Parasite distribution

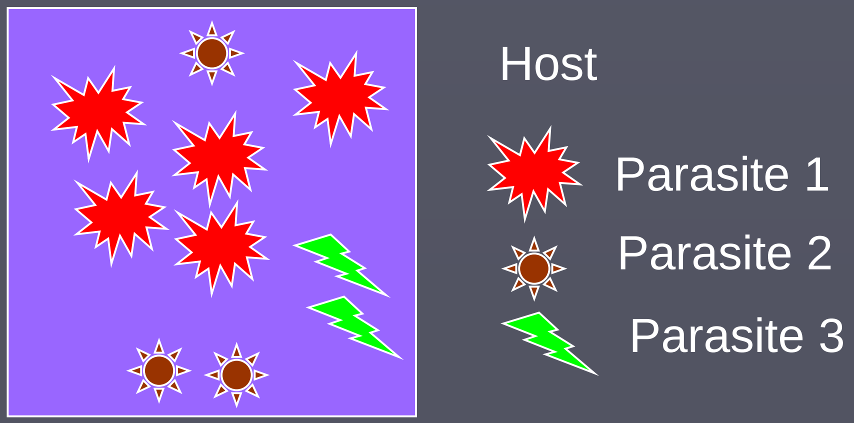
Parasite Populations

- Population – a group of individuals of a given species at a given time and in a given area

- Population characteristics:
- natality
- mortality
- age structure
- reproductive capacity
- dispersion
- growth
- density

Infrapopulation of parasites

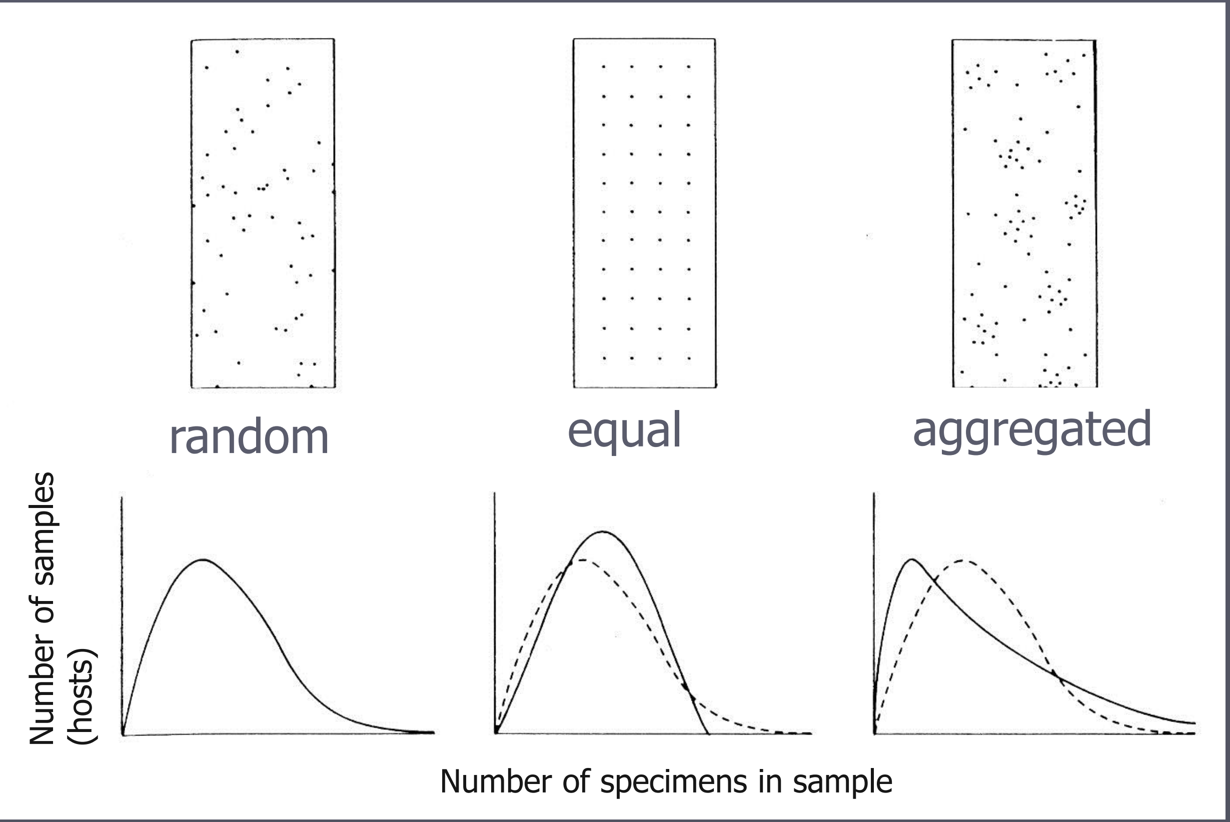
- a set of all individuals of one species of parasite on/in one host individual
- Short life span – limited by life span of the host individual
- Individual host - one or more infrapopulations of different parasitic species



Distribution of parasites

Distribution of parasites in the host population

- frequency distribution



Variance = mean
Poisson distribution

Variance < mean
Positive binomial function

Variance > mean
Negative binomial function

Aggregation of parasites

- Hosts = components of a suitable habitat in an inhospitable environment

  Some components contain more parasites than average, others less so

- Tendency to aggregate: main characteristics of parasitic infection

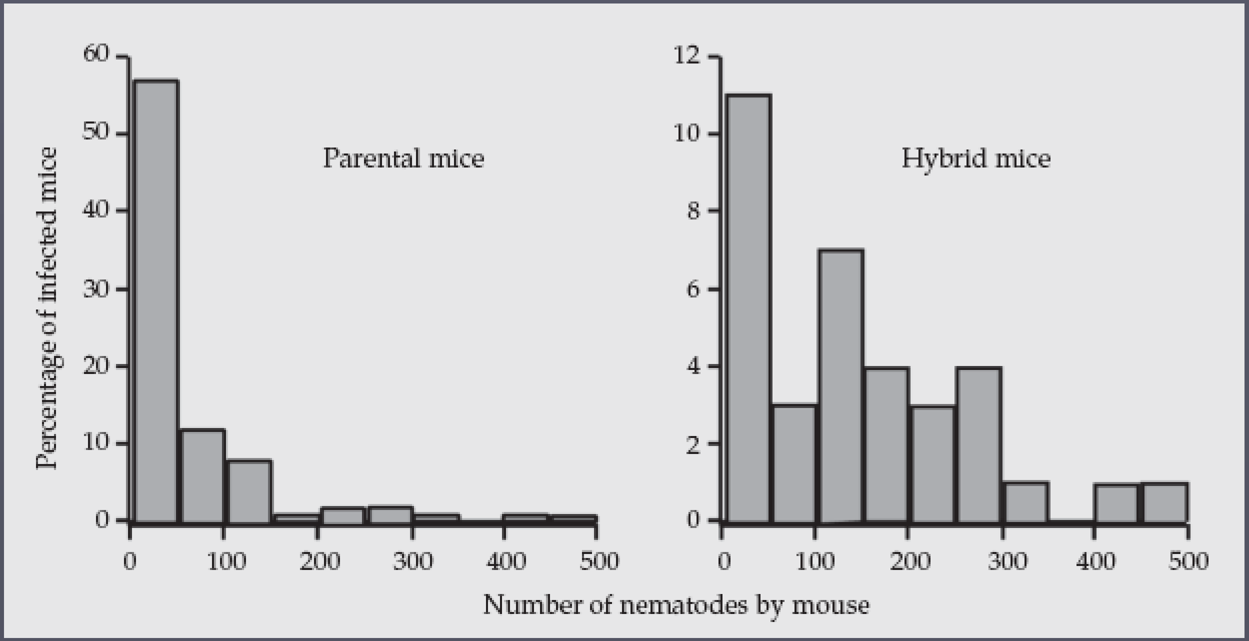
- The distribution of parasites over time is not static

- It cannot be expressed by a single measurement

- At multiple levels: at the level of individuals (within the population), at the level of microhabitats (within the host)

Aggregation of parasites

- Most hosts have a low frequency of parasites or are not parasitized at all, few hosts have a high number of parasites



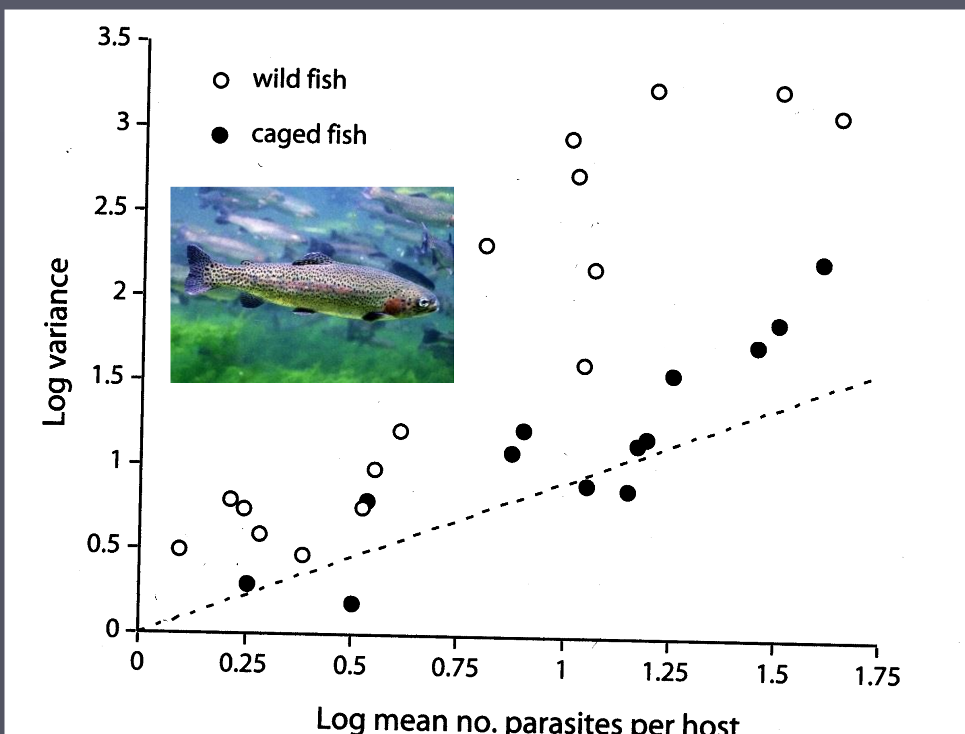
Distribution of the number of nematodes (*Aspiculuris tetraptera* and *Syphacia obvelata*) in the parental mice (*Mus musculus* and *Mus domesticus*) and their hybrids (Moulia et al. 1991).

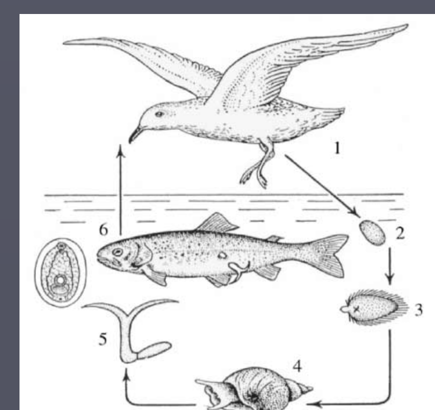
Causes of aggregation

- Temporal and spatial heterogeneity of host exposure
- Intraspecific variability of the host - immune response, size, age, sex, physiology or behavior of the host, genetically fixed differences in susceptibility to parasites
- The result of a combination of several factors
- Variability in different host-parasite systems → the degree of aggregation depends on the properties of the parasites and hosts

Causes of aggregation: heterogeneity in host exposure to parasites

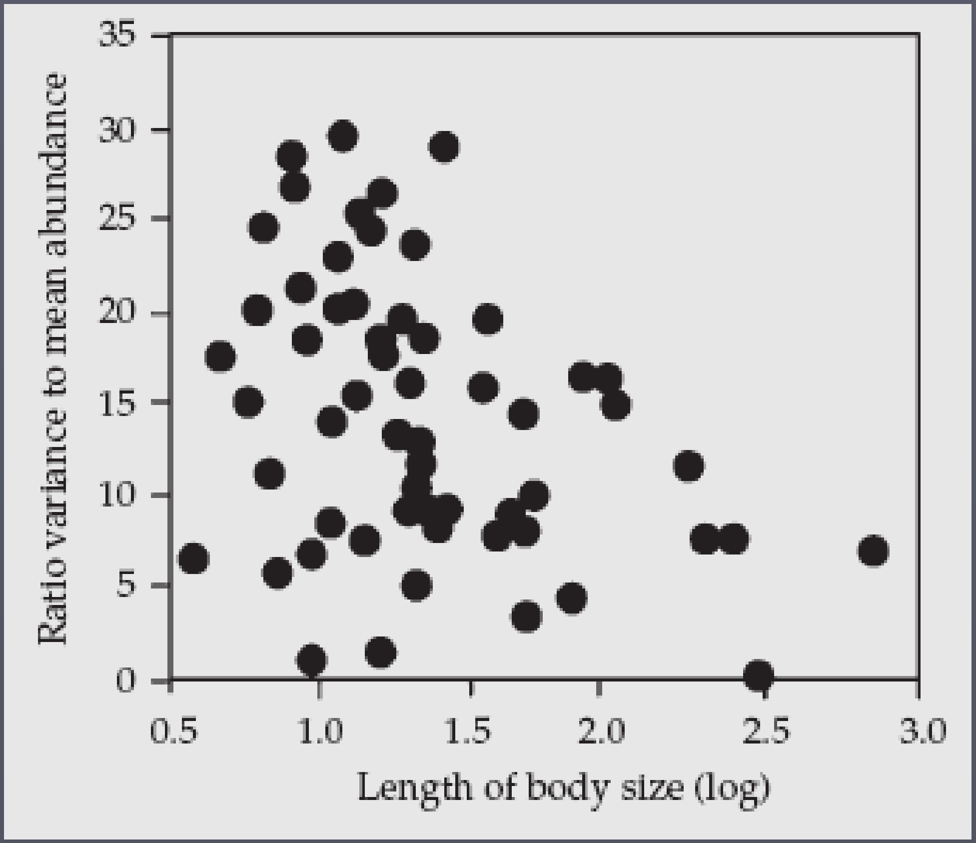
- Ex. Karvonen et al. (2004) - heterogeneity in exposure of hosts to metacercariae *Diplostomum spathaceum* (Trematoda) in rainbow trout *Oncorhynchus mykiss* leads to parasite aggregation





Causes of aggregation: parasite size

Ex. Poulin & Morand (2000) 59 species of gastrointestinal nematodes in mammals

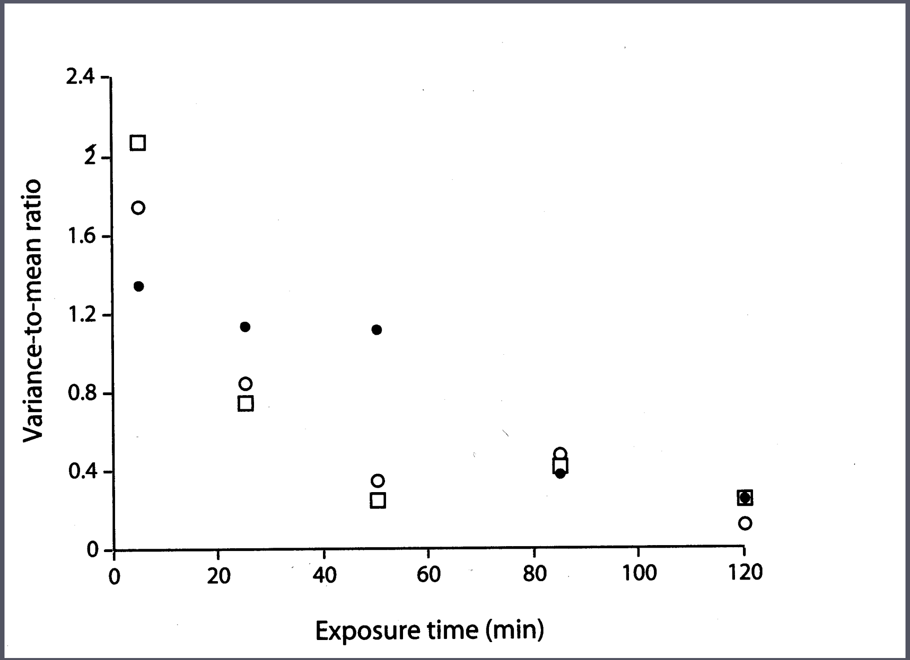


Causes of aggregation: exposure time

- Ex. Experimental infection with ectoparasite (*Argulus foliaceus*) in *Oncorhynchus mykiss*

  \- same infectious dose, different exposure time

  \- differences in host exposure may generate an aggregated distribution



Causes of aggregation: diverse distribution of the parasite in time and space

- ex. Keymer & Anderson (1979)

  experimental study – aggregated distribution of infectious stages in space leads to aggregated distribution of parasites in the host population

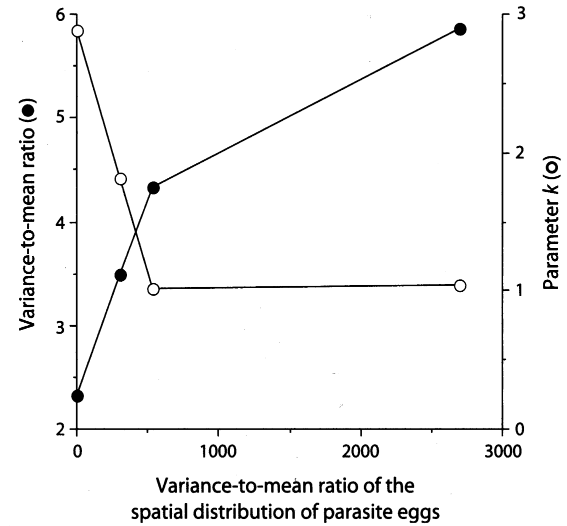
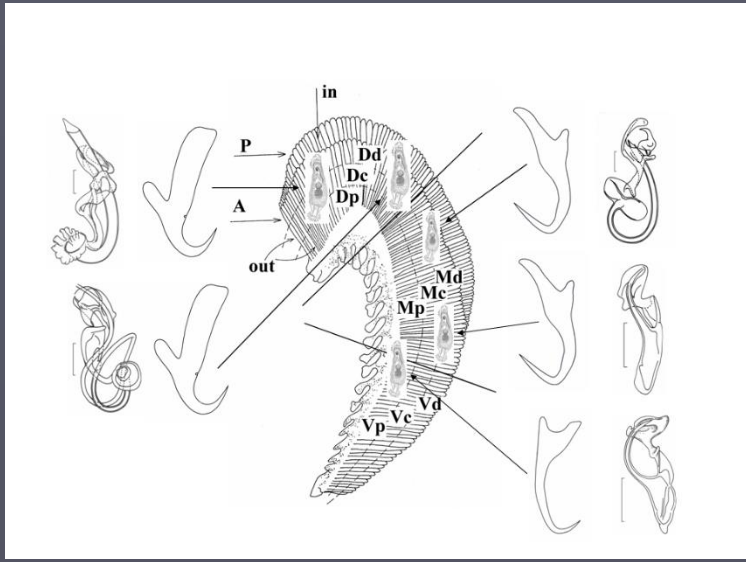


Figure 6.6 Relationship between the aggregation of parasites among their hosts (measured using both the variance-to-mean ratio and the parameter *k* of the negative binomial distribution) and the spatial distribution of parasite eggs. Data are from experiments in which equal numbers of beetles, *Tribolium confusum*, were exposed to identical numbers of eggs of the cestode *Hymenolepis diminuta*, for which it acts as an intermediate host; only the dispersion of eggs varied between treatments. (Modified from Keymer and Anderson 1979)

Consequences of aggregation

- Advantages of aggregation for parasites

- Encounters for reproduction, the "mating rendez-vous" hypothesis - in the case of low population densities (Monogenea)



- Factor facilitating species coexistence (high aggregation at intra-species level than in inter-species level)

Consequences of aggregation

- „crowding effect“ (Read, 1951)

  - in large infrapopulations

  - strong aggregation could reduce the fitness of parasites

  - high numbers of parasites on/in host specimen = smaller average size of parasites (e.g. Cestoda)

  - growth and fecundity are density dependent (for many parasites)

Consequences of aggregation

- Population of adult parasites in the definitive host - more small individuals with low fecundity, several large individuals with high fecundity (superior parasite genotypes?)

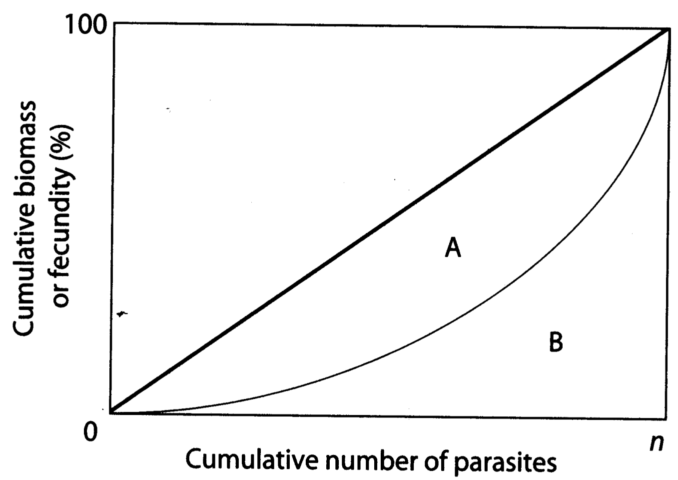


Figure 6.10 The Gini coefficient used to quantify inequalities among parasites in size or egg production is simply the relative discrepancy between the observed distribution of biomass or fecundity among parasites (curve) and their hypothetical uniform distribution (straight line). It can be quantified as the ratio of area A to area (A + B). The cumulative biomass or fecundity is plotted against the cumulative number of parasite individuals, with parasites ranked from the smallest or least fecund to the largest or most fecund prior to being summed up. (From Dobson 1986)

Consequences of aggregation: genetic diversity in the parasite populations

- Impact on genetic variability of parasitic populations – reduction of genetic variability
- Ex. The genetic variability of parasitic helminths is lower than in free-living invertebrates
- Different heterozygosity in parasitic and free-living organims

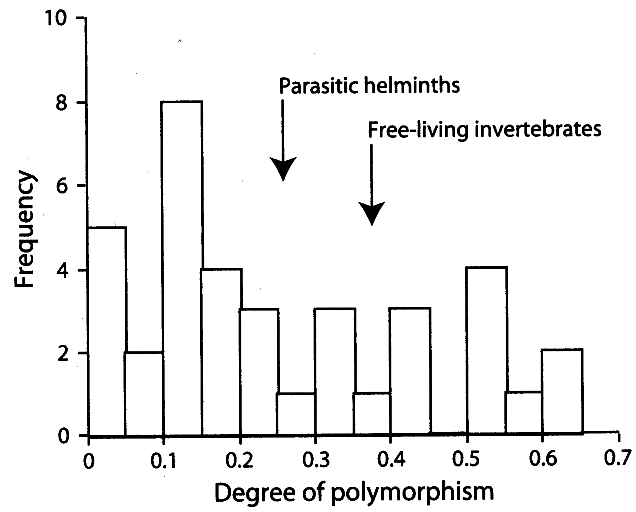


Figure 6.11 Frequency distribution of levels of genetic polymorphism among thirty-seven parasite populations, representing twenty-four helminth species. Polymorphism is measured as the proportion of polymorphic loci among those surveyed. The mean for the helminth populations is shown, along with that for free-living invertebrates in general (Data from table 16.2 in Bush et al. 2001)

Consequences of aggregation: genetic diversity of parasites

Distribution of rare alleles - eggs produced from the same adult are genetically more similar than eggs of different adults

Cornel et al. (2003) model of the spread of rare, recessive but beneficial, alleles of trichonstrogylid nematodes parasitizing ruminants (i.e. aggregation is associated with a certain degree of inbreeding)

Consequences of aggregation: shift in sex ratio

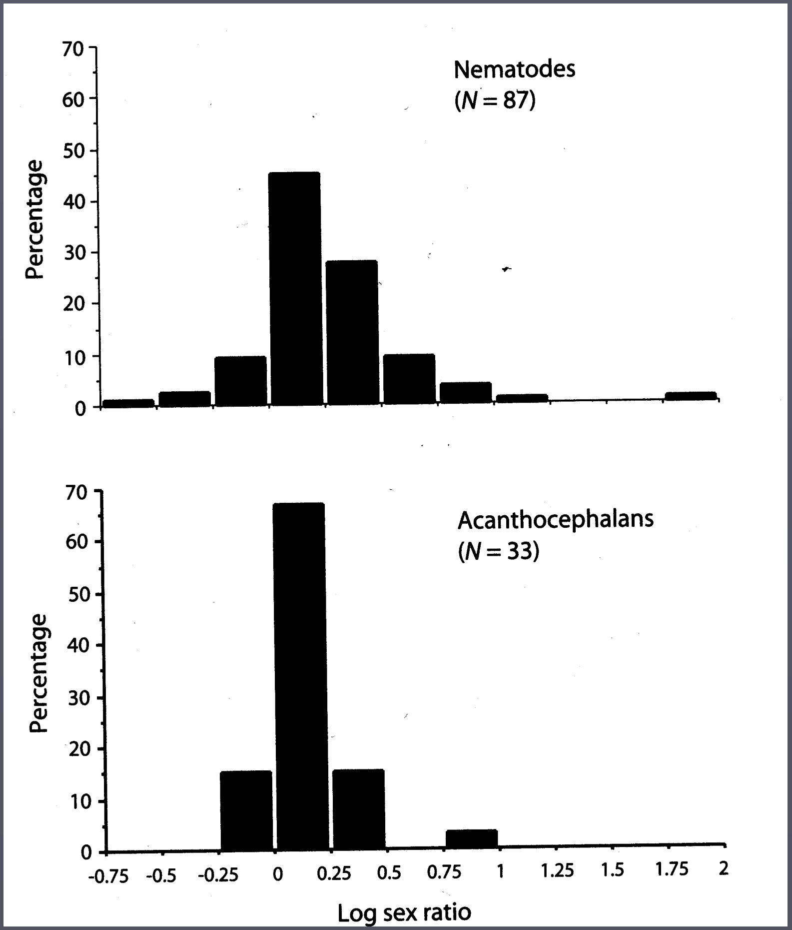
- Effect on sex ratio
- Ex. in polygamous parasites

  Nematoda and Acanthocephala

  in favour of females

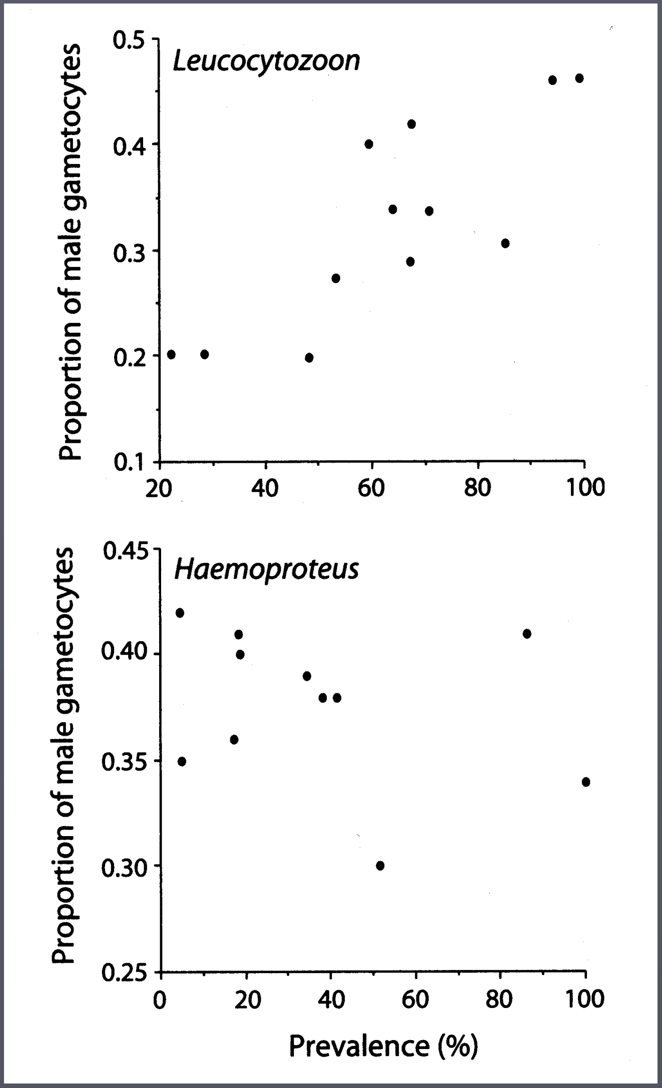
  - the result of differential mortality

  (females live longer)



Consequences of aggregation: shift in sex ratio

- Apicomplexa - sexual stages = gametocytes
  - the benefit of females
  - for some representatives of *Plasmodium*, pronounced in Toxoplasma
  - inbreeding - selection for low production of male gametocytes
  - Apicomplexa in birds - not always a shift in the sex ratio



Quantification of aggregation

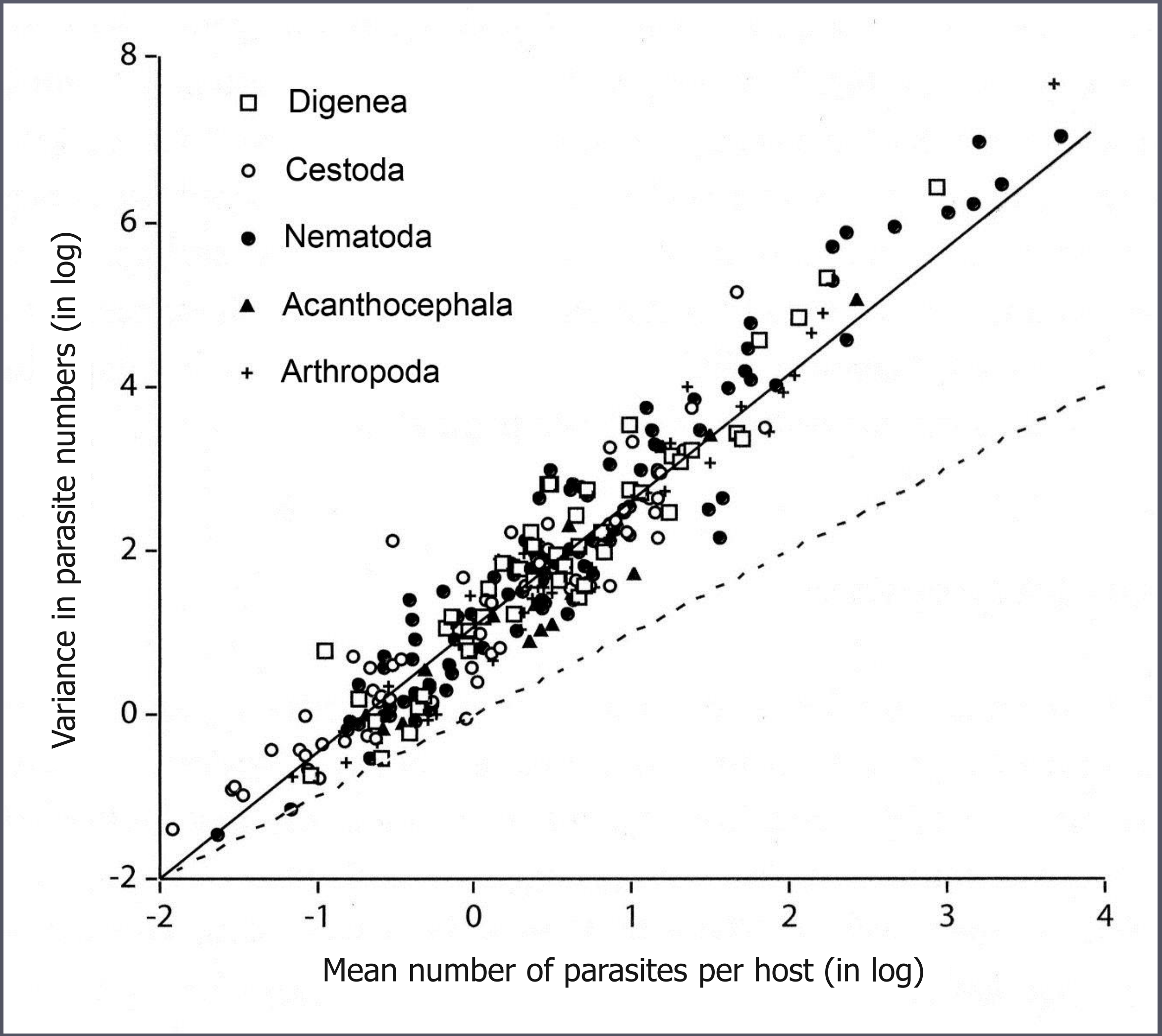
- Variance to mean ratio
- Parameter of negative binomial distribution (k)
- Discrepancy index (D)
- Taylor's rule

Variance to mean ratio

- The simplest and commonly used
- Ratio of variance to mean number of parasites per host
- Variance - a measure of mathematical variability within a population
- Var (M) / M = 1 random distribution
- Var (M) / M <1 uniform "under-dispersed"
- Var (M) / M> 1 aggregated "over-dispersed"

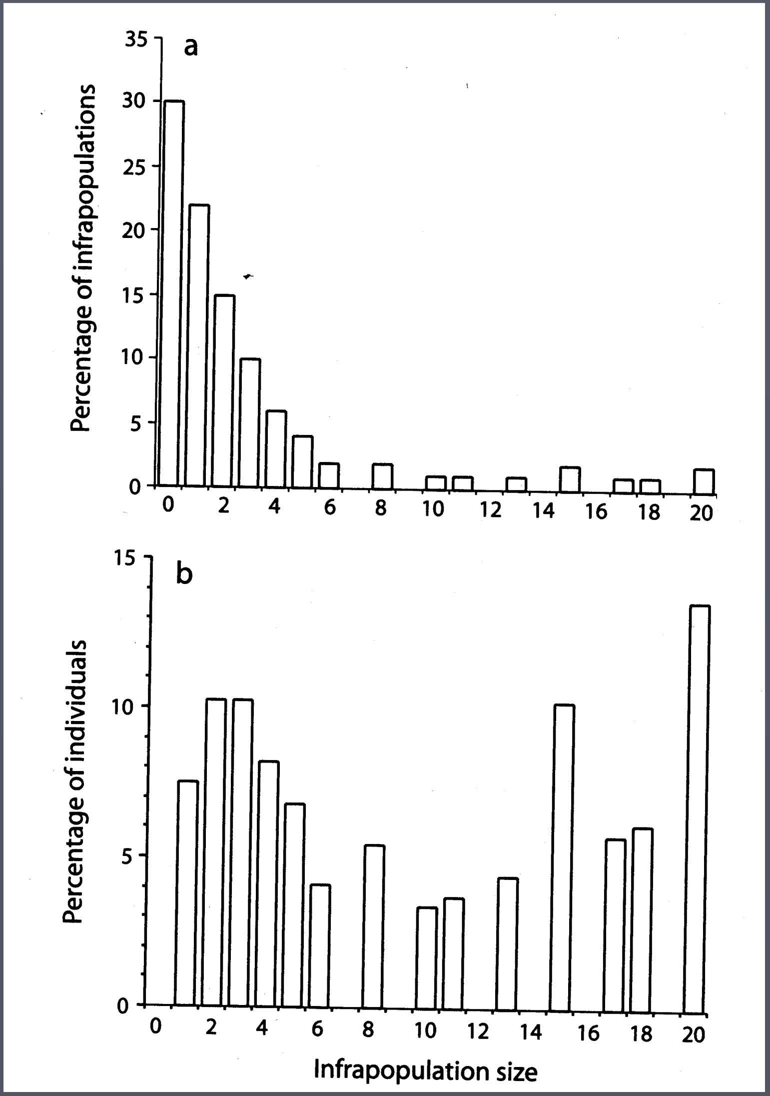
- Increasing value of the coefficient = increasing the rate of aggregation
- It quantifies variability in the intensity of infection between hosts or variability in the size of parasite infrapopulations

Aggregation of metazoan parasites



Variance to mean ratio as an indicator of aggregation

- Unsuitable if analyzing frequency distribution of parasites between infrapopulations of different sizes



Parameter of negative binomial distribution

- Defined by the average abundance (*M*) and the dispersion parameter *k*

- Negative binomial distribution

  $s^2 = M+M^2/k$

- With negative binomial distribution

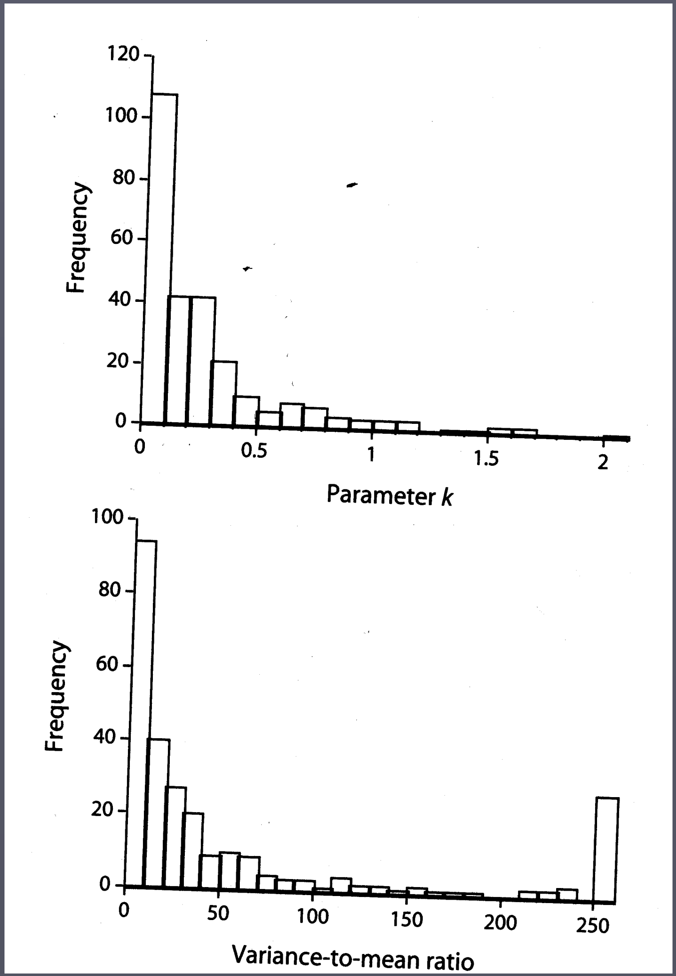
  $k = M^2/(s^2-M)$

- if $k \rightarrow 0$ aggregation increases, if *k* is high (> 20) random distribution (Poisson function)

Comparison of frequency distribution of parasites expressed using different aggregation indices

- (1) based on parameter k
- (2) the ratio of variance to diameter

Ex. 269 metazoan populations parasites in vertebrates



Discrepancy index

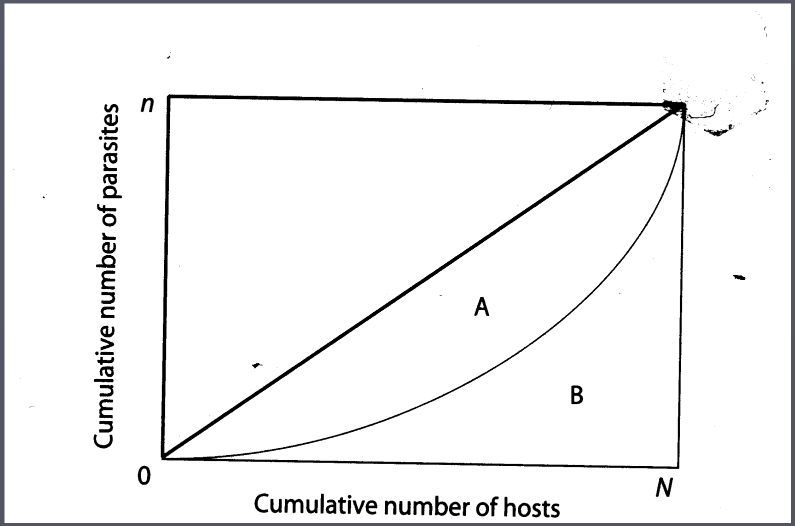
- Poulin (1993)
- It quantifies aggregation as the deviation between the observed distribution and the hypothetical distribution of parasites, where all hosts are used equally and all parasites occur in infrapopulations of similar size

$$D = 1 - \frac{2\sum_{i=1}^{n}\left(\sum_{j=1}^{i} x_j\right)}{xn(n+1)}$$

x is the number of parasites on host *j* (hosts are sorted in order from the least infected, i.e. *j* = 1, to the most infected) and *n* is the number of hosts in the sample

Discrepancy index

- Cumulative number of parasite individuals vs. cumulative number of host individuals, hosts ranked from the least to the most infected
- Relative discrepancy A/(A + B)
- Minimum index value = 0 - no aggregation
- Maximum value = 1 - aggregation is the highest



Taylor's rule

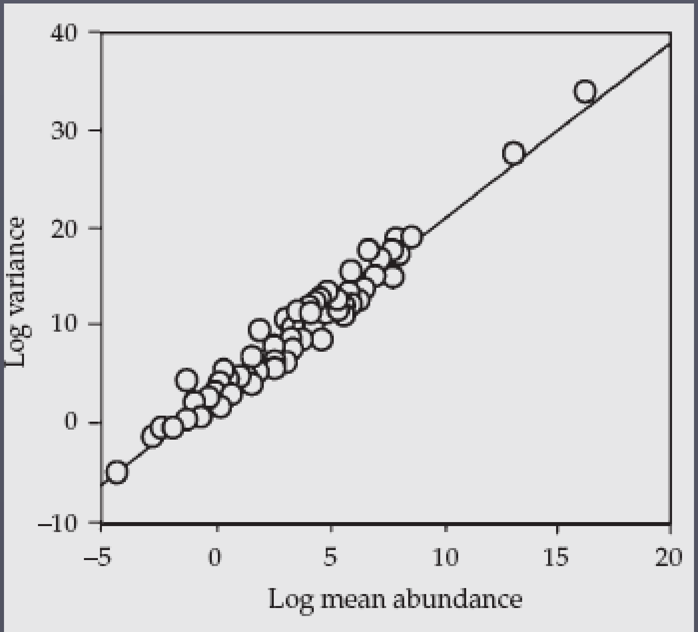
- Taylor (1961)
- Taylor's rule - relation between abundance (M) and variance Var (M)

$$\log(V) = b\log(M) + \log(a)$$

a: intercept, b: slope of the line, exponent of the rule

b represents the aggregation index

There is a relationship between the parameter k and the parameters a and b of Taylor's rule

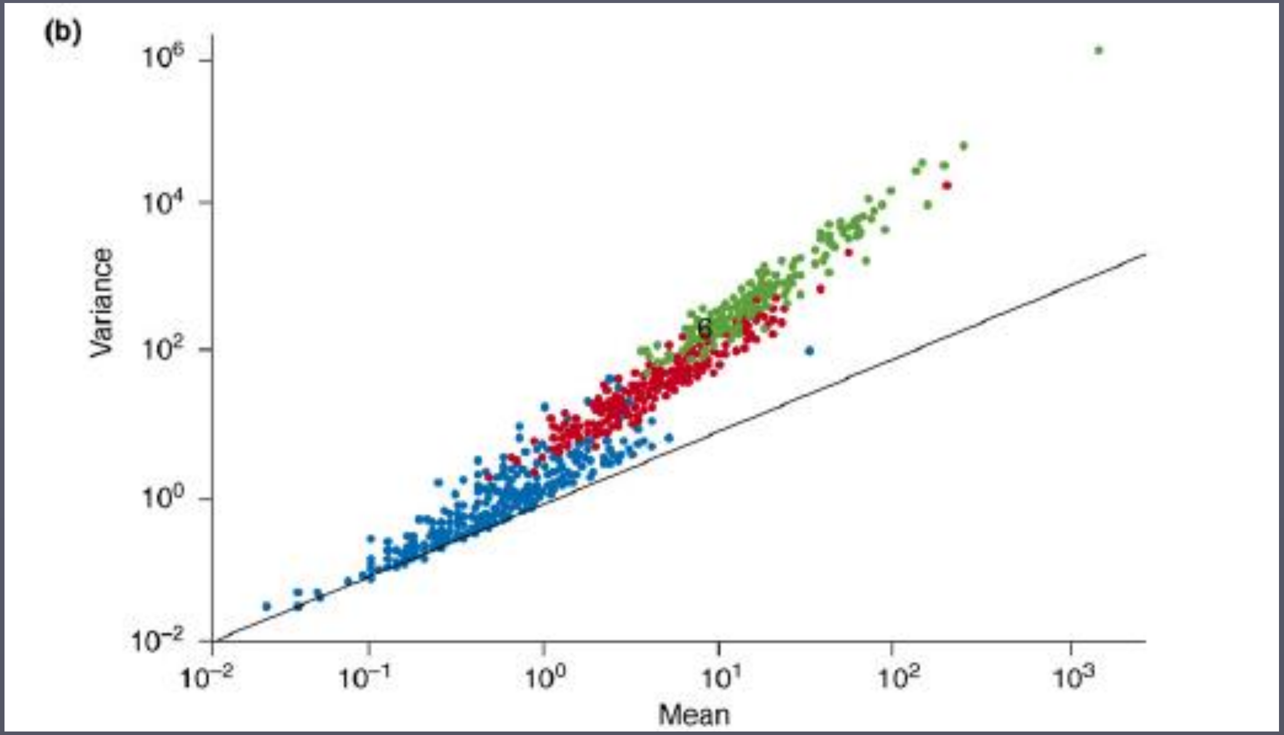


$$1/k = aM^{(b-2)} - (1/M).$$

Taylor's rule: parameter b

- describes how species use the environment, i.e. parasites use the host
- variable between species 1 <b <2
- the causes of variability between or within species (in terms of space and time) are not entirely clear (e.g. Kilpatrick and Ives, 2003)

Taylor's rule and vaccination



Measles in 366 communities from England and Wales. The data are divided into the pre-vaccination period (1944–1966, green dots), the 80% vaccination period (1980–1990, red dots) and the 90% vaccination period (1990–1997, blue dots).
The line corresponds to the Poisson distribution, where V = m.

Increasing and decreasing aggregation

- Increasing aggregation

  - reproduction of the parasite takes place inside the host (density dependent)

  - heterogeneity in host susceptibility to infection (differences in ecology, behaviour, genetic differences)

  - heterogeneity in host exposure depends on the distribution of infectious stages over time and space

- Decreasing aggregation

  - host mortality is dependent on parasite density

  - host fertility decreases depending on density;

  - host immunity protects against reinfection

Strategies for parasites to achieve a mean aggregation value?

- When?

High host mortality (and parasite mortality) at high aggregation

Reduced parasite contacts at low aggregations

- Compromise - mean aggregation values observed in many parasitic populations