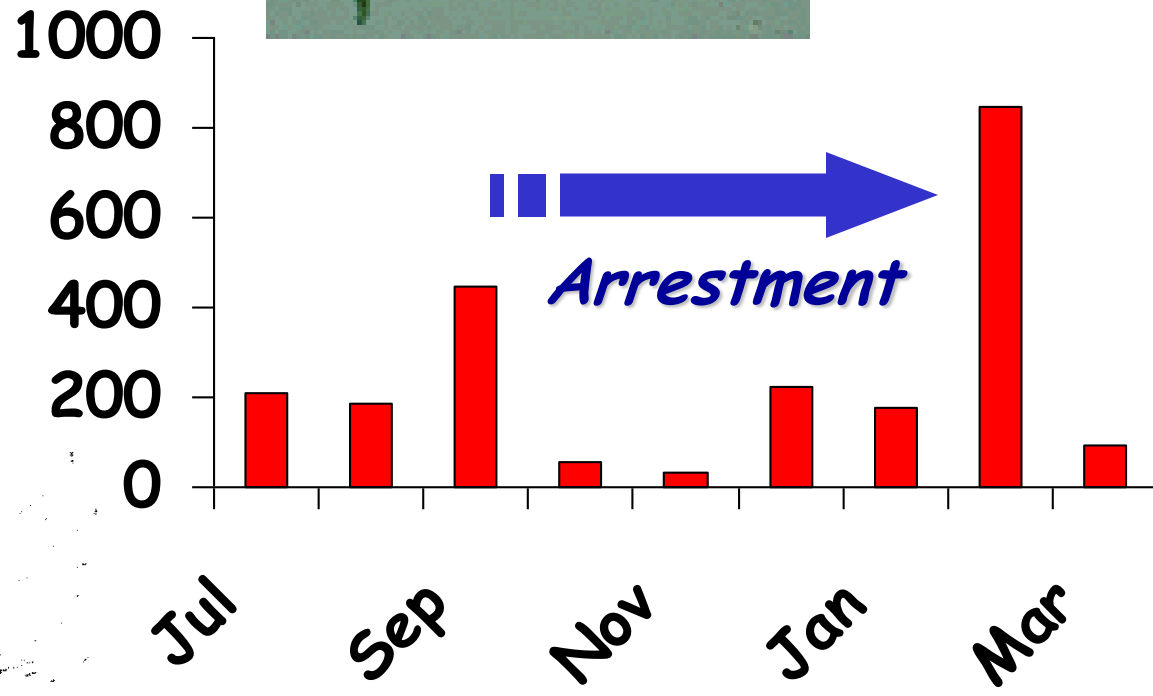
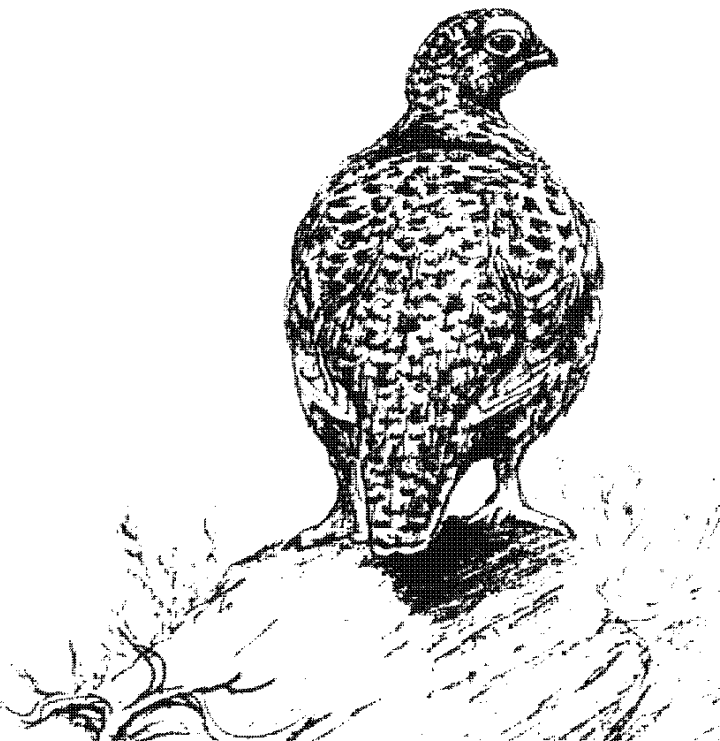


2b. Parasite induced reduction in host fecundity



2c. Time delays in parasite life cycle

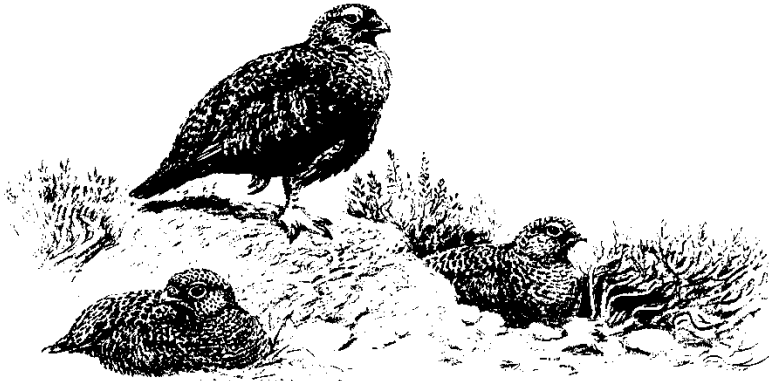
Time of Parasite Recruitment



Do Parasites influence Host Dynamics?

2. Destabilising Features at individual level

Red Grouse



Trichostrongylus tenuis



Destabilizing Features:

1. Regular distribution $\kappa \rightarrow \infty$
MMMmm a a bit
2. Parasite induced reduction in host fecundity $\delta < \alpha$
Yep
3. Time delays in life cycle
Yep

Trophic Interactions

What are the consequences for population & community?

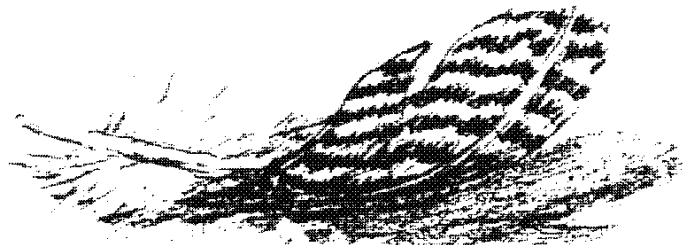
1. Individual level productivity

*Frequency Dist. Fecundity Reduction
& Time delay*

2. Population level dynamics

3. Community level interactions

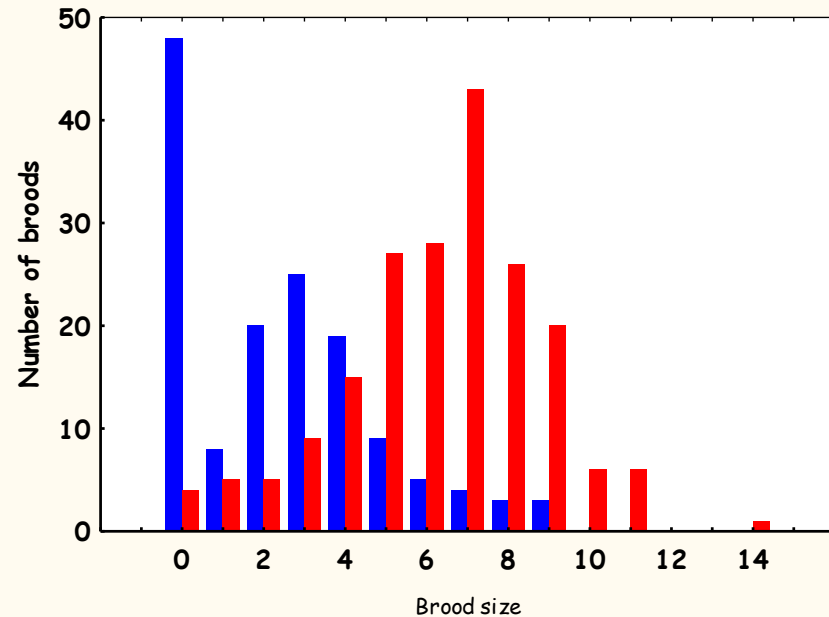
Understanding ~ Monitoring Experiments & models



1. Individual Level Productivity

Grouse brood frequency distributions

High & Low Worms



Worms

Female Condition

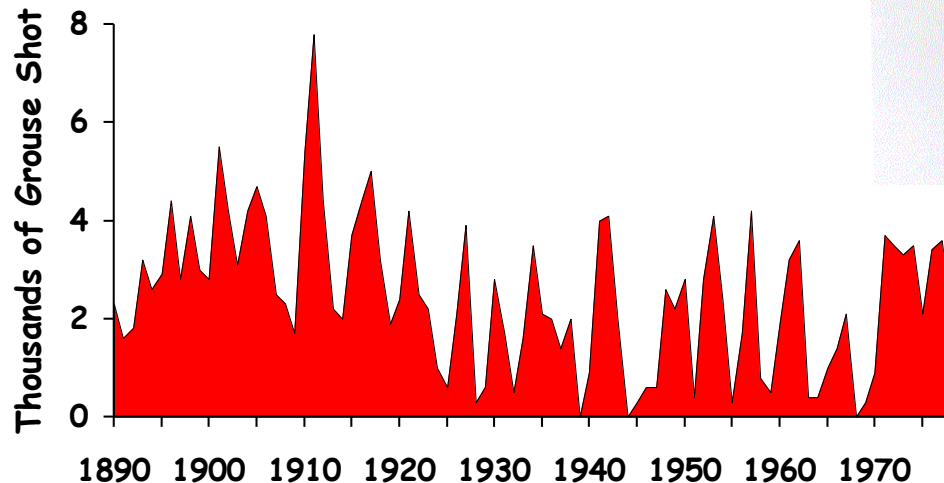
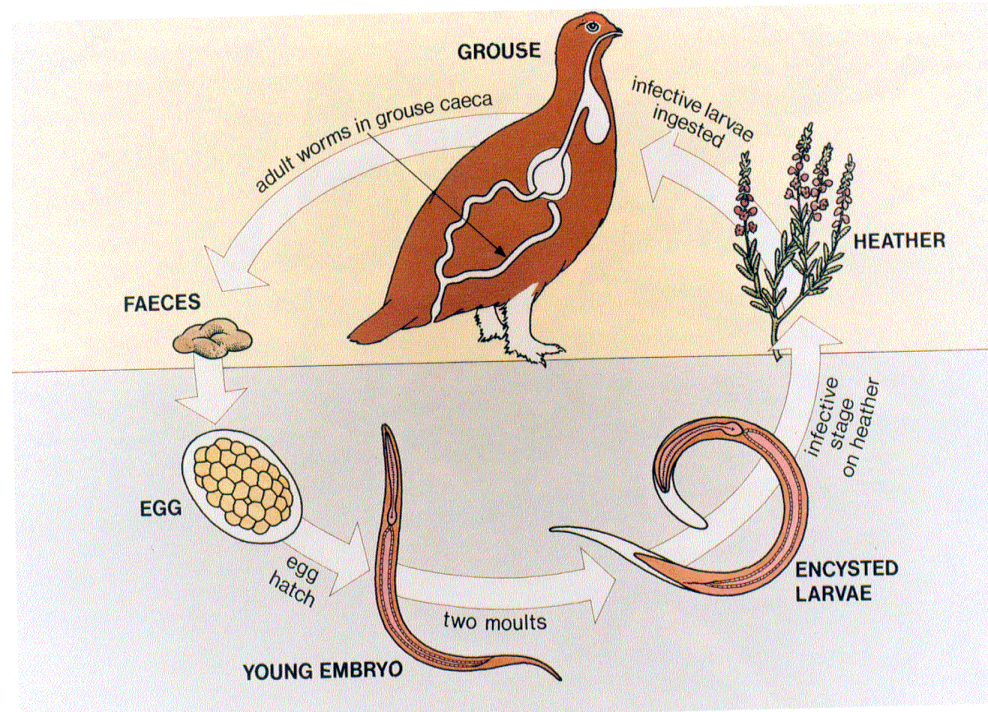
Chick survival



2. Population Level Dynamics

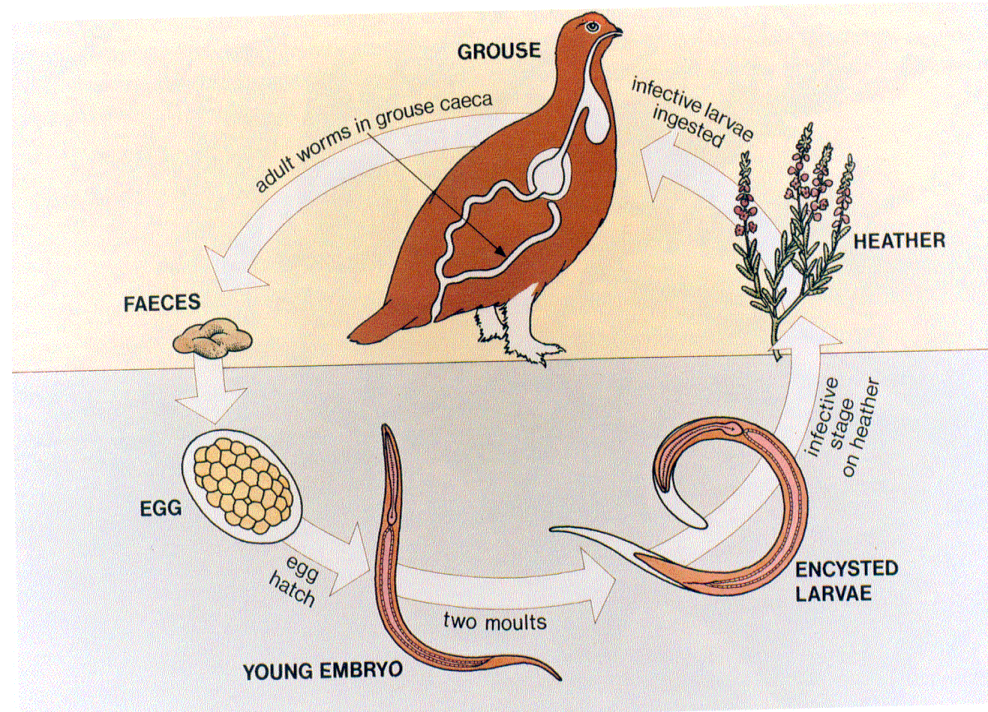
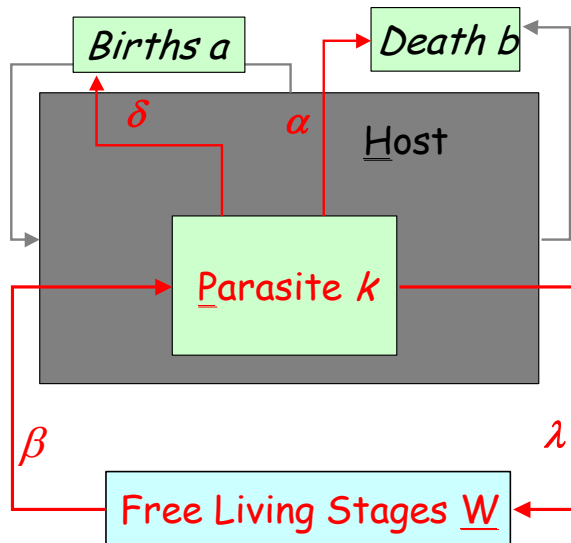
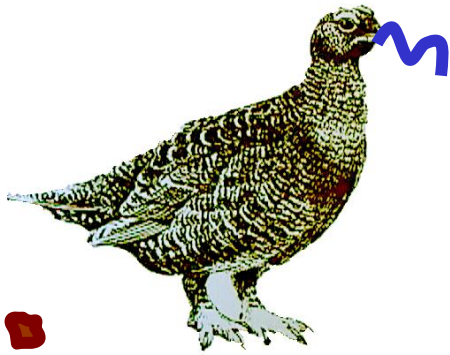
Dobson & Hudson Macroparasite model

Grouse



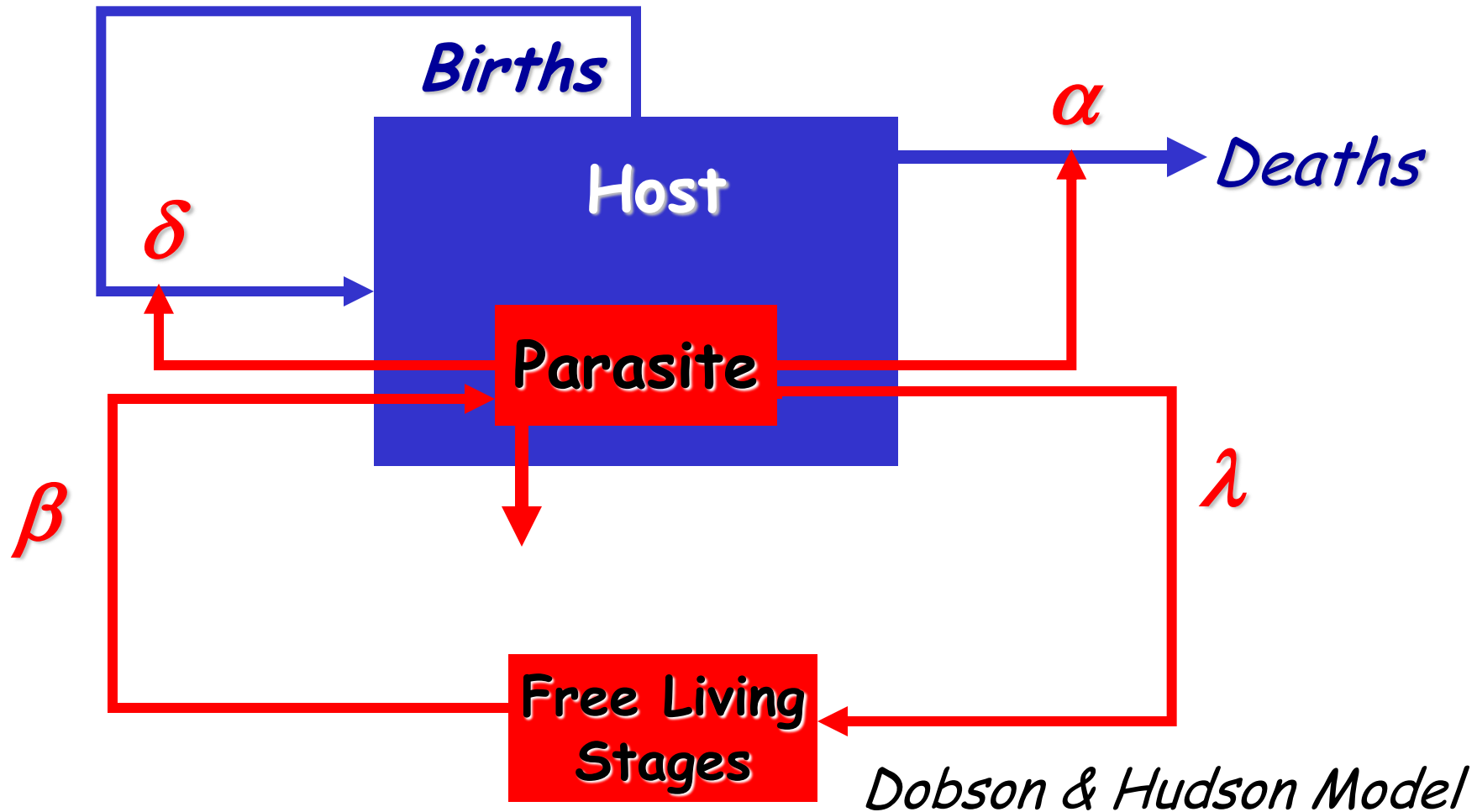
2. Population Level Dynamics

Dobson & Hudson Macroparasite model

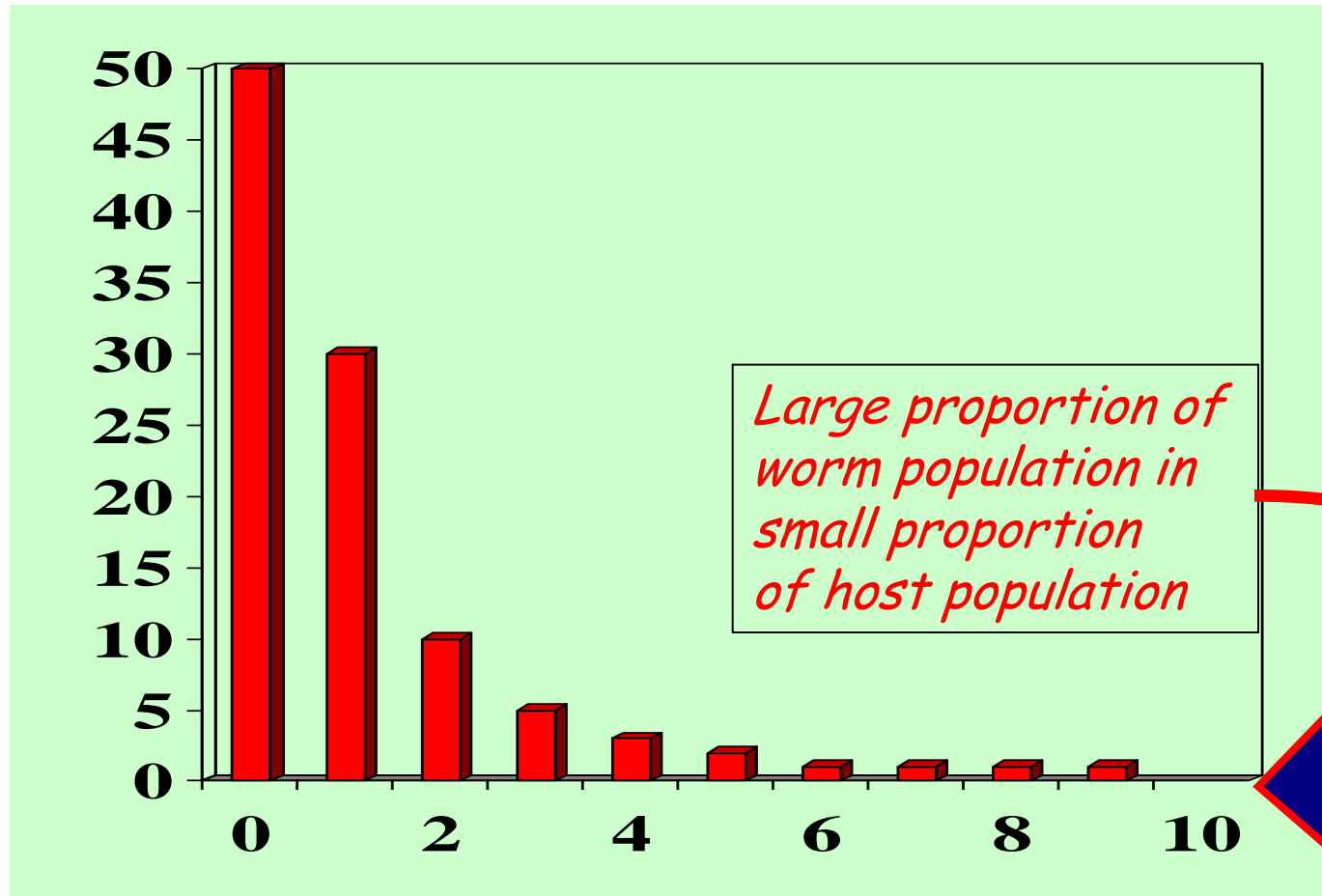


Do Parasites influence Host Dynamics?

3. Population level effects

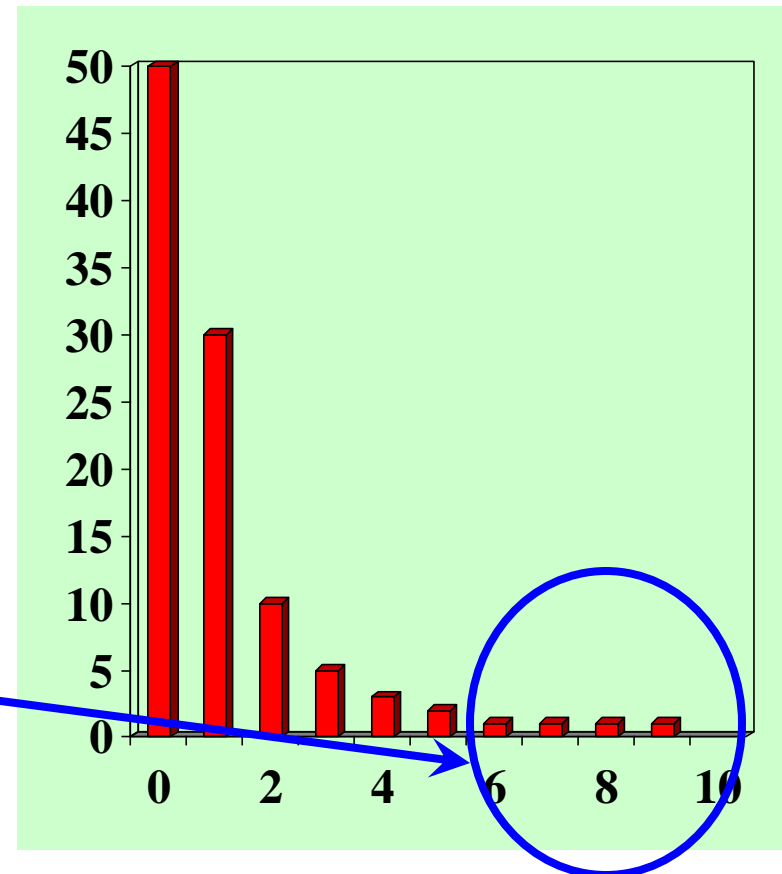


Macroparasites invariably have an aggregated distribution



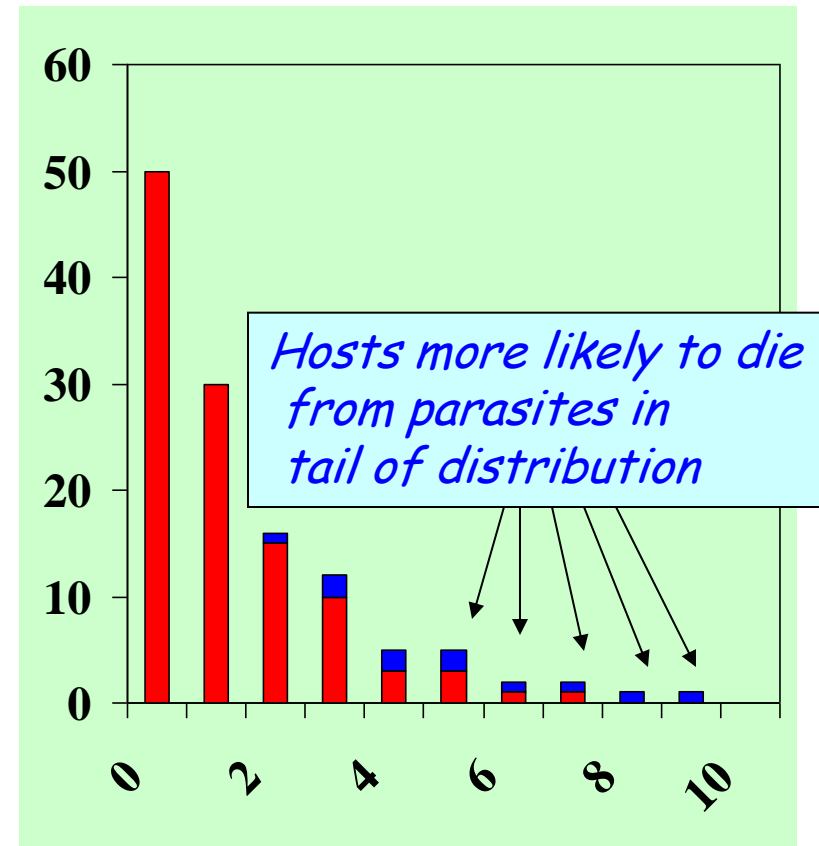
Aggregated distributions = Biological interest

- Overall parasites experience higher densities
- *Mortality and morbidity just in the tail*
- *So impact on host and selection pressure will be higher here*



Aggregated distributions = Biological interest

- *Highly virulent parasites have low means because they kill the hosts in the tail of the distribution*
- Some selection against this because of reduced mating opportunities in dioecious species
- *So selection towards moderate virulence*



2. Population level dynamics

Dobson & Hudson Macroparasite model

$$\frac{\delta H}{\delta t} = aH - bH - (\alpha + \delta)P$$

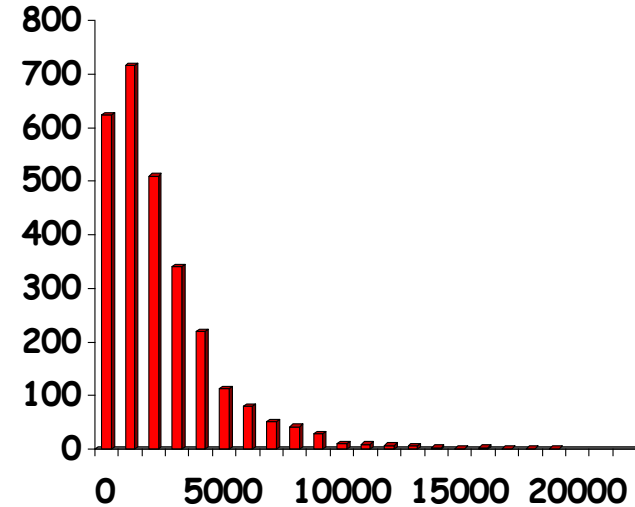
2. Parasite impact on fecundity

$$\frac{\delta W}{\delta t} = \lambda P - \gamma W - \beta WH$$

3. Parasite impact on mortality-host and parasite!

$$\frac{\delta P}{\delta t} = \beta WH - P(\mu + \beta + \alpha) + \alpha \frac{P^2}{H} \left(\frac{k+1}{k} \right)$$

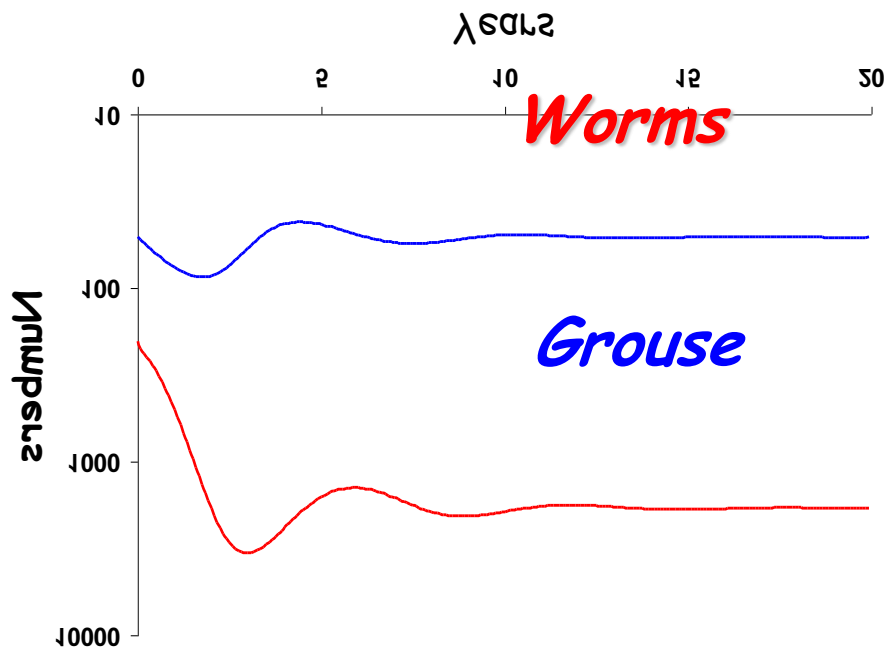
1. Individual risk of parasite induced impacts (-ve binomial)



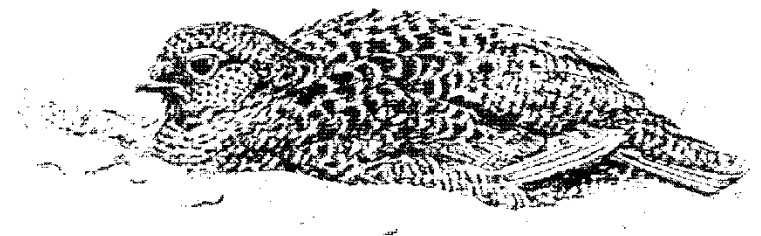
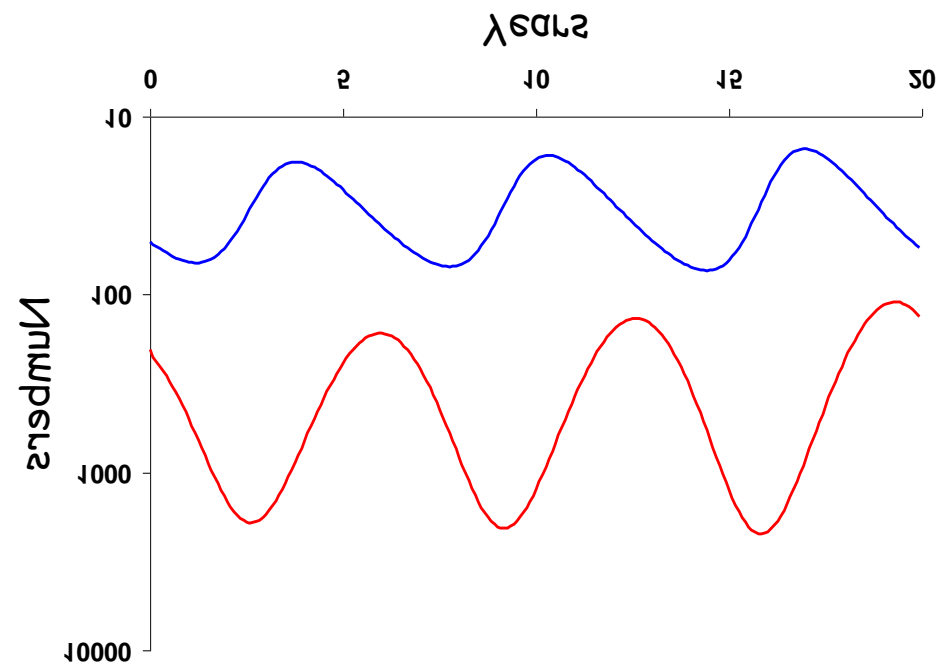
2. Population level dynamics

Dobson & Hudson Simulations

Low impact on fecundity

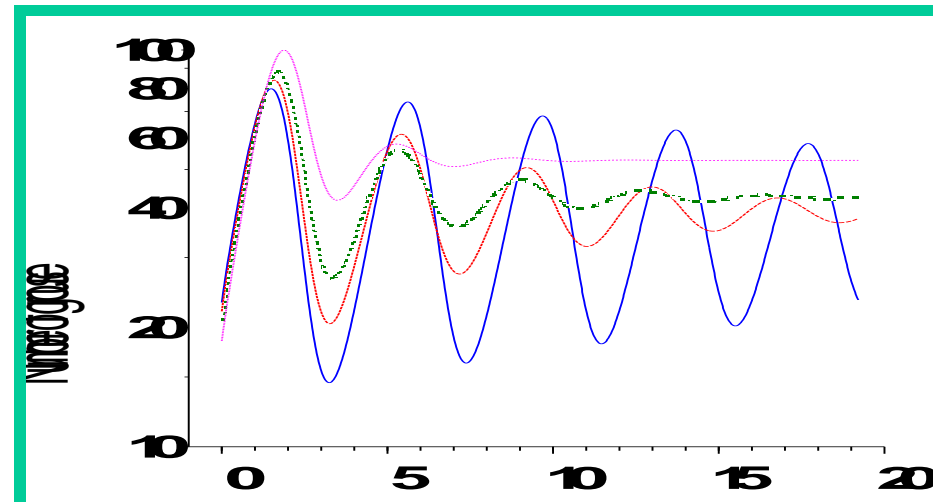
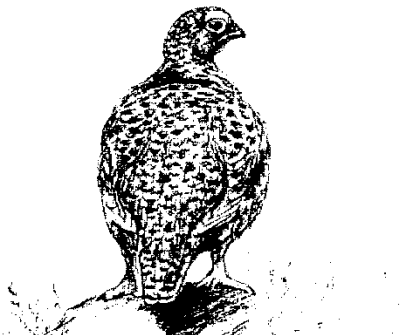
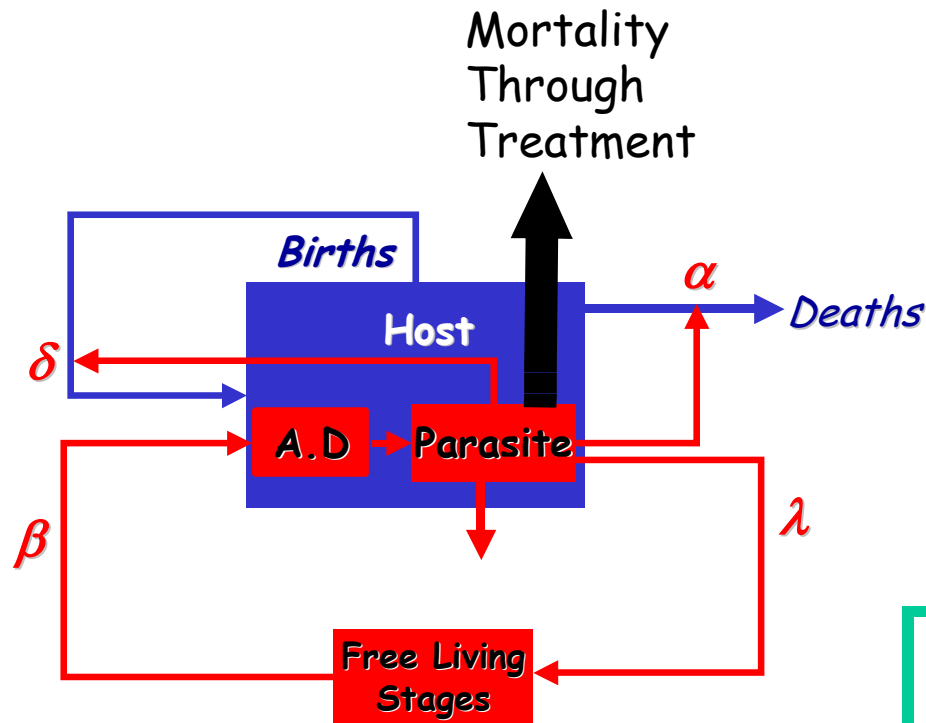


High impact on fecundity

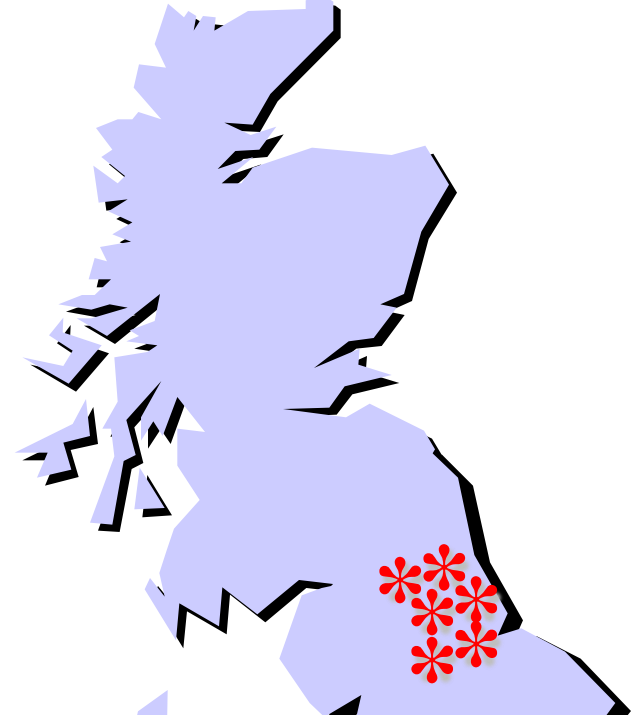


Do Parasites influence Host Dynamics?

3. Population Level Consequences



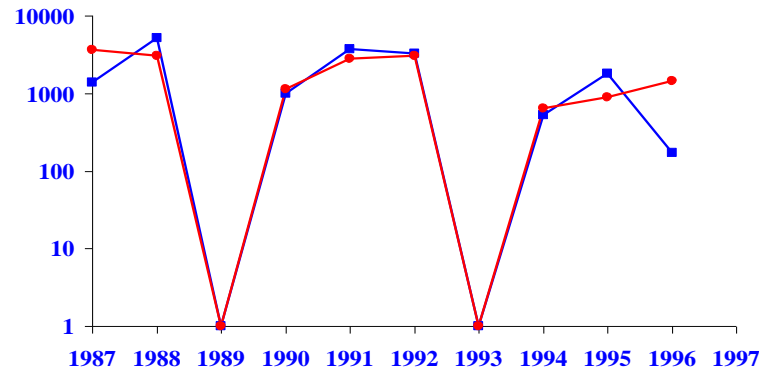
2. Population Level Experiments



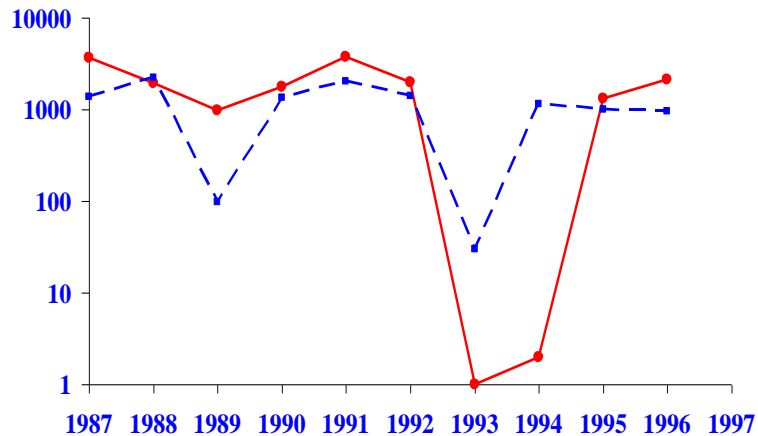
2. Population Level Experiments

Reducing Parasites Reduces Variance in Growth Rate

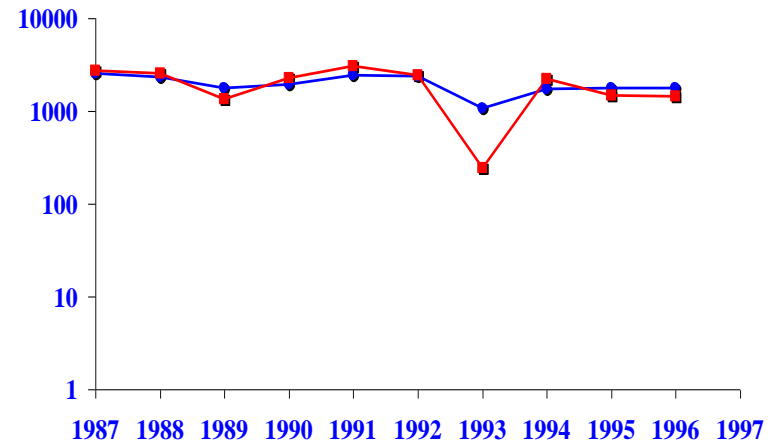
a. Control



b. One Treatment

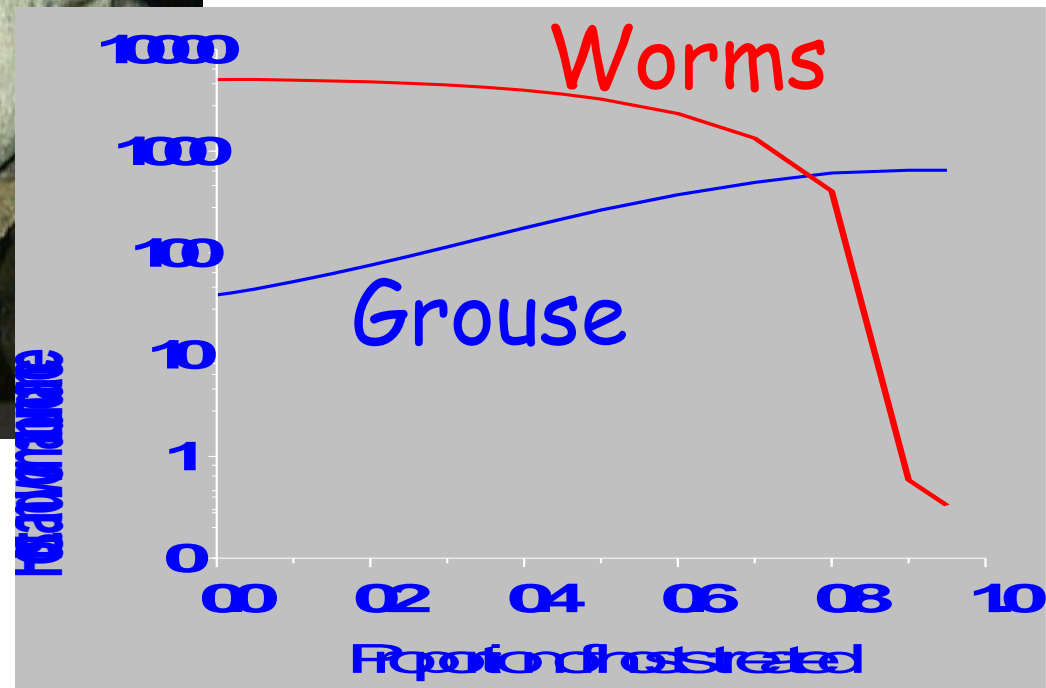
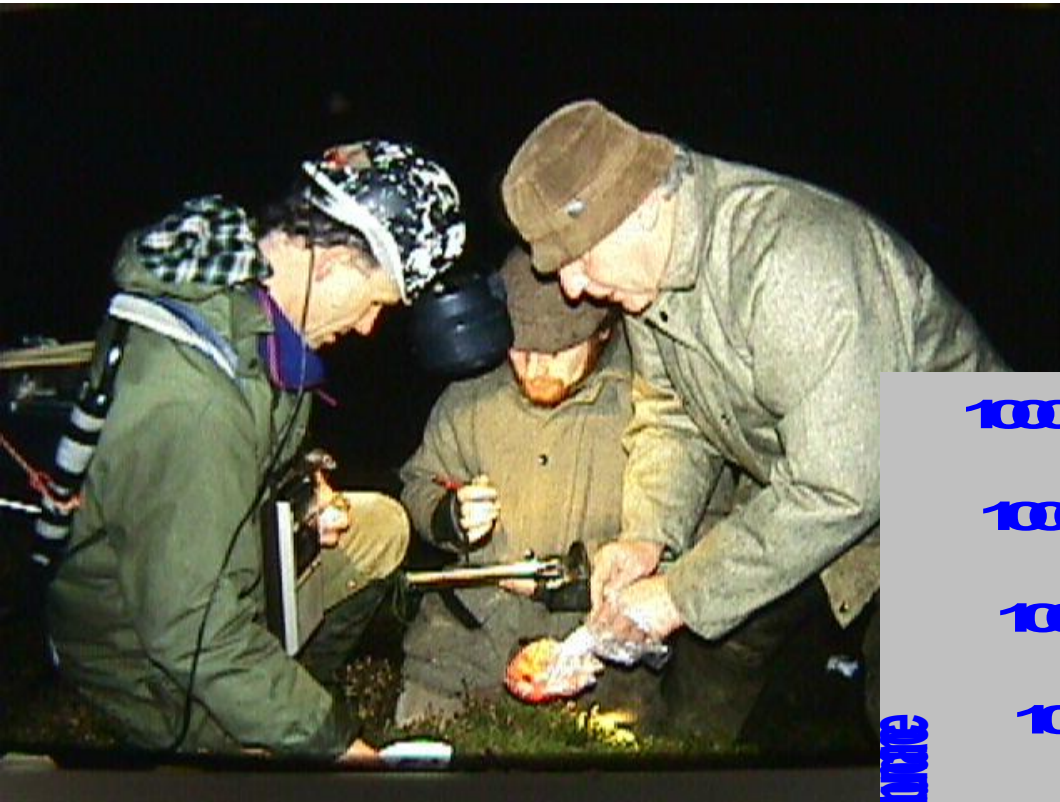


c. Two Treatments



Do Parasites influence Host Dynamics?

3. Controlling infection: Direct Treatment

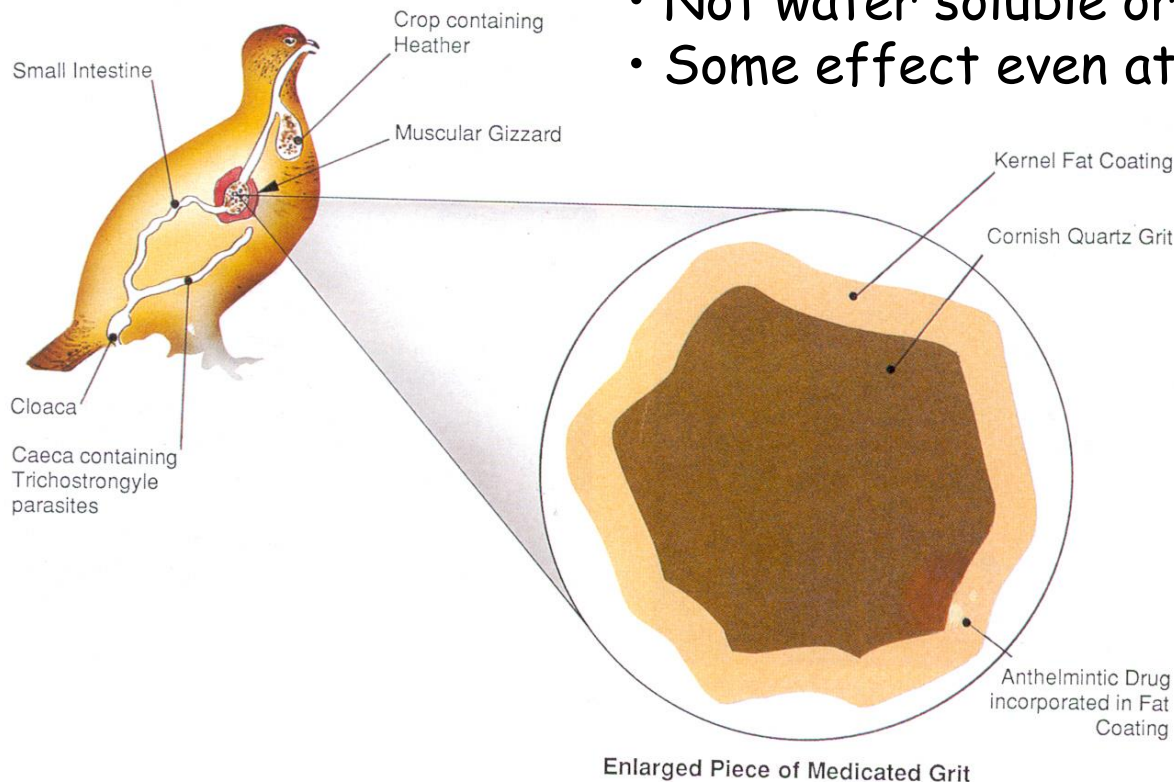


Do Parasites influence Host Dynamics?

3. Controlling infection: Medicated grit

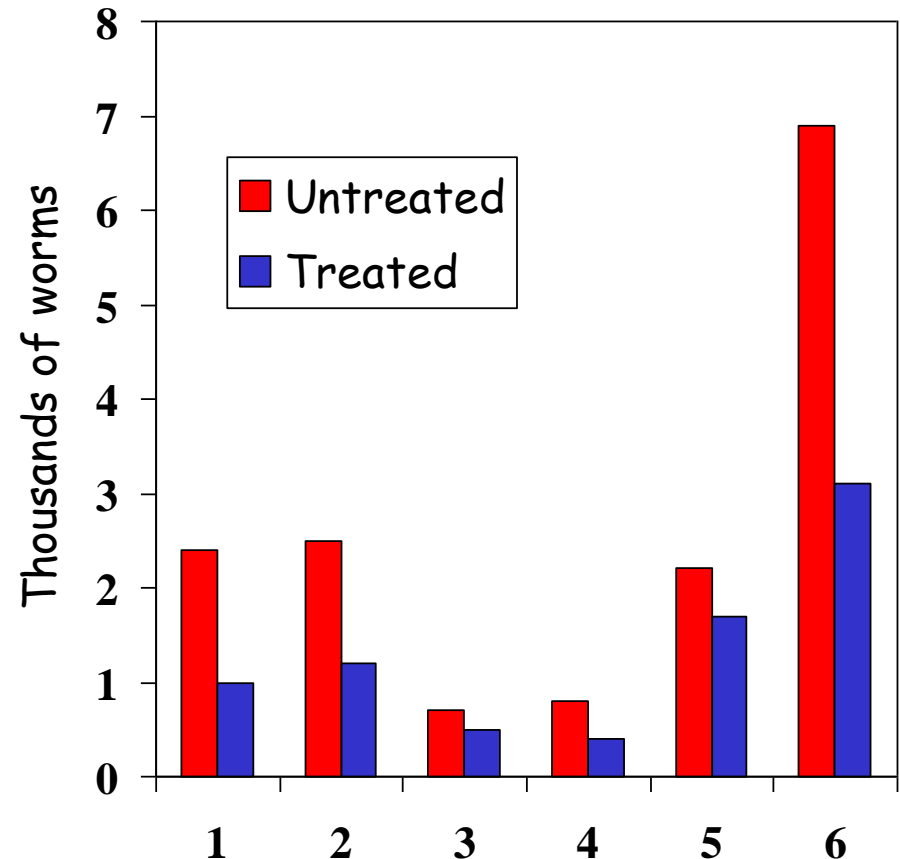
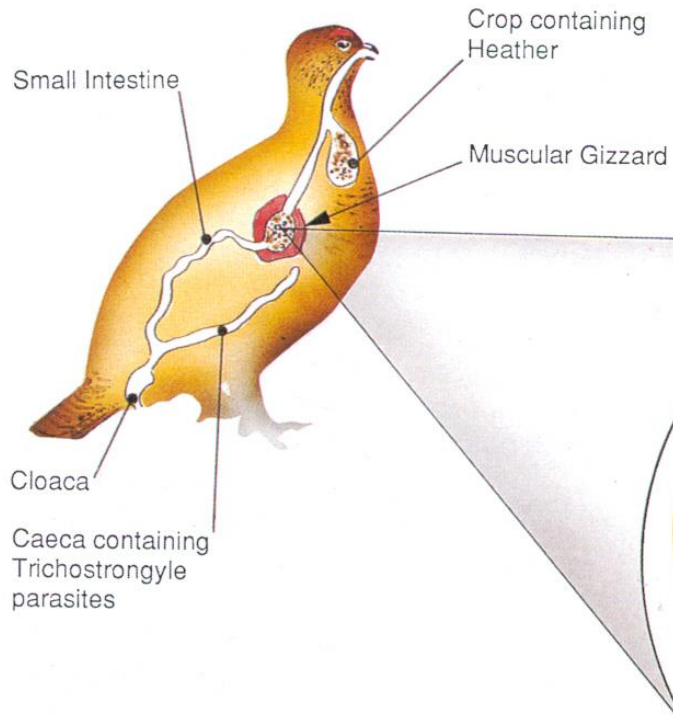
Fenbendazole effective:

- Split dose treatment over 15 days
- Safe to wildlife
- Not water soluble or break down in light
- Some effect even at low doses

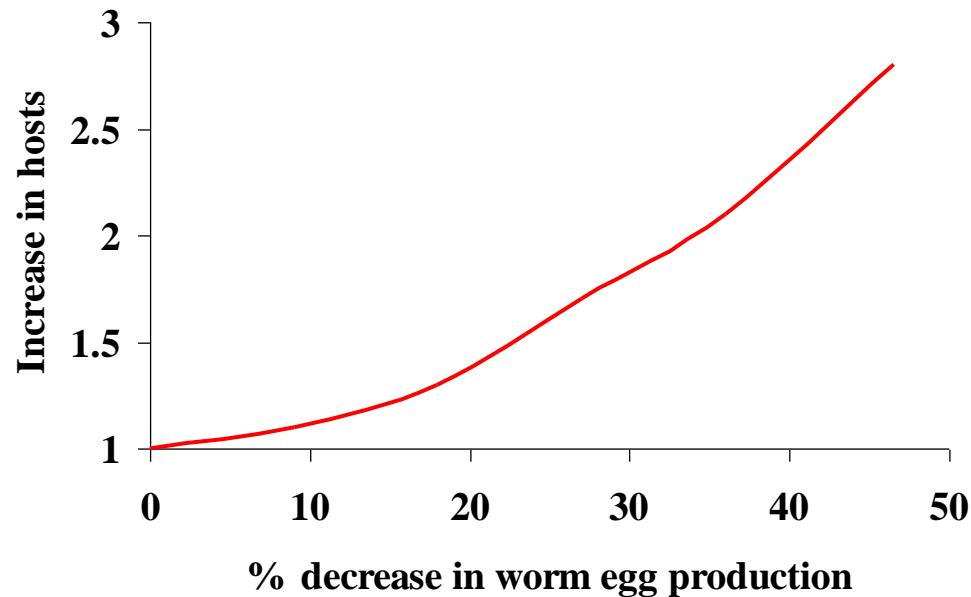
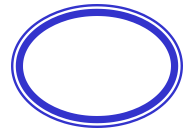
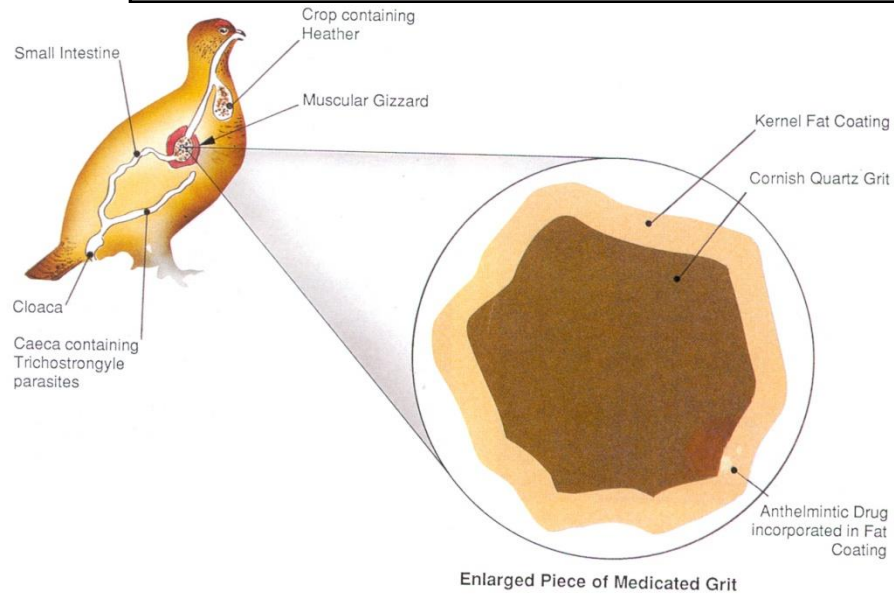


Do Parasites influence Host Dynamics?

3. Controlling infection: Medicated grit

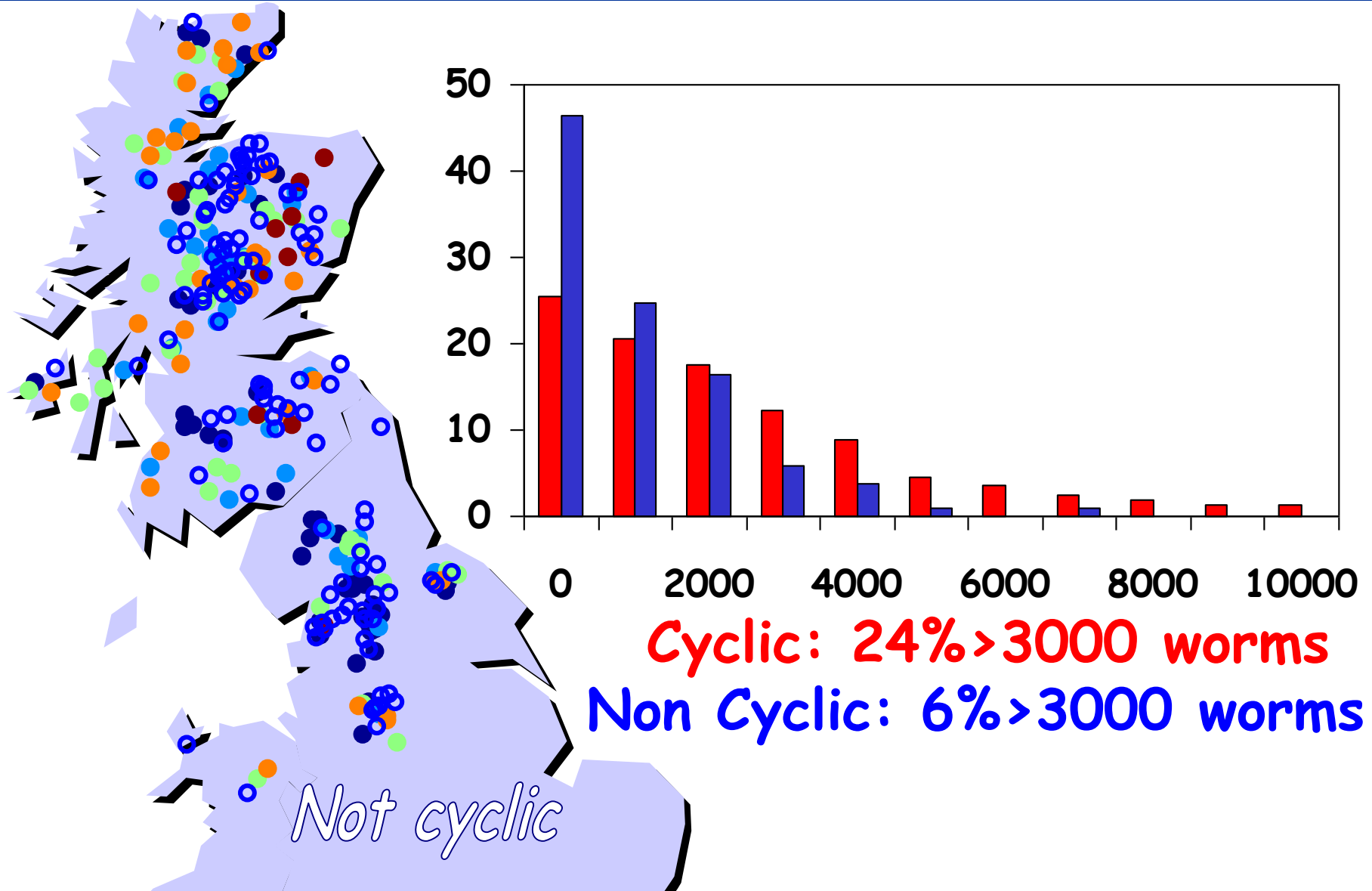


Medicated Grit & Reduced Worm Fecundity



Do Parasites influence Host Dynamics?

3. Why are some populations not cyclic?



Do Parasites influence Host Dynamics?

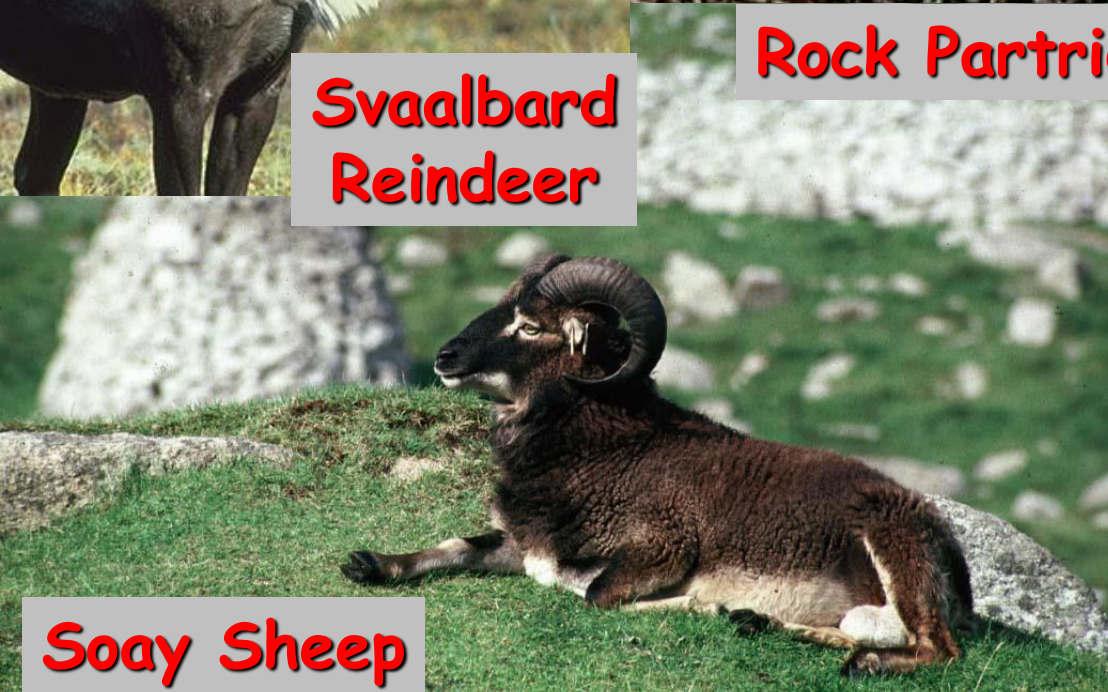
Are grouse a special case?



**Svaalbard
Reindeer**



Rock Partridge



Soay Sheep

Willow Ptarmigan



Trophic Interactions

What are the consequences for population & community?

1. Individual level productivity

Frequency Dist. & Fecundity Reduction

2. Population level dynamics

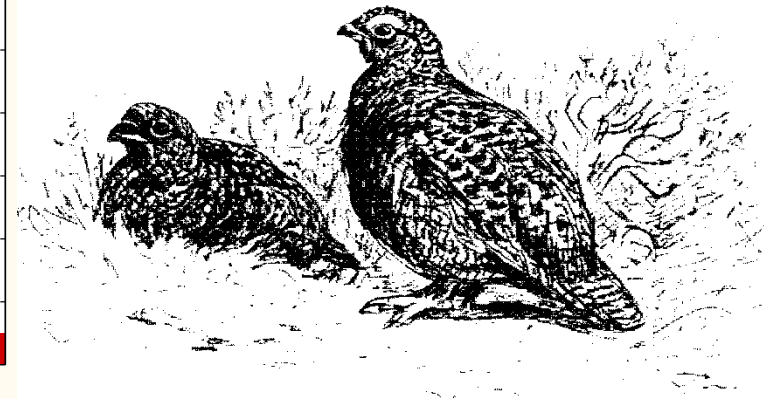
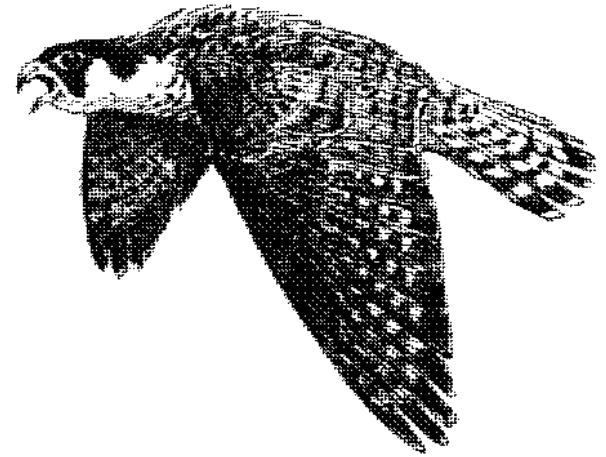
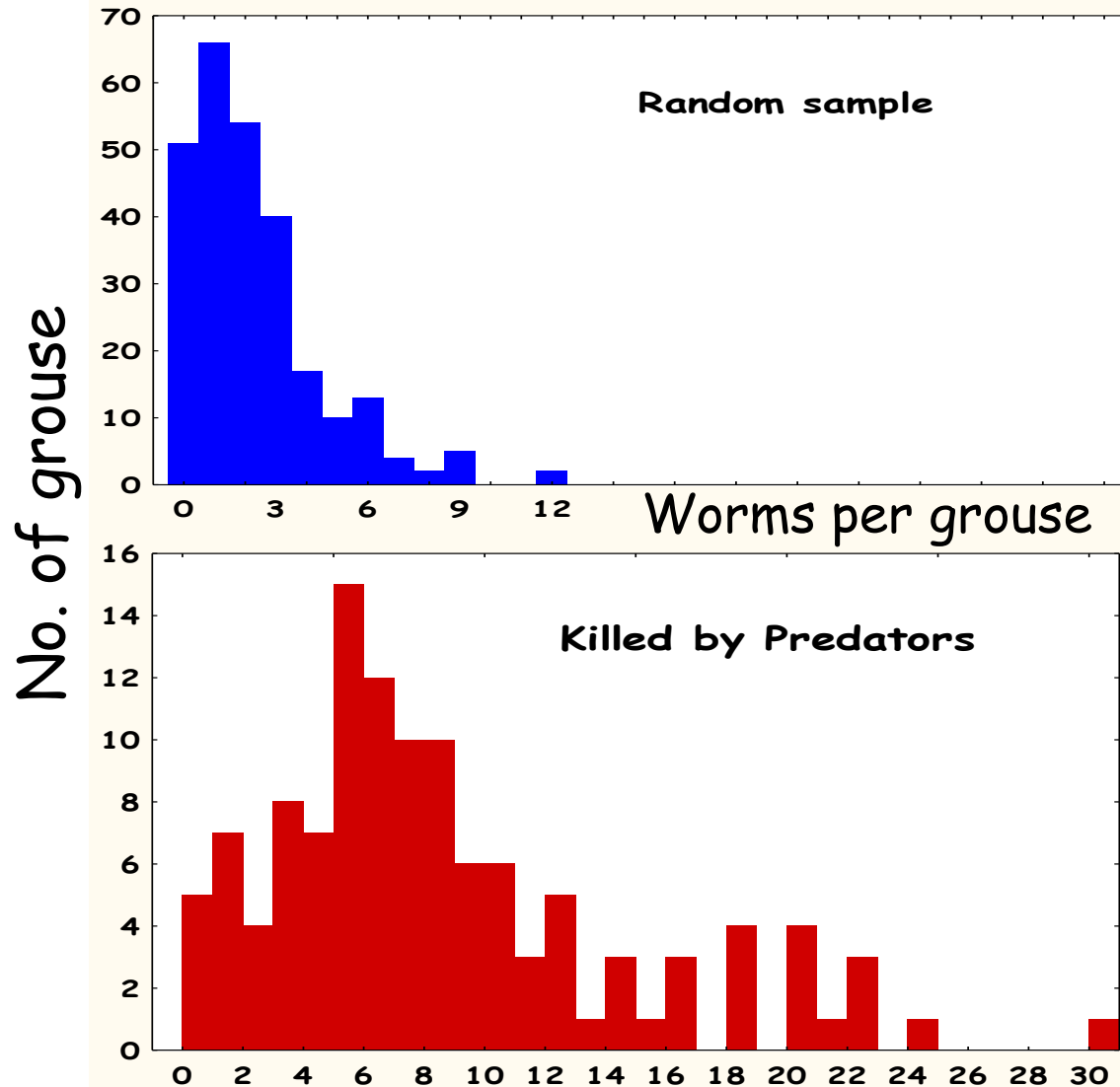
Parasites play a major role & captured in model

3. Community level interactions

Understanding ~ Monitoring Experiments & models

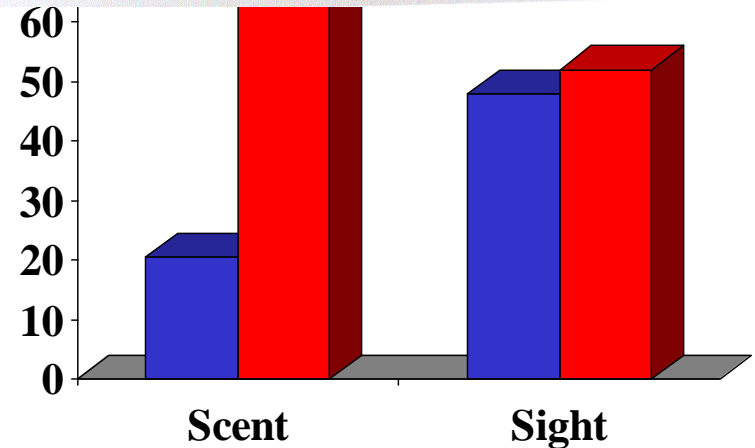
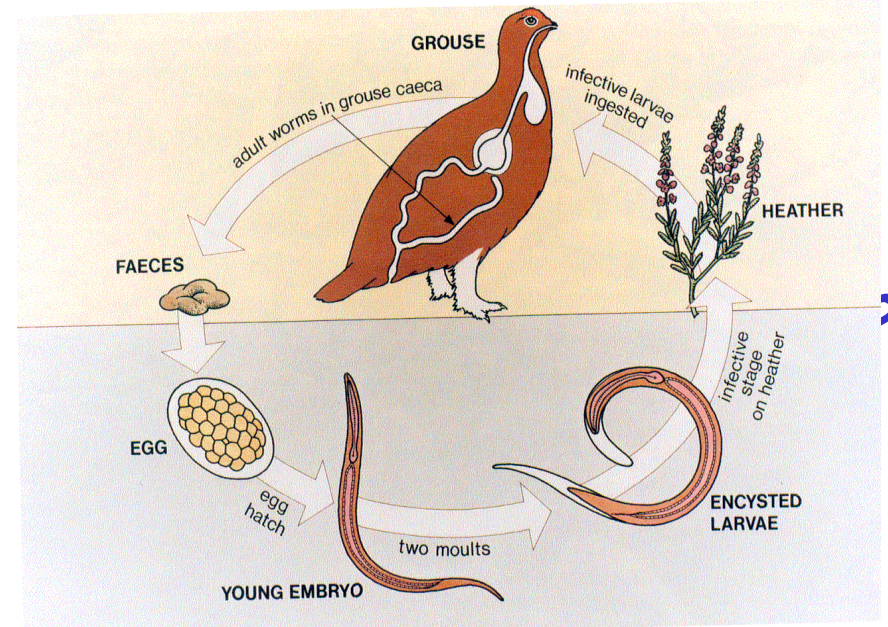
Interactions with Predators

Predators selectively kill heavily infected Hosts



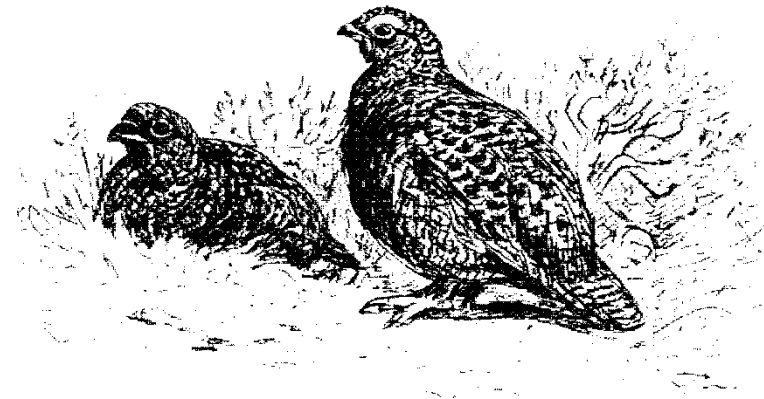
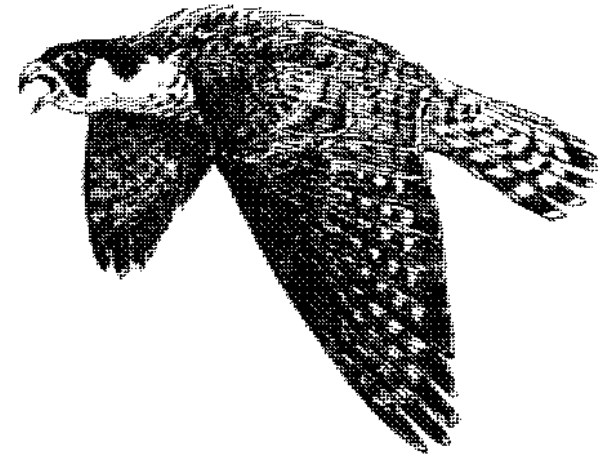
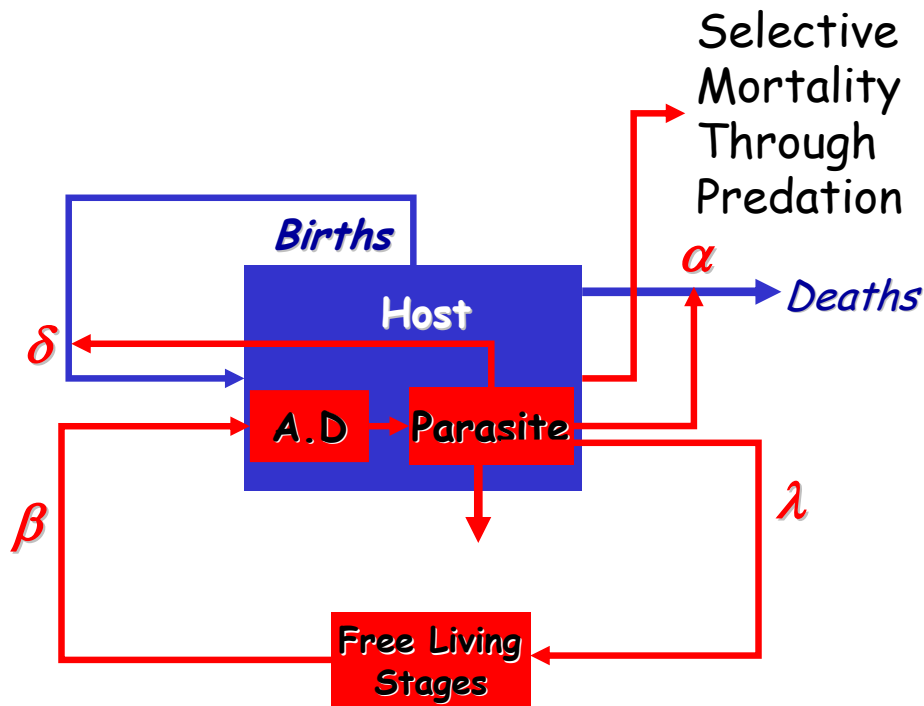
Interactions with Predators

How Do Predators Identify Heavily Infected Grouse?



Do Parasites influence Host Dynamics?

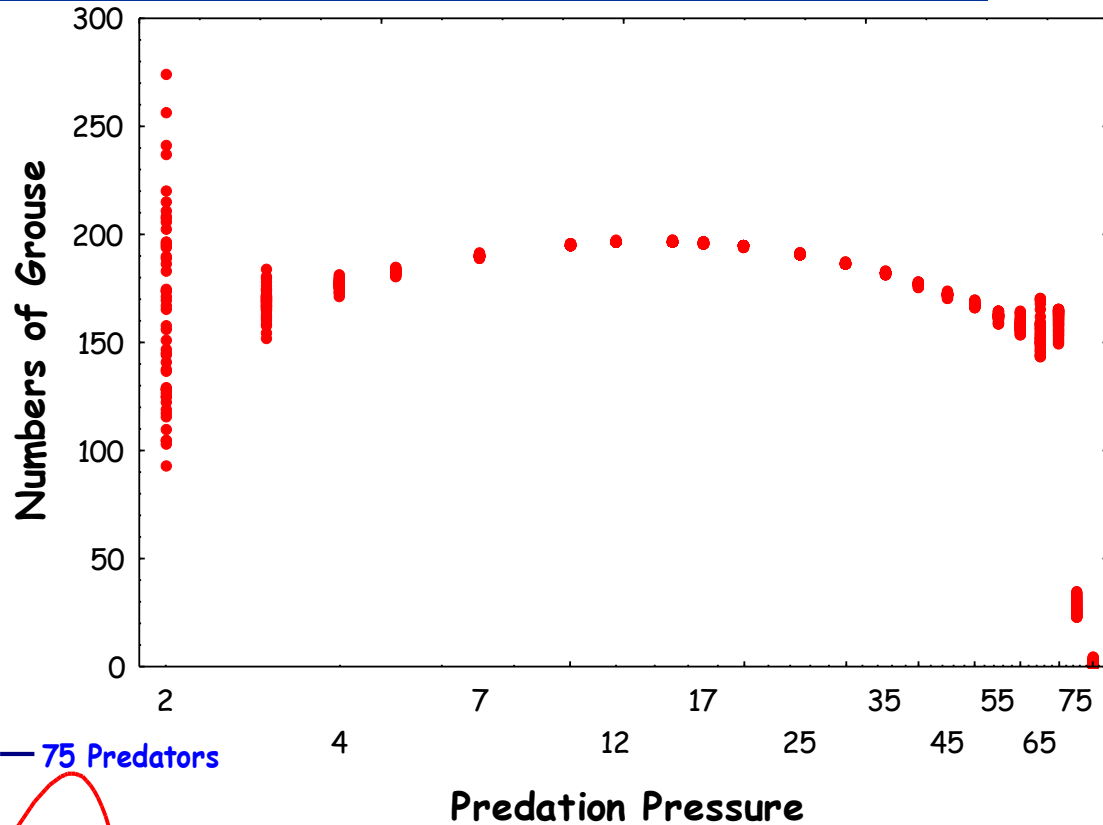
3. Population Level Consequences



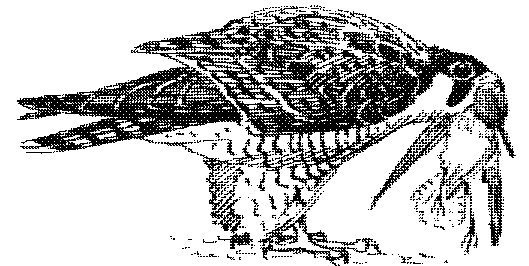
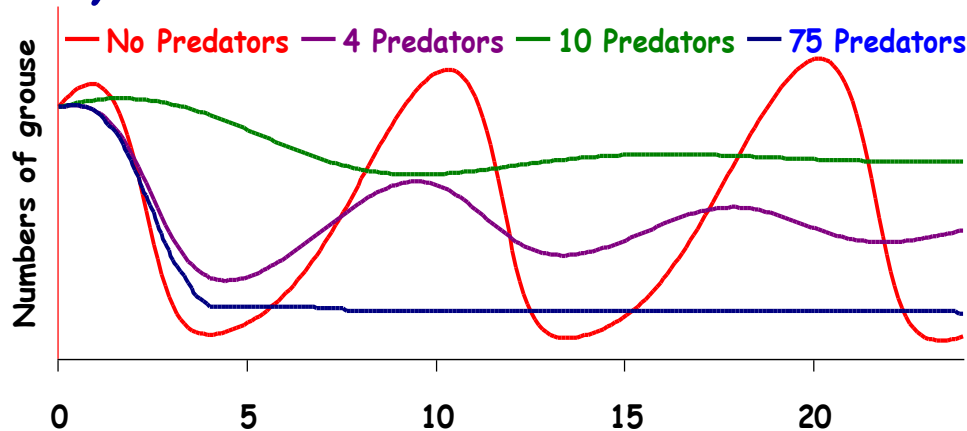
Interactions with Predators

Consequences of Selective Predation

Selective predation
~ dampens cycles
~ increases equilibrium



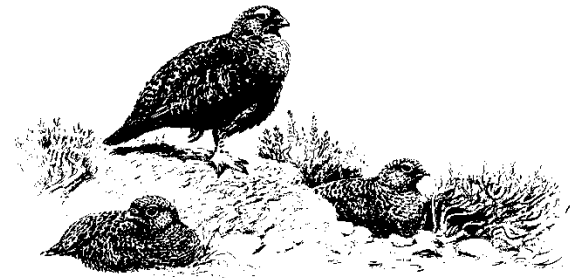
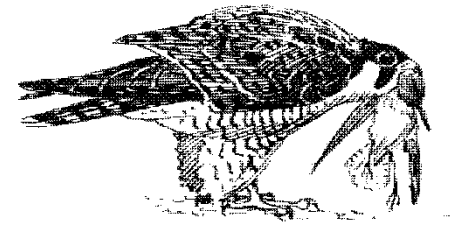
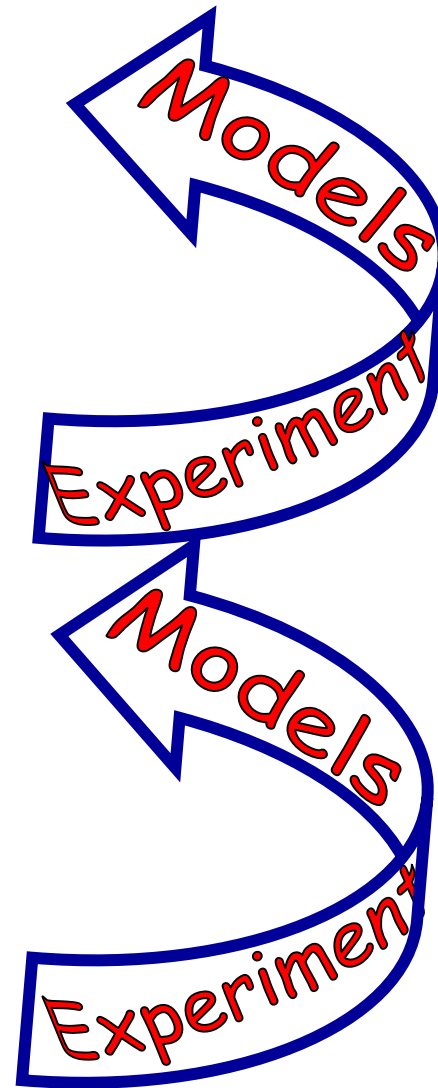
Dynamics



Community Level

*Population Level
Patterns*

*Individual level
Processes*



Global Burden of Intestinal Nematode Infections



- How many people are infected globally?
- What impact does this have on them?
- How much has the situation changed in last 50 years?

M.-S. Chan (1997) *Parasitology Today*, 13, 438-443



Summary

- Understanding the ecology and evolution of host-parasite relationships requires us to develop a quantitative understanding of their natural history.
- This requires us to study parasitic relationships at a range of spatial and temporal scales.
- Mathematics will be as powerful here as microscopes!
- Parasitism is arguably the commonest life-style on the planet – at least 40% of metazoan species are parasitic, maybe 90% of all species.
- Not all parasitism leads to disease.