



### Andrewartha and Birch 1951

- Worked on insects in very dry climates - Australia - harsh environment
- Spatial Aspect Metapopulations
- Is it applicable to vertebrates?

# **Quail in Southwest**

- California Quail Leopold 1977
- Forbs in late winter-spring; Complex model
- Residual soil moisture on April 30
- Percent adults in females
- $r^2 = 96\%$
- Gambel Quail Gallizioli 1965
- Latest: Natural compounds in forbs mimic estrogens and produce physiological changes in hens.







# David Lack 1954

- Natural Regulation of Animal Populations
- Argues for food as primary factor in birds because:
  - 1. Few birds die of disease or predation
  - 2. Birds are more numerous where food is abundant
  - 3. Each species eats different foods in same habitat; otherwise lives in different habitats
  - 4. Birds fight for food, especially in winter





- If find a population decreasing, must consider the hypothesis:
  - Individuals in population have changed and now are more susceptible to same environmental mortality factors.
- He was studying microtines which are highly irruptive or cyclic



#### Behavior limits breeding population Watson

#### and Moss (1970)

### • Must show:

- 1. A substantial part of the population does not breed.
- 2. Such non-breeders are physiologically capable of breeding if the more dominant or territorial animals are removed.
- 3. Breeding animals are not completely using up some resource.
- 4. This mortality or depressed recruitment changes to just compensate for changes in other sources of mortality or depressed recruitment.







### Behavior limits breeding population Watson

#### and Moss (1970)

5. If 1-4 true and numbers change following changes in food, then both food and behavior are limiting population.

#### Red Grouse Habitat and Food

- Abundant on moors in Scotland
- Main food is heather (Calluna vulgaris)
- Total quantity of heather vastly exceeds requirements at all times
  - Few signs of grazing
  - Less than 5% removed
  - But they sometimes select heavily for nitrogen and phosphorous

### **Red Grouse Food Selection**

- Collected Red Grouse and compared crop contents to heather <u>clipped</u> in area.
- Placed grouse in portable pens and compared diet quality to current years and tips of current growth
- Grouse selected heather higher in nitrogen and phosphous than available when N and P low.



### **Timing**

- Territories distributed annually in Oct.-Nov.
- Held till late May
- 3 categories of individuals:
  - Territory holders
  - Floaters
  - Others

### **Tests of territories**

- How would you test what determines size of territories?
- Androgen implant makes cocks take a bigger territory.
- Estrogen implant -> lose hen, less territorial behavior, loses territory

### **Red Grouse Nutrition Experiments**

- Red Grouse populations on areas over base-rich rocks are more dense than in areas with poorer (less productive) soils
- Experimental treatments: (overhead)

### **Territories**

- Change from year to year
- Overhead

### Size of territories

Bigamous cocks have significantly larger territories than cocks with one hen whose are larger than unmated cocks.

More aggressive cocks have larger territories.

### Does territorial behavior limit population

### size in grouse?

- 1. Many birds fail to get territories in the fall. - They all die before spring. - Thus do not breed.
- 2. These birds can breed if remove territory holders.
- 3. Food limiting? Difficult Birds take less than 5% of annual production of heather.



# Summary

## Where to now St. Peter?

• Key feature missed until recently