Grazing and Top Down vs. Bottom Up Regulation

Grazers

- Generally herbivores

- Remove tissue from a large number of ‘prey’ individuals

- Are rarely lethal

What limits grazer population density?

Top down vs. bottom up regulation

Top down

Bottom up

We have already seen that predators can control prey densities

Direct effects

Indirect effects

But can plant abundance also control grazer densities?

How can we answer this question?

We could apply the Lotka-Volterra model…

Prey (Plants)

$$\frac{dN}{dt} = rN - \alpha NP$$

Predator (Grazer)

$$\frac{dP}{dt} = \beta NP - qP$$

α is the *per capita* impact of the predator on the prey

β is the *per capita* impact of the prey on the predator

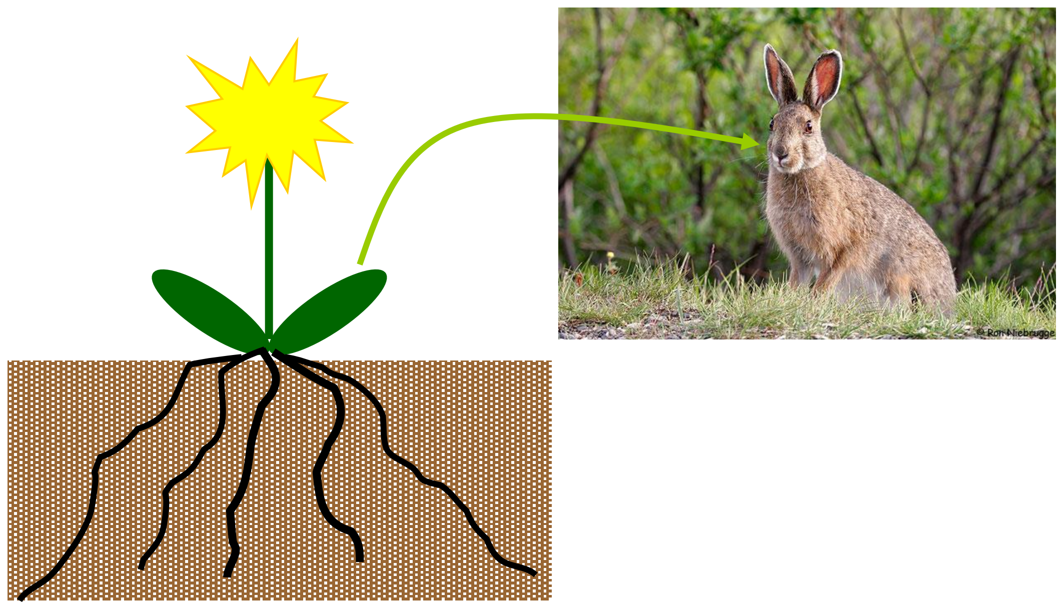
q is the predator death rate

But this implies that grazers kill ‘prey’ individuals outright

But by definition, grazers do not kill ‘prey’ individuals

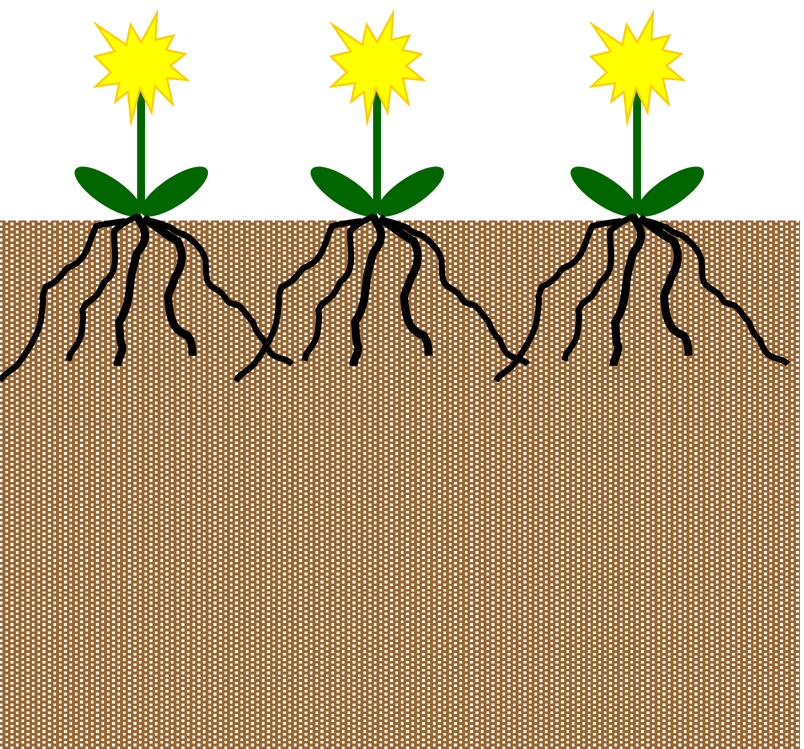
- **Plant parts differ in nutritional quality, so only some parts are eaten**

- **Plant parts differ in levels of chemical defense, so only some parts are eaten**

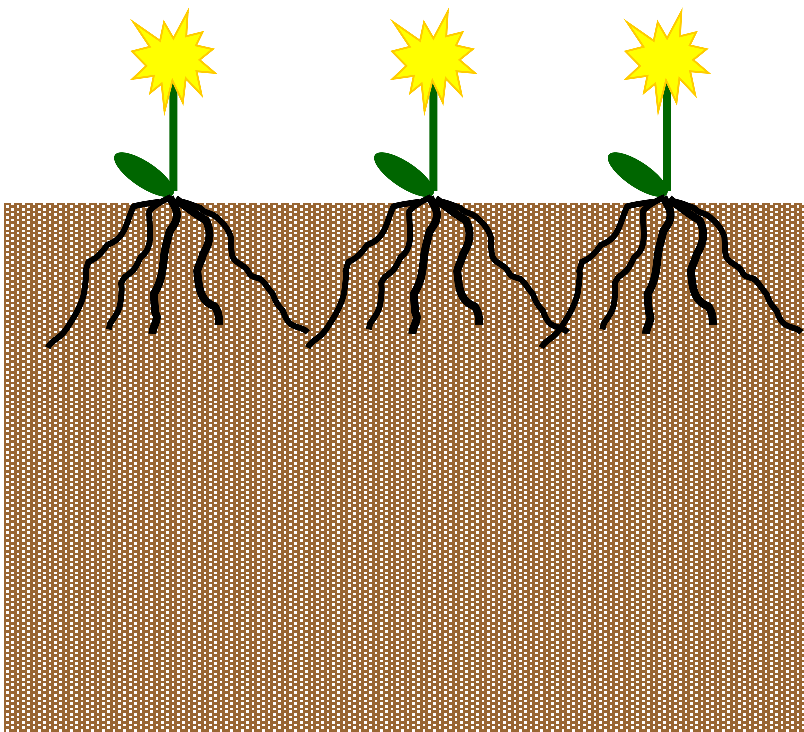


As a result, graze biomass changes, but population density does not

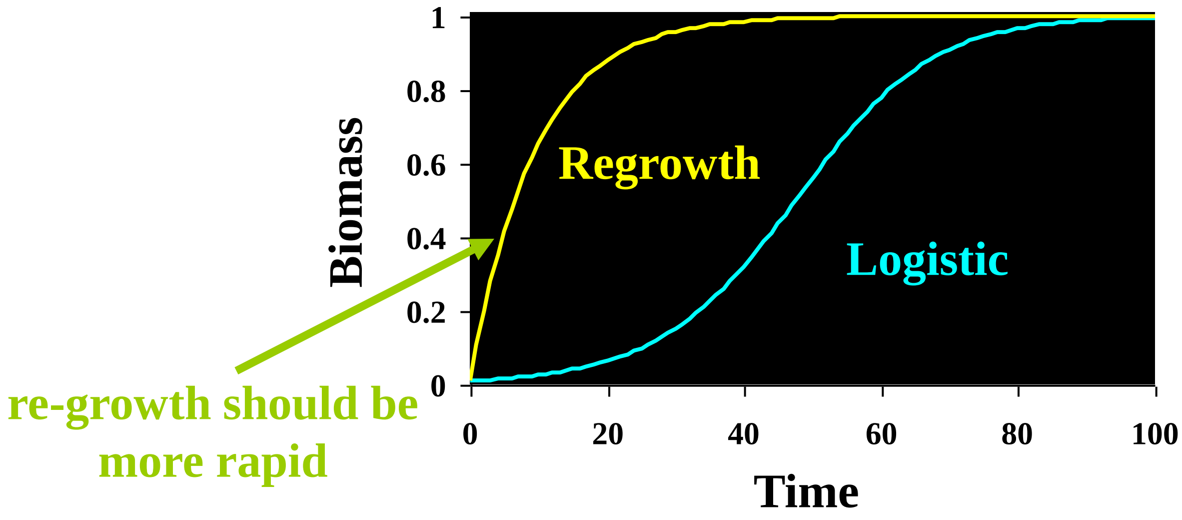
Before grazing

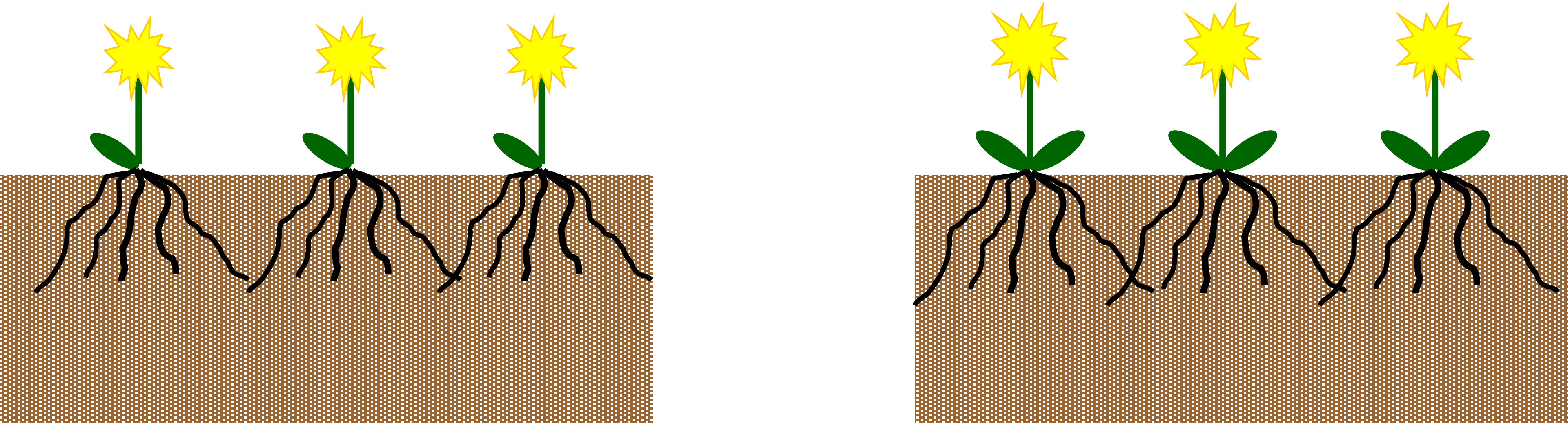


After grazing



The re-growth of graze biomass should not be logistic





A reasonable model of plant-grazer interactions

A Lotka-Volterra model with the following changes:

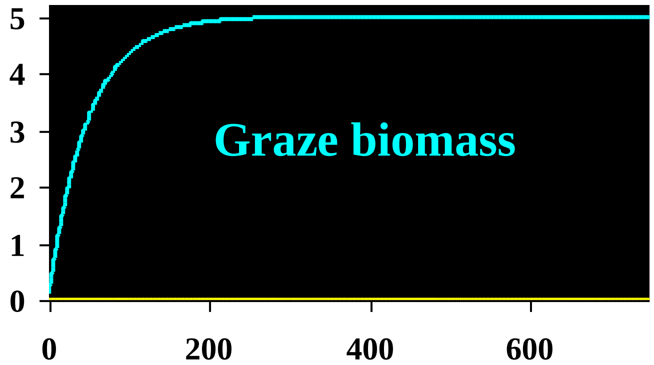
1. Prey (plant) biomass changes in response to grazing, but prey (plant) population density does not.

2. Prey (plant) biomass increases in a ‘re-growth’ rather than logistic fashion.

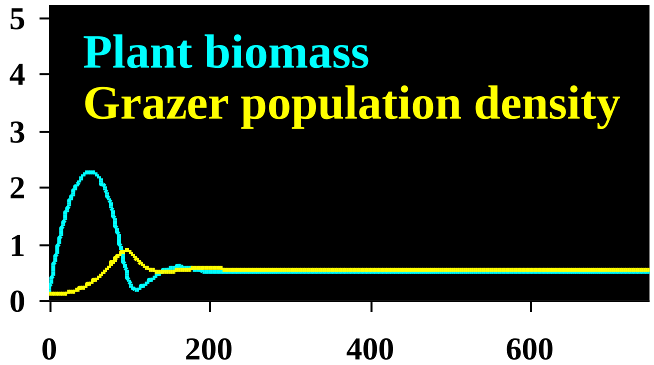
3. A Type II functional response

What does the model tell us?

No Grazers



Grazers



- Interactions between grazers and plants limit plant biomass
- Interactions between grazers and plants limit grazer population densities
- Interactions between grazers and plants lead to stable equilibria, not permanent cycles

A comparison of interactions

Predation

• Predators can control prey population density

• Prey density can control predator density

• Can cause cycles

Grazing

• Grazers can control plant biomass

• Plant biomass can control grazer population density

• Generally does not cause cycles

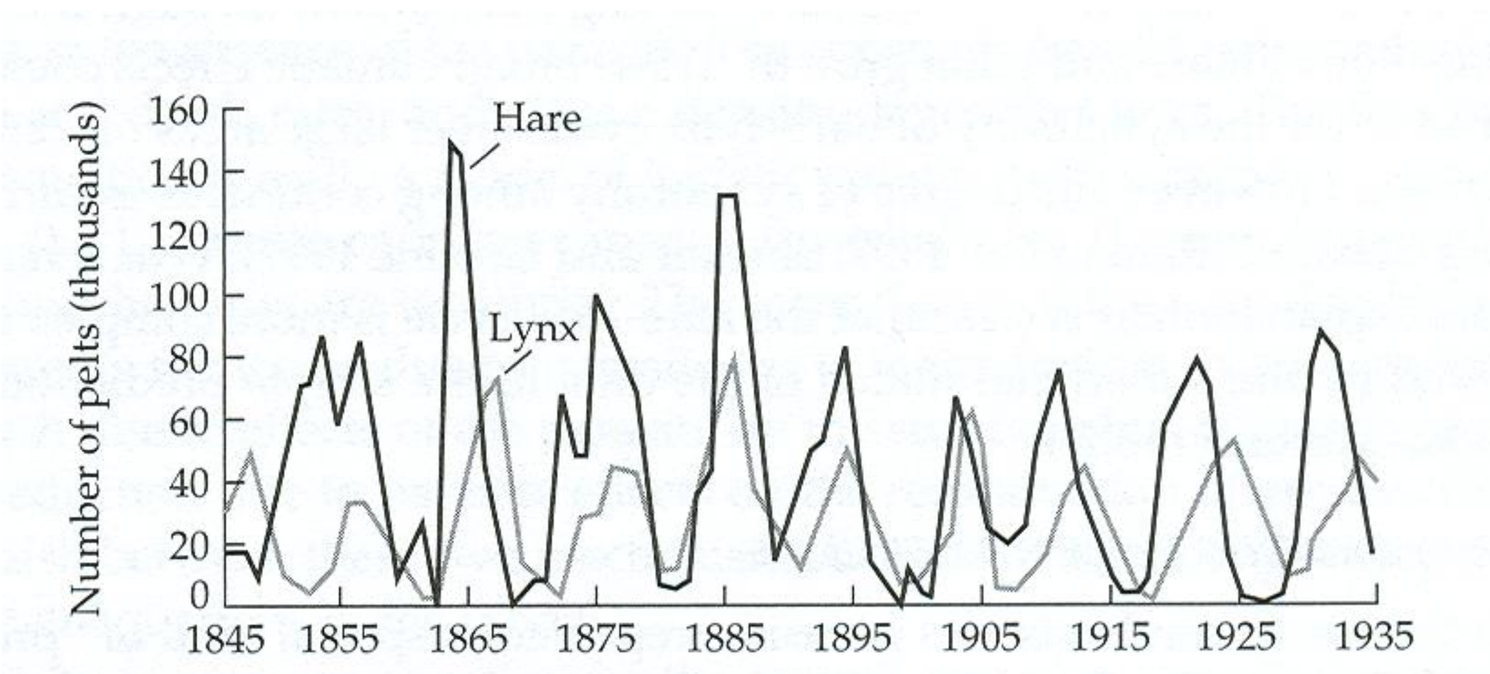
Top down vs. bottom up regulation

Top down

Bottom up

Mathematically, both can work… But what about real data?

Another look at snowshoe hare cycles



Year

The strong cyclical nature of this data would seem to be more compatible with top down regulation. However the simple re-growth model considers only graze quantity and ignores graze quality

An alternative hypothesis

- Hare population density is regulated from the bottom up
- This bottom up regulation is due to both graze biomass and graze quality
- Lynx density simply tracks hare density

Interactions between the hare and its food plants

Grey willow
Salix cinerea

Soapberry
Sheperdia canadensis

Bog birch
Betula glandulifera

Evidence for importance of vegetation (Quantity)

Pease et. al. 1979

• **Studied a population of hares in Alberta from the peak of the cycle to its trough (1970-1975)**

• **Measured food availability to hares during these years**

• **Results showed that in the peak years of 1970 and 1971 food plant biomass was too low to support observed hare population densities**

Evidence for importance of vegetation (Quality)

Bryant et. al. 1979

• **Studied the chemical composition of plants used by hares as food**

• **Found that secondary shoots (produced after intense hare grazing) had significantly greater concentrations of toxic chemicals that deter feeding by snowshoe hares**

• **These results suggested that hare population cycles might be driven by fluctuations in the level of plant defenses**

This led to a new hypothesis

<u>The ‘bottom up’ or ‘food shortage’ hypothesis</u>

1. Hare population density increases, causing increased removal of plant tissues

2. As a result, plant biomass decreases, plant quality decreases, and plants become increasingly well defended with toxic chemicals

3. Consequently, hare population begins to decline due to a shortage of food

4. As hare population density decreases, plant biomass increases and the concentration of toxic chemicals is reduced

5. Lynx do nothing but track the density of the hare population

Comparison of the two hypotheses

Table 10-2 Comparison of the predation and food limitation interpretations of the lynx and hare population cycles; interpretations are identical, except for items 1, 3, and 4

Predation Hypothesis	Food Shortage Hypothesis
1. Hare populations increase due to low predator populations.	**1. Hare populations increase due to food abundance.**
2. Lynx populations keep pace with hare populations.	2. Lynx populations keep pace with hare populations.
3. Lynxes become so numerous that they depress hare populations.	**3. Hare browse declines in quantity and nutritional content; toxic allelochemicals increase.**
4. Hare numbers decline due to intense lynx predation.	**4. Hare numbers decline due to starvation; lower fecundity.**
5. Lynxes starve; population crashes.	5. Lynxes starve; population crashes.
6. Hare populations recover.	6. Hare populations recover.

Which is correct?

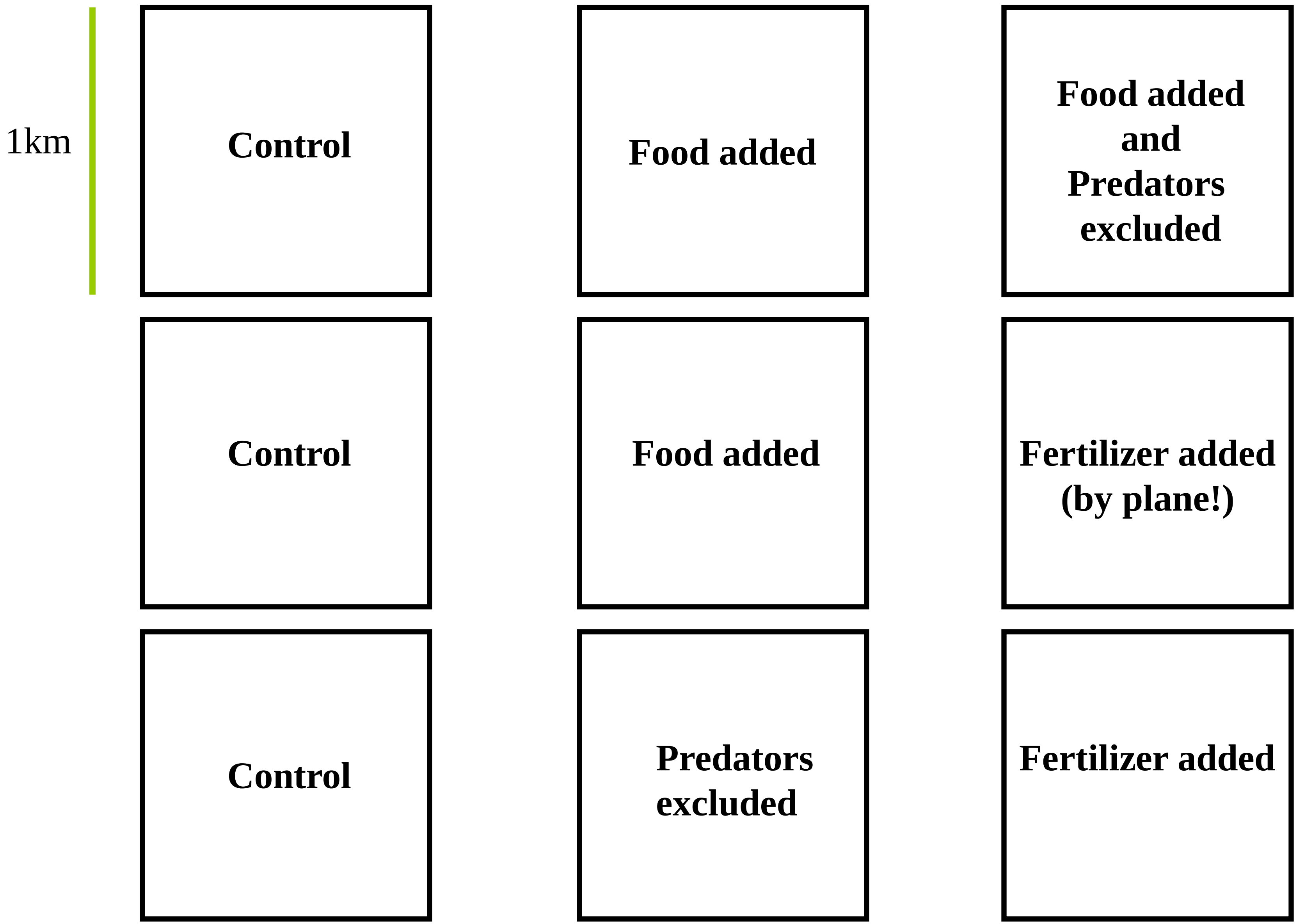
Kluane studies (Krebs et. al.)

- Studied an entire lynx-hare cycle from 1986-1994 in the Canadian Yukon

- Experimentally manipulated both predation and food supply

- Followed lynx and hare densities within 1km square enclosures

Design of the Kluane study



Results of the Kluane study

Food added

Hare density was tripled during peak years

Predators excluded

Hare density was doubled during peak years

Predators excluded & Food added

Hare density was increased eleven fold during peak years

Both food supply and predators play a role in regulating hare population density

What about other systems?

(An example from the diverse mammal community of the Serengeti)


Cheetah


Elephant


Oribi


Leopard


Hippo


Hyenah


Impala


Black Rhino


Serval


Golden Jackal


Wildabeest


Zebra


Lion

Predator species differ in the size of prey they consume

(Sinclair et. al. 2003. *Nature* 425:288-290)

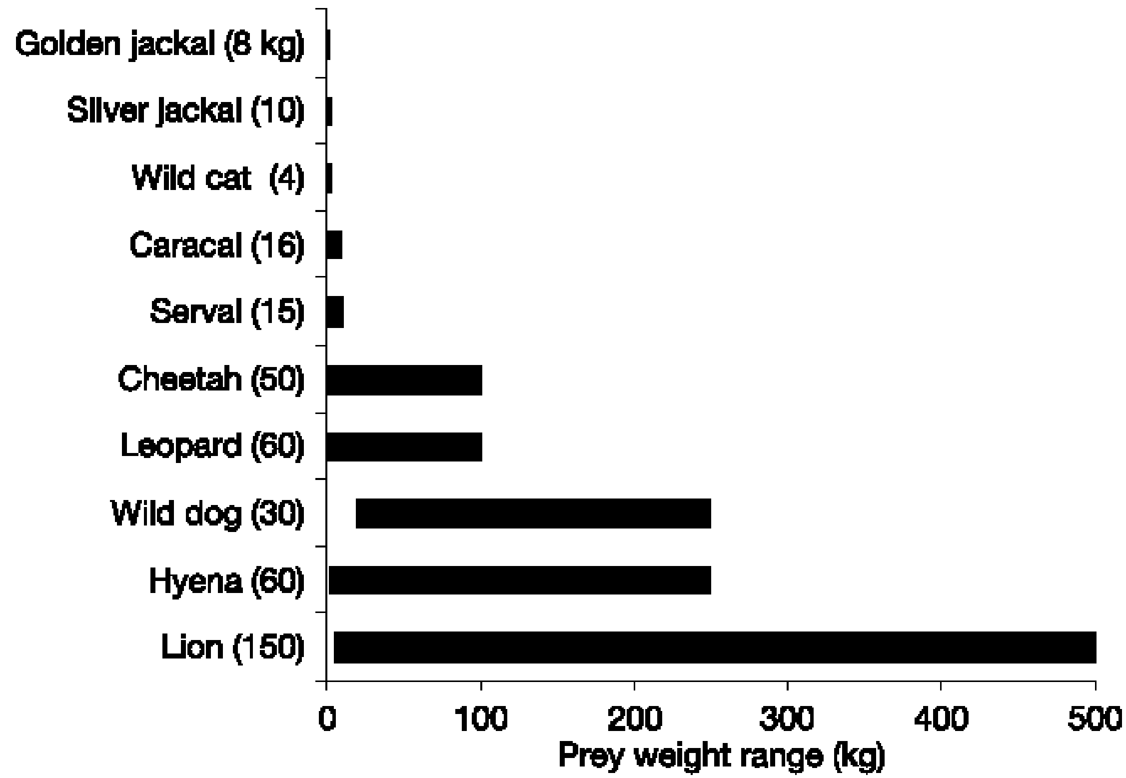


Figure 1 The range of weights of mammal prey consumed by carnivores of different sizes in the Serengeti ecosystem. There is a large overlap in diet at small prey sizes. Data are from our unpublished observations and published sources[17,26].

Therefore, prey species differ in their # of predators

(Sinclair et. al. 2003. *Nature* 425:288-290)

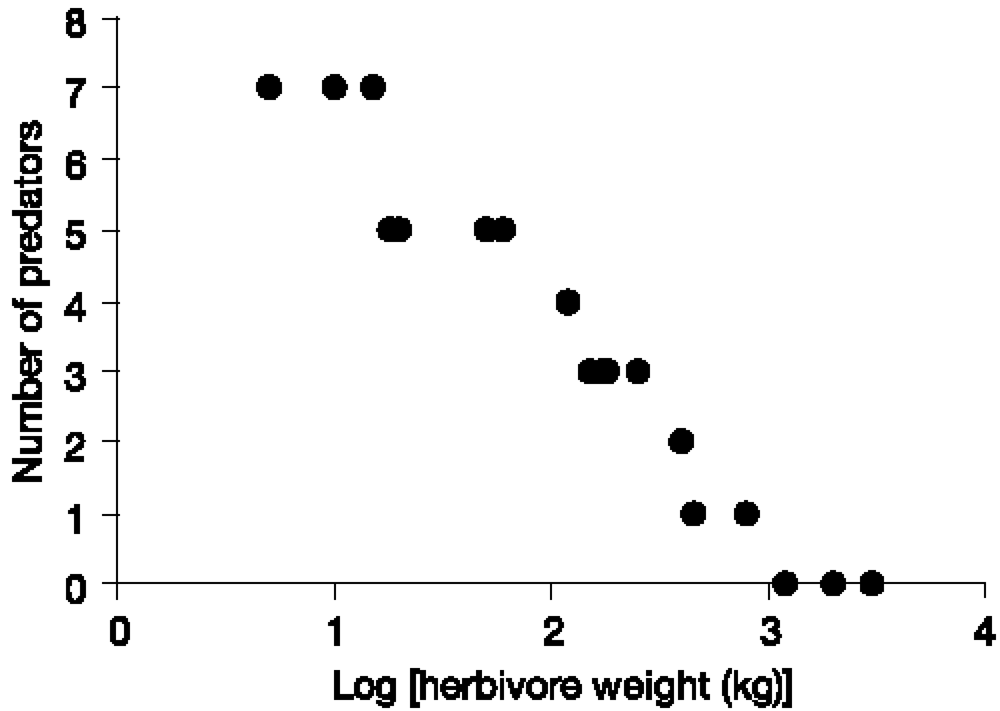
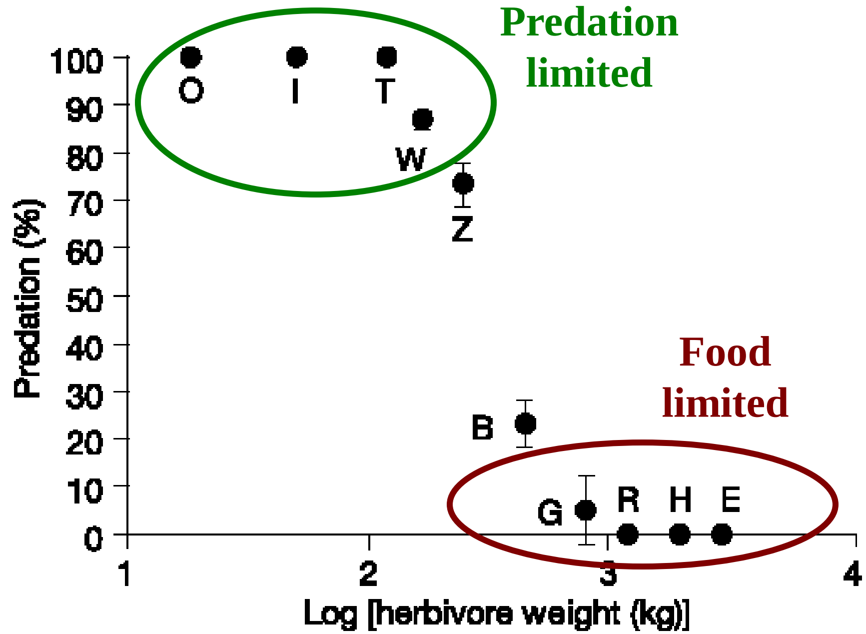


Figure 2 The number of mammal carnivore species that prey upon the savannah ungulates of different body sizes in Serengeti. Adult female body sizes are from published sources[26] and provided in Supplementary Information.

As a result, some prey species experience more predation

(Sinclair et. al. 2003. *Nature* 425:288-290)

Oribi

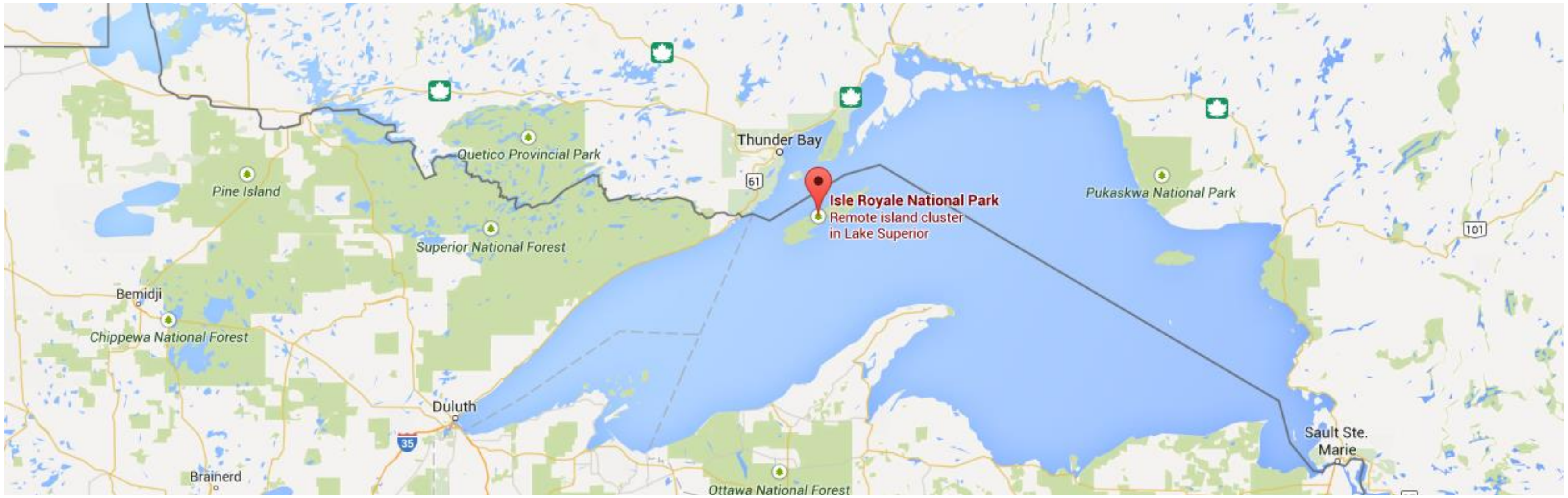


Elephant

Figure 3 The proportion of annual adult mortality accounted for by predation in ten non-migratory ungulate populations for which data were available in the Serengeti ecosystem. There is a threshold in body size of about 150 kg above which predator limitation switches to food limitation. Error bars are 95% confidence limits. Species are: O, oribi; I, impala; T, topi; W, wildebeest; Z, zebra; B, African buffalo; G, giraffe; R, black rhino; H, hippo; E, African elephant. Data are provided in Supplementary Information.

Moose and Wolves on Isle Royale

Isle Royale National Park



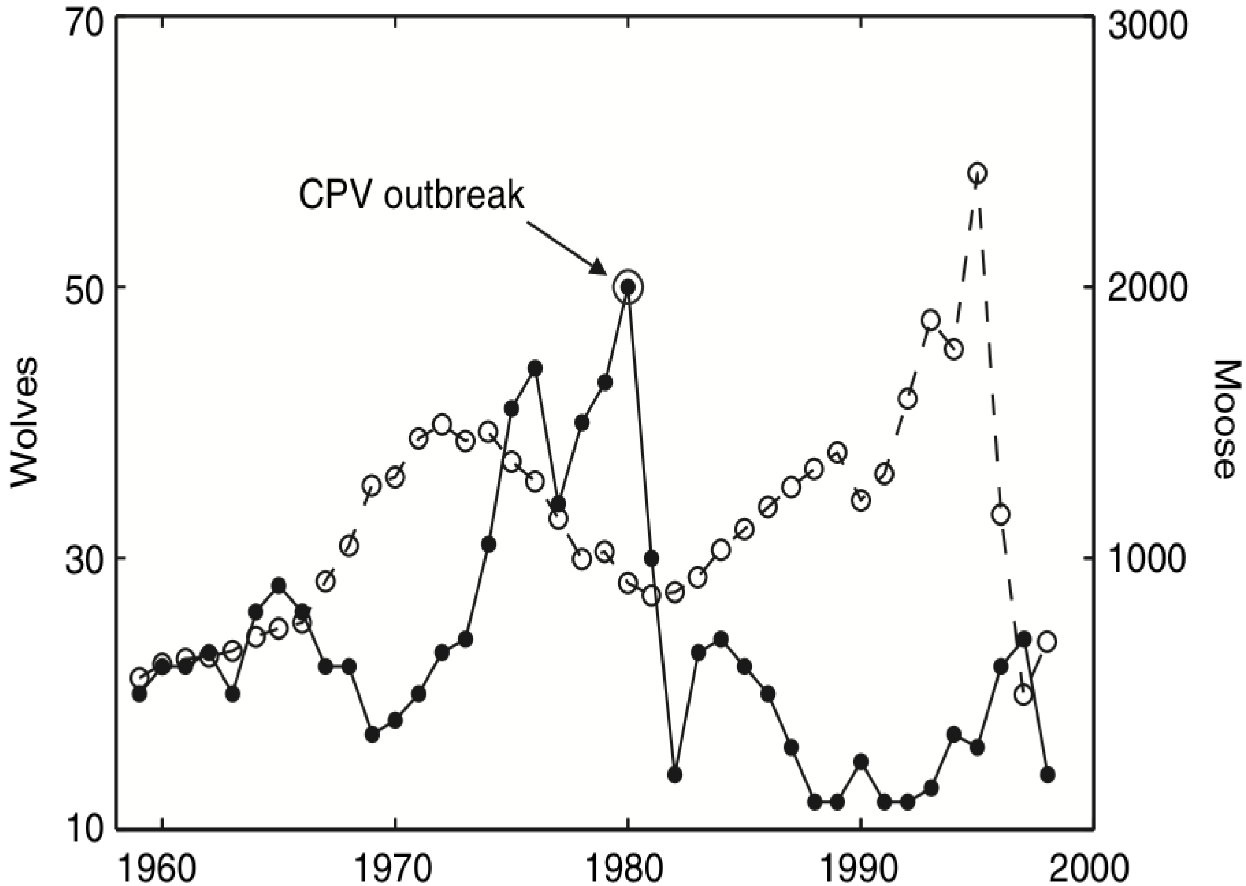
Moose on Isle Royale

- Colonized island around 1890
- Initially rapid population increase
- Experience repeated die offs and population fluctuations

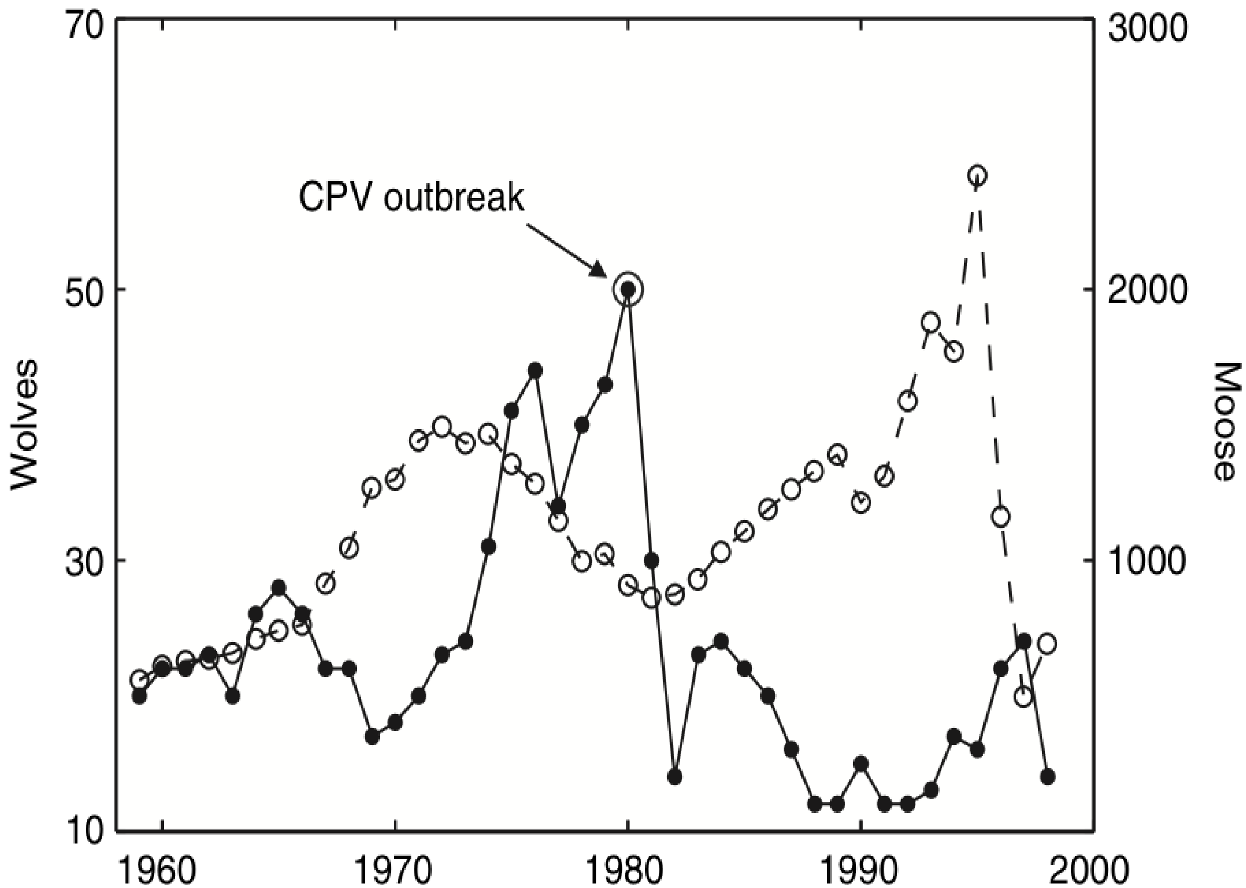
Enter Wolves

- **Arrive on Island in late 1940s**

Population Trends of Wolves and Moose



What Regulates Moose Population Growth?



Could we use this data to find out?

Wilmers, C. et al. 2006 Ecology Letters 9, 383-389

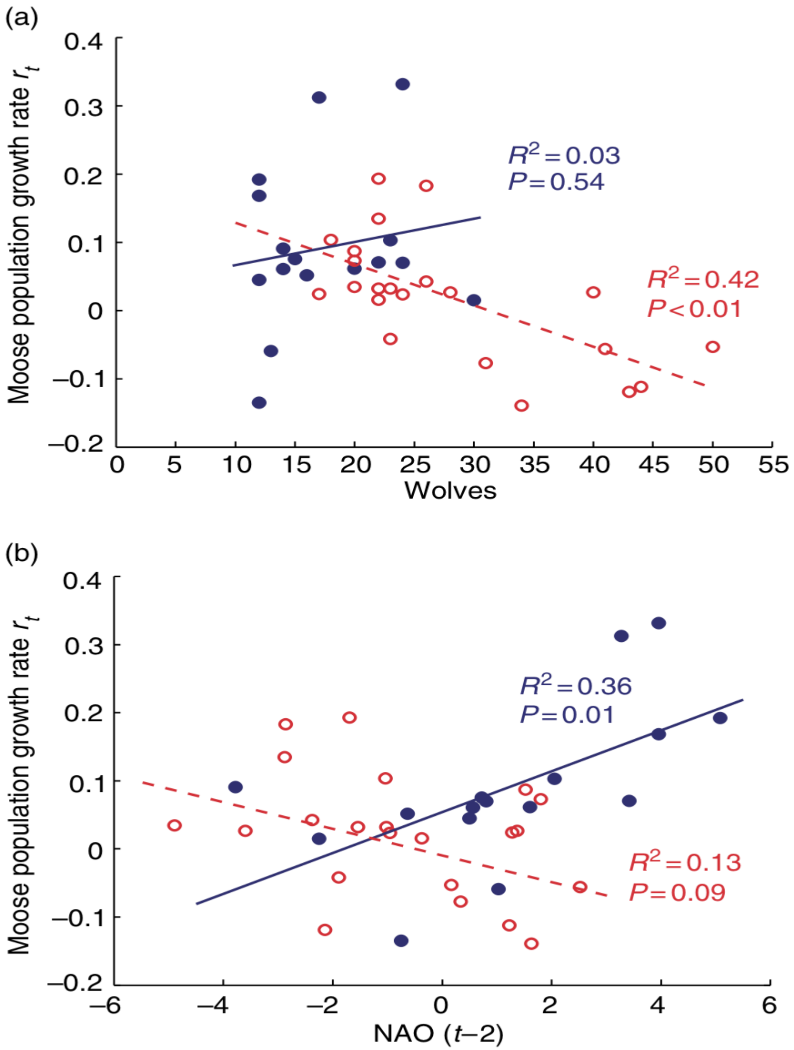
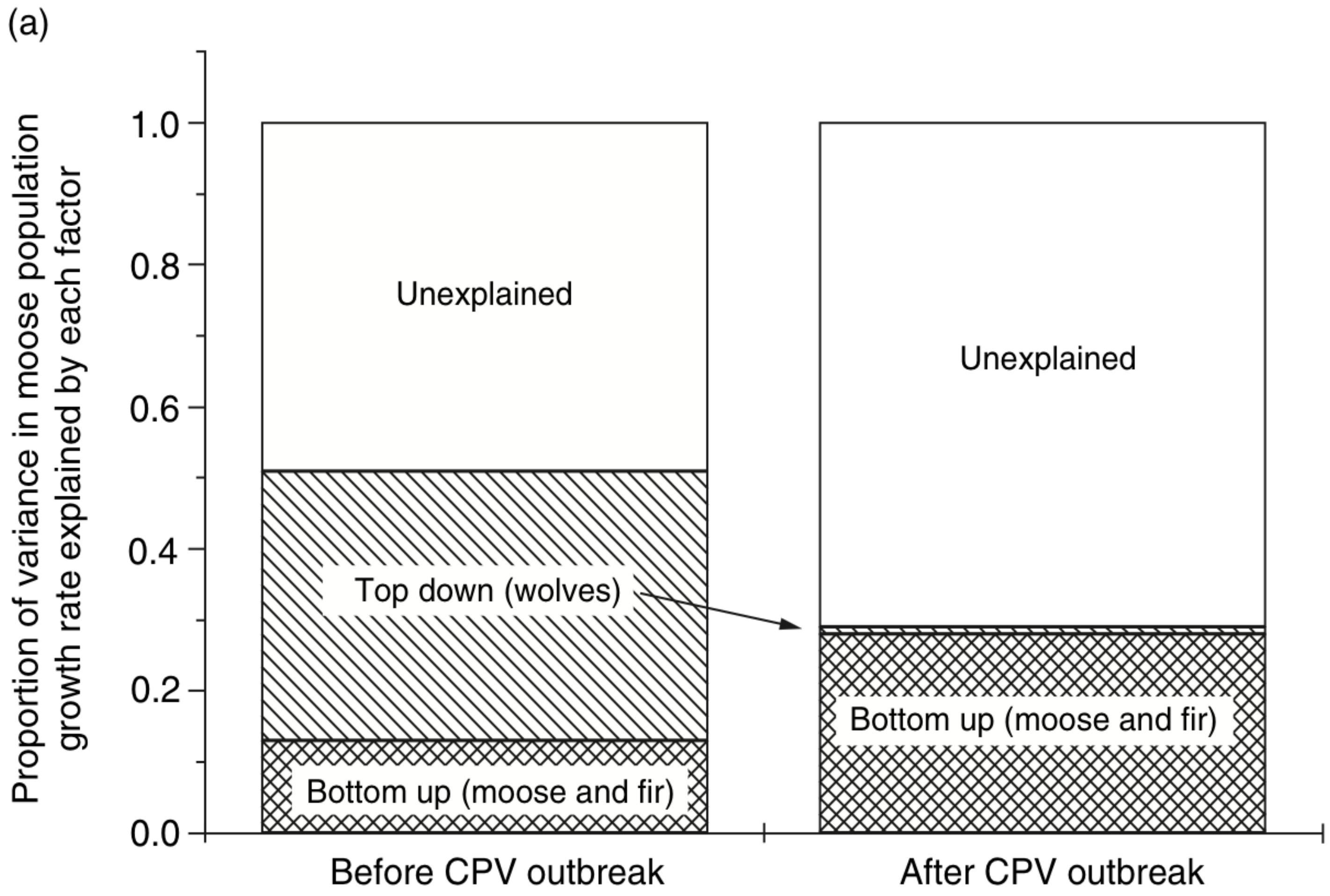


Figure 2 Progression of canine parvovirus (CPV) effects on moose population dynamics on Isle Royale. (a) Wolves have significant negative effect on moose population dynamics before (open circles) CPV outbreak and no effect after (closed circles) outbreak. (b) Climate, as measured by the North Atlantic Oscillation (NAO), has an insignificant effect on moose population dynamics before the crash in the wolf population and a highly significant influence after the crash.

Before Parvovirus outbreak

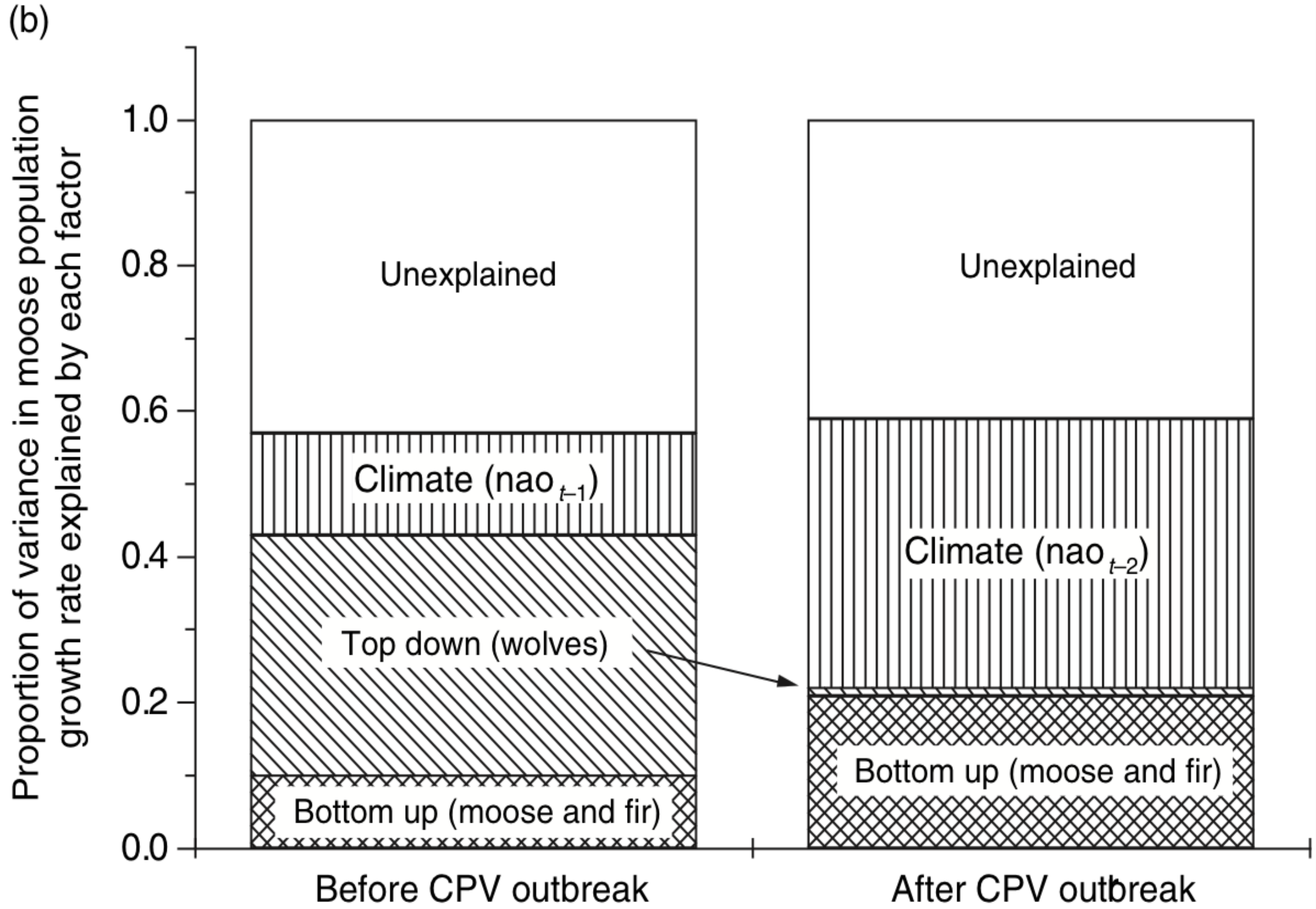
After Parvovirus outbreak

Statistical Model 1: Moose, Food, and Wolves



(b)

Statistical Model 2: Moose, Food, Wolves, and Climate



Summary of wolf moose interactions

- Prior to 1980, wolves regulated moose population densities
  ➔ "Top-down" regulation

- After 1980, moose population densities were regulated by availability of food
  ➔ "Bottom-up" regulation

Summary: Grazing and Top Down vs. Bottom Up Regulation

- Interactions between grazers and plants can control both the density of grazers and plants

- Plant-grazer interactions are less likely to cycle than are predator-prey interactions

- Mathematical models show that both bottom up and top down population regulation are possible and not mutually exclusive

- Empirical studies show that prey density is regulated by both predators and food supply. The relative importance of each depends on species, location, and point in time.