Evolution of life strategies of parasites

Life strategies

- Combination of physiological and demographic components: body size, life expectancy, age at sexual maturity, fecundity, size and number of offspring
- Some combinations are favored by selection because they lead to higher fitness in a given environment
- Some components are variable at the population level, others are fixed at a higher taxonomic level

Theory of life history

- To analyze the relationships between life traits (maintenance, reproduction and survival)
- Total contribution to individual's fitness

- Do organisms with late maturity live longer?
- Do larger organisms have fewer offspring than smaller organisms?

- Simultaneous maximization in more traits is not possible → the evolution of life traits is limited and is characterized by a trade-off between the individual traits

Trade-off

- The connection between the traits of life, leads to the simultaneous evolution of traits

- A benefit obtained by a change in one trait (component) is offset by a cost in the other trait (component)

- Negative relationship between two traits, e.g. number and size of offspring, onset of reproduction and survival

Relationships between parasites and components of the host's life history

- Parasites can control the evolution of host's life history traits

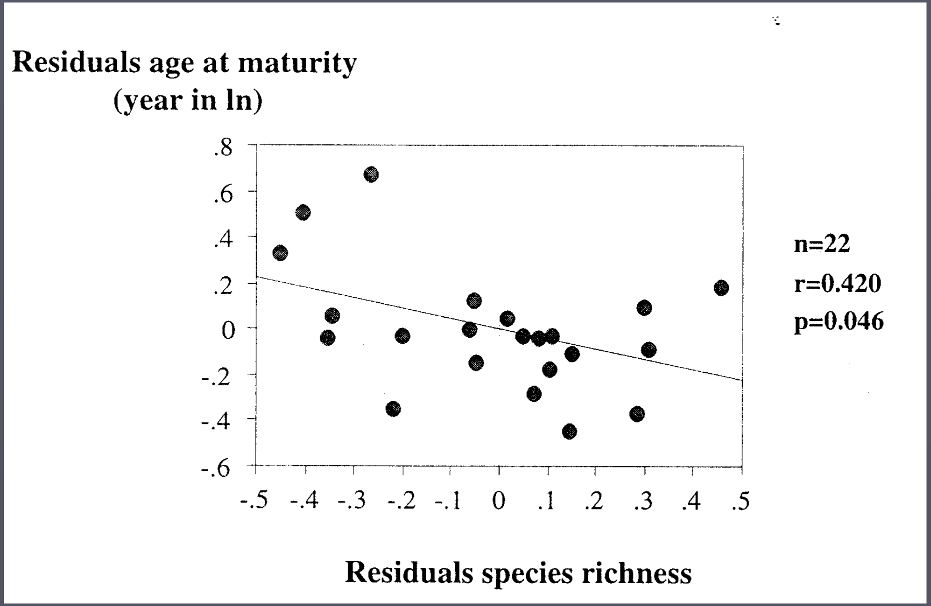
- Parasites represent an important selection pressure on the host

- The trade-off in host energy allocation depends on the selection pressure of the parasite

- Survival and reproduction
- Immune function

Relationships between parasites and components of the host's life history

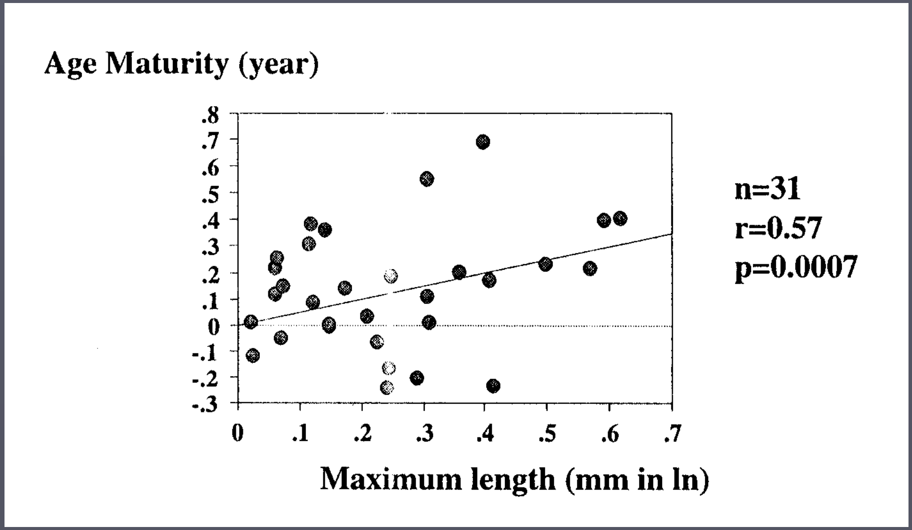
- Age at sexual maturity versus parasite species richness
- Parasites that accumulate with the age of the host reduce its age in sexual maturity

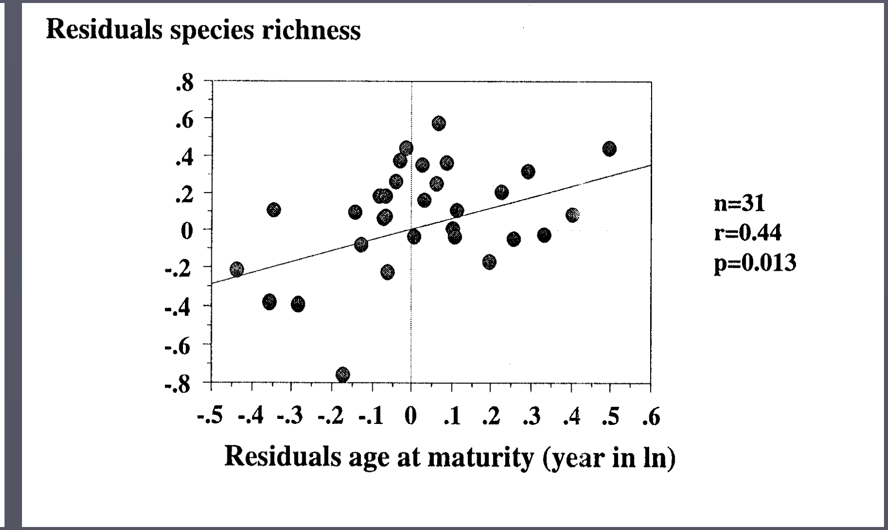


Ex. Fish species colonized by a higher number of parasitic species (larval stages) mature earlier

Relationships between parasites and components of the host's life history

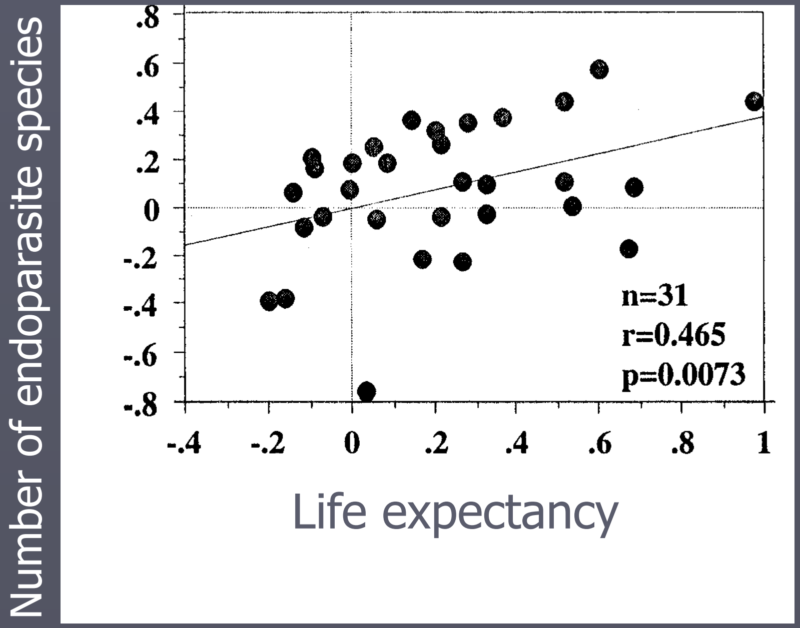
- Age at sexual maturity versus parasite species richness
- Fish with delayed onset of sexual maturity have a higher number of parasitic species





Relationships between parasites and components of the host's life history

- Life span versus parasite species richness
- Ex. Long-lived fish are parasitized by a higher number of endoparasites

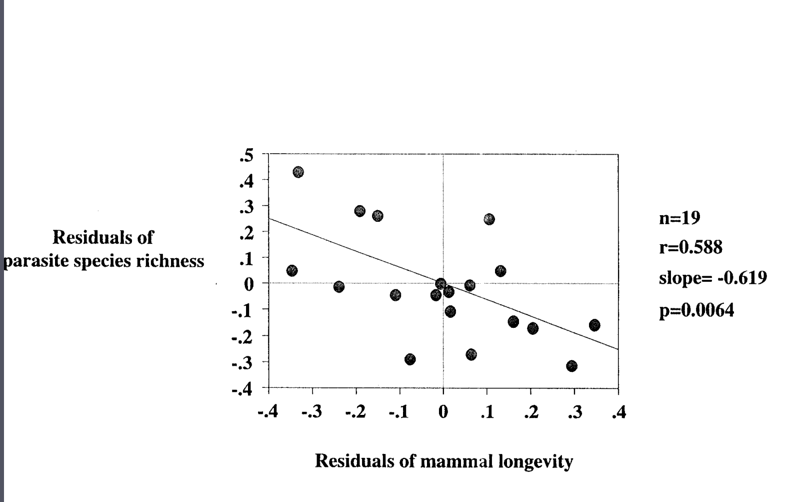


Relationships between parasites and components of the host's life history

- Host basal metabolism versus parasite species richness
- BMR - the minimum energy costs needed to ensure the activity of the organism
- Metabolic costs of immunity

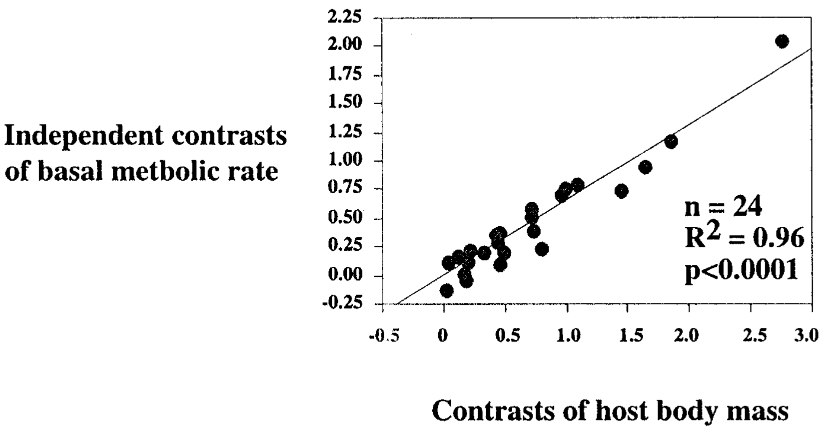
Ex. Mammals at higher risk of parasitism have higher metabolic requirements to initiate an immune response

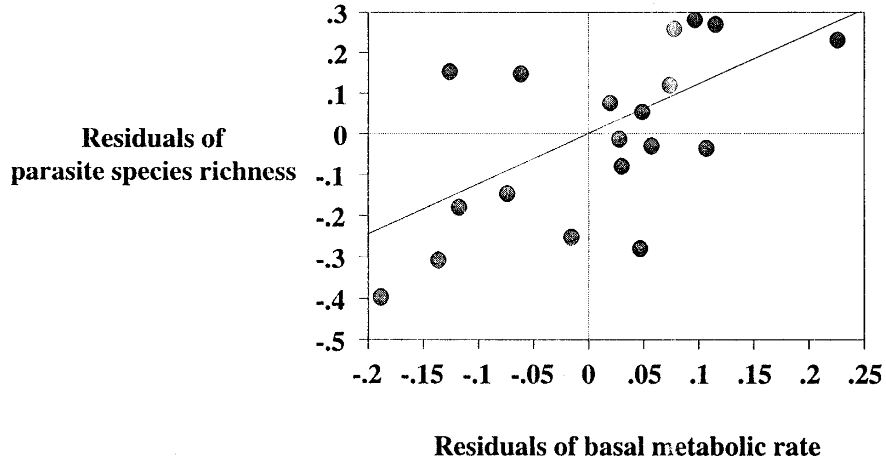
Mammals with higher parasitic load have a shorter lifespan (consequence of physiological losses)



Relationships between parasites and components of the host's life history

- Mammals with higher metabolic rates have a higher number of parasitic species





n=19

r=0.620

slope= 1.235

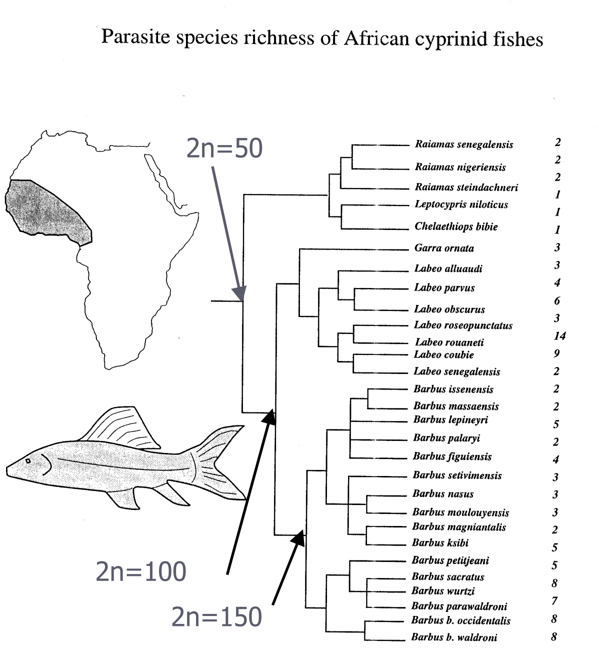
p=0.0035

Relationships between parasites and components of the host's life history

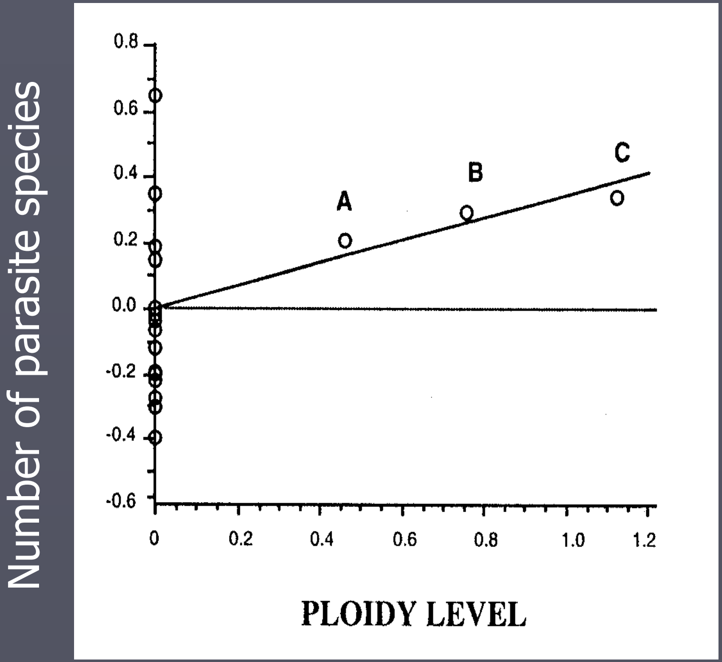
- **Host ploidy versus parasitism**

  chromosomal duplication - an important role in adaptive immunity

Ex. Positive relationship between parasite species richness and ploidy of African cyprinid fish



Parasite species richness of African cyprinid fishes

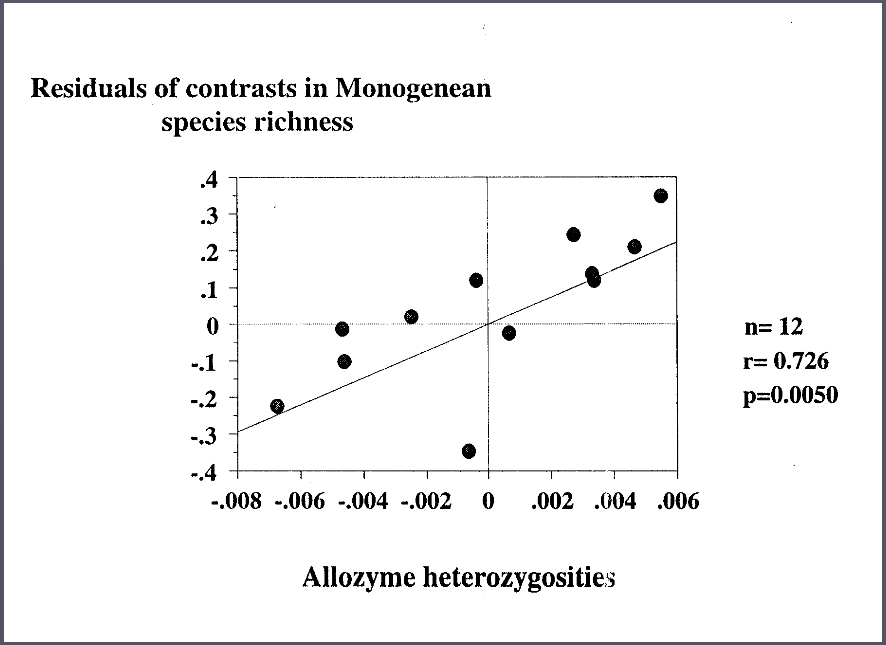


Relationships between parasites and components of the host's life history

- Host genetic diversity versus parasite species richness

Ex. Positive relationship between number of monogenean species and genetic heterozygosity in cichlid fish (factor of parasite diversification)

- size of host population is also important factor of parasite diversification



Phenotypic plasticity and adaptation of parasites

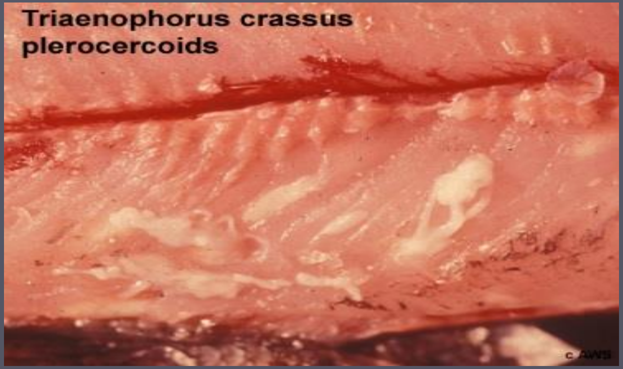
- Adapting the strategy of parasite life history to changes in environmental conditions

- 1. Phenotypic plasticity
  - adaptation to local conditions, small developmental changes, selection of the best strategy, change in one generation
  - one genotype produces numerous phenotypes
- 2. Adaptation
  - selection prioritizes genotypes producing the most appropriate phenotypes, evolutionary change, spread of genotypes in a population, adaptive genetic response – change in multiple generations

Phenotypic plasticity and adaptation of parasites

- Phenotypic plasticity - body size

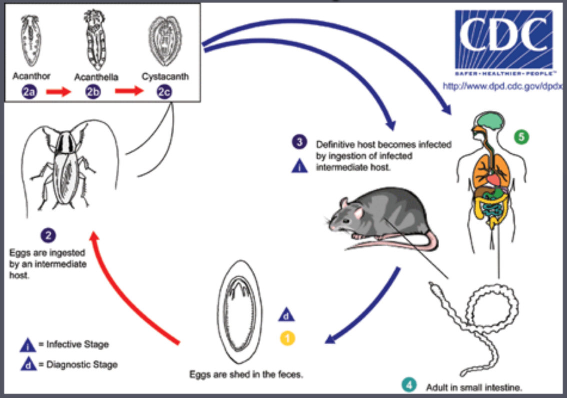
Ex. Freshwater fish tapeworm *Triaenophorus crassus* –
adult weight 5.7 -124 mg, difference in size 20x
Freshwater fish nematode *Raphidascaris acus* 0.7- 61.2mg,
difference in size 90x,
even higher differences in fecundity



influence of parasite distribution (aggregation)
host immune response generates phenotypic variability in body size within a parasitic population

Phenotypic plasticity and adaptation of parasites

- How quickly the adaptation appears?
- Rapid adaptation - Ex. egg production and the rate of development of the nematode parasites *Heligmosomoides polygyrus* in mice - changes observed after 11 generations from the former population
- Potential for rapid adaptation sometimes limited - *Moniliformis moniliformis* - changes not observed after 60 generations compared to the former generation



Evolution of parasite life strategies

- Body size
- Age at the time of reaching sexual maturity
- Egg production

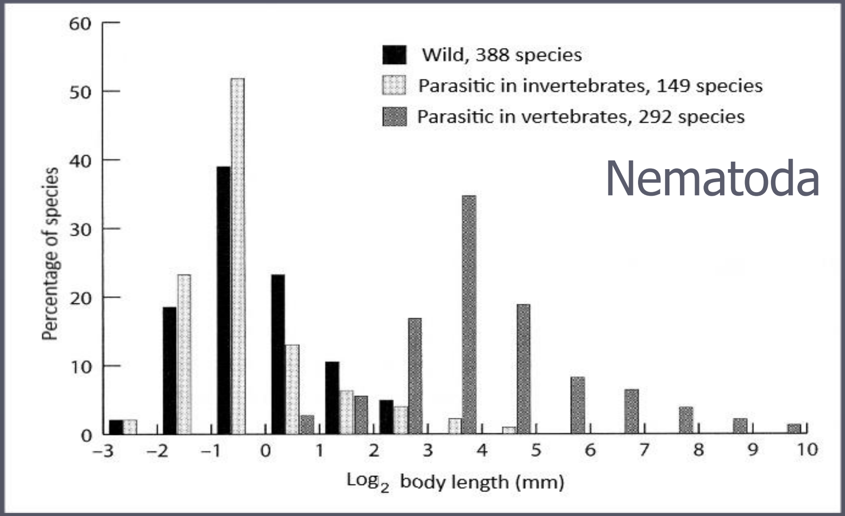
- Animal body size - increasing in evolutionary time (Cop's rule)
- Parasite body size

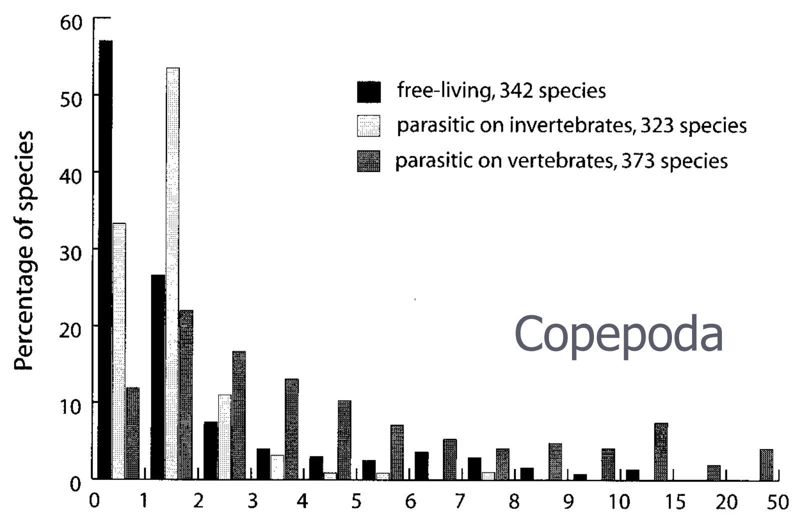
  in general evolution from wild to parasitic = size reduction

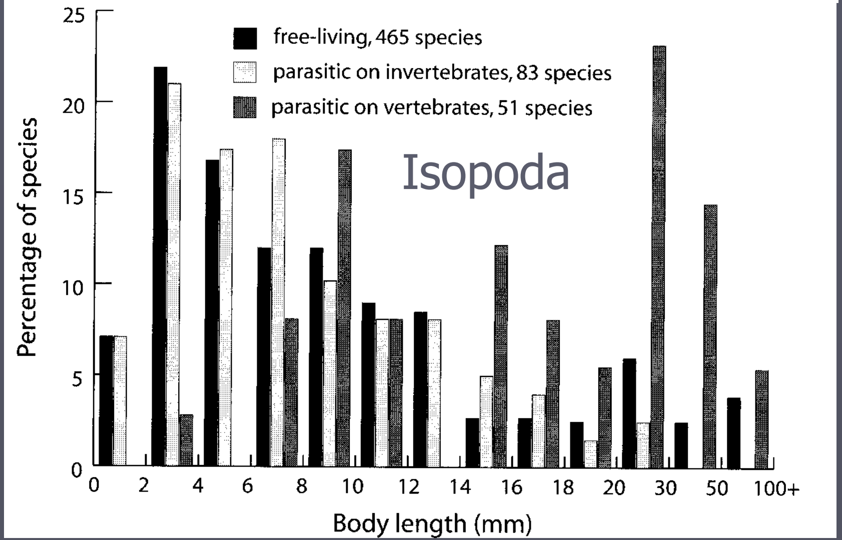
  (limited habitats)

Resizing as an adaptation to parasitism

Frequency distribution of body size







Evolution of body size of parasites

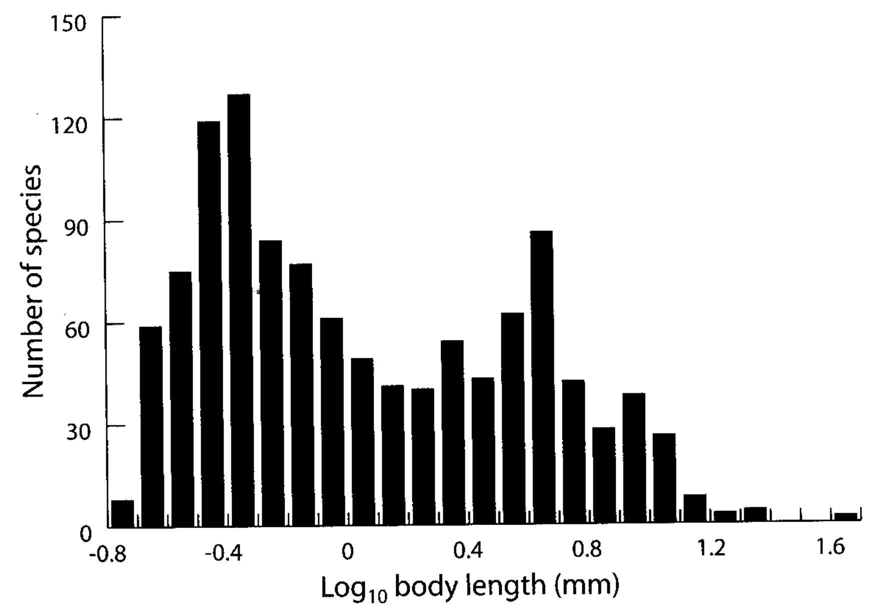
- Frequency distribution of body size
  → it indicates which size groups have undergone diversification

The evolution of body size differs among parasite groups
→ it does not always lead to reduction

It is asymmetric (in digeneans and nematodes),
log-normal in ectoparasites of fish (selection favors intermediate sizes)

Evolution of body size of parasites

- The problem of using the body size distribution for evolutionary conclusions !!
- The polyphyletic origin of the taxon affects the shape of the distribution



Ex. Frequency distribution of body size among 1131 species of monogeneans parasitizing on fish or other aquatic vertebrates

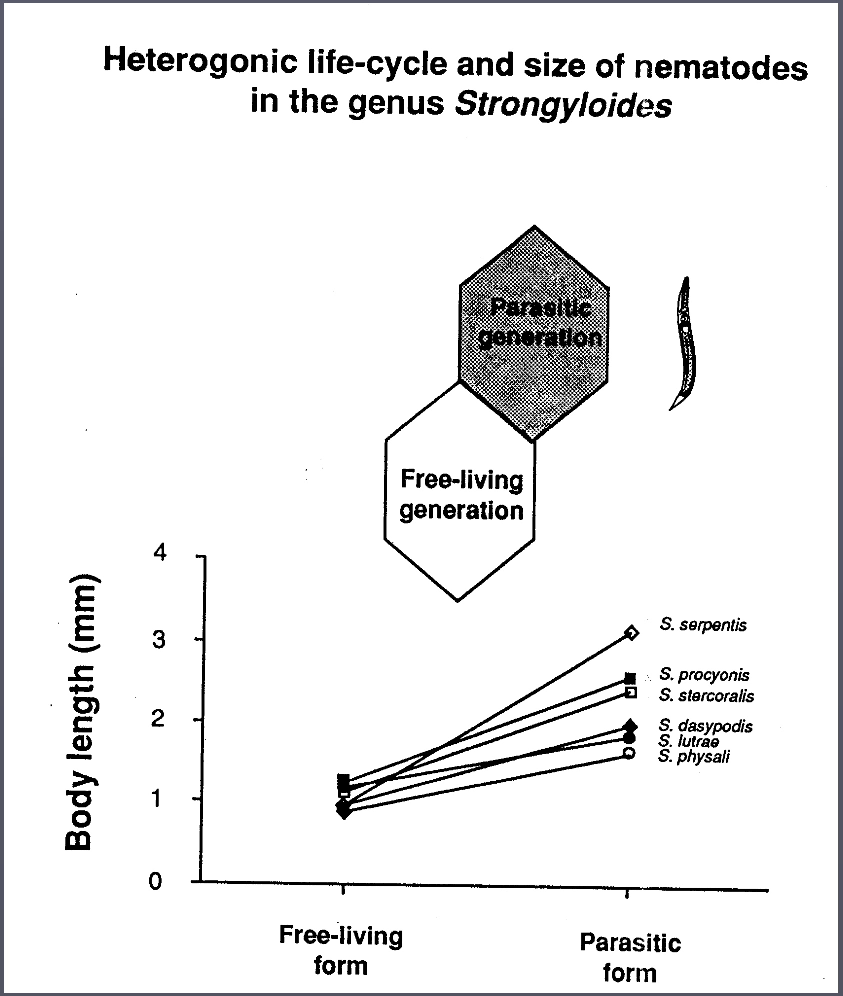
The evolution of body size - the transition from wild to parasitic life strategy

- Lack of fossil records

- Use of phylogenetic analyses - comparison of body size of basal and derived taxa

- Ex. Digenea - no consistent trend
- Ex. Monogenea - reduction of average body size in evolutionary time (consequence of invasion of spatially limited microhabitats)
- Recently evolving groups tend to be smaller in size than their ancestors

Body size of parasites - wild and parasitic generations



Heterogonic life-cycle and size of nematodes in the genus *Strongyloides*

Factors affecting the evolution of the parasite body size

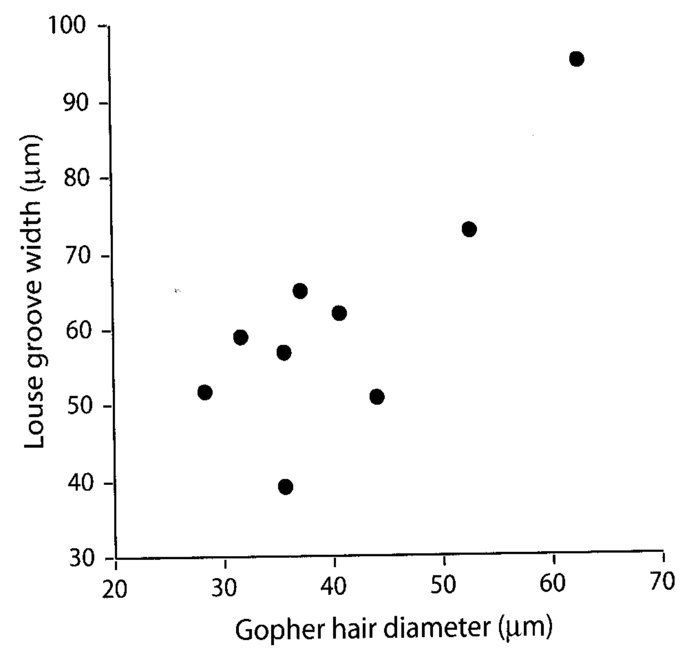
- Host body size
- Larger parasites on larger hosts (interspecies comparison)

Host taxon level
- larger host = wider space (elephant vs. mouse)
- larger host = more food sources
- larger host = longer living = more stable environment
→ favors parasites with later sexual maturity and larger size

- Larger parasites on larger hosts, smaller parasites on a wide range of host sizes
- Positive relationship between host body size and parasite body size

Factors affecting the evolution of the body size of parasites

- Flea body size and host bird (or mammal) size (Kirk, 1991)
- Lice body size and host rodent body size
- *Enterobius* (Nematoda) body size and host primate body size (Harvey & Keymer, 1991)



The relationship between the width of the groove on the head of the lice and the diameter of rodent hair (Morand et al. 2000) - the relationship between parasite body size and host body size is associated phenomenon

Factors affecting the evolution of the body size of parasites

- Oxyurid Nematoda in invertebrates and vertebrates - a strong relationship between parasite and host body sizes → host size an important factor in the evolution of nematode body size
- Acanthocephala - positive correlation between parasite size and host vertebrate host weight
- The largest Digenea in the largest hosts

  (didymozoid Digenea 12m in *Mola mola*)

- !!! The positive relationship between host body size and parasite is not universal, e.g. Copepoda parasitizing in fish

Effect of host body size on parasite life components

- Influence of host body size mediated by other factors

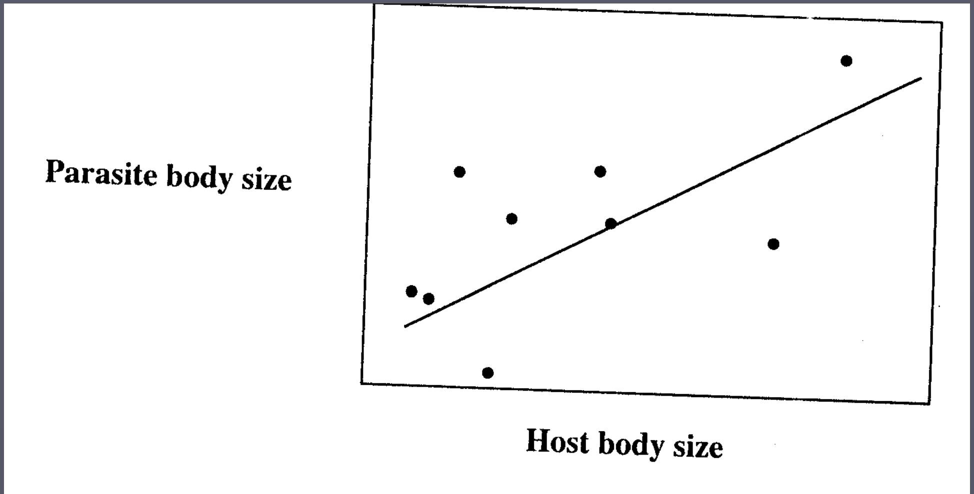
  - host life span affects the growth of the parasite

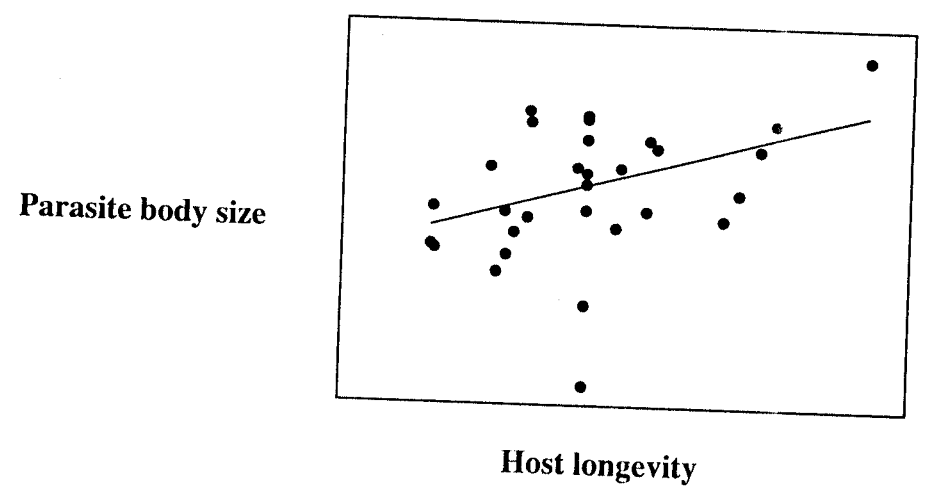
  - variability in the immune response limits the size and sexual maturity of parasites

  - availability of nutrients in the host - location in the host limits the size of parasites

Ex. The size of the tapeworms in the intestine of small mammals depends on the position of attachment - it determines the mortality of parasites

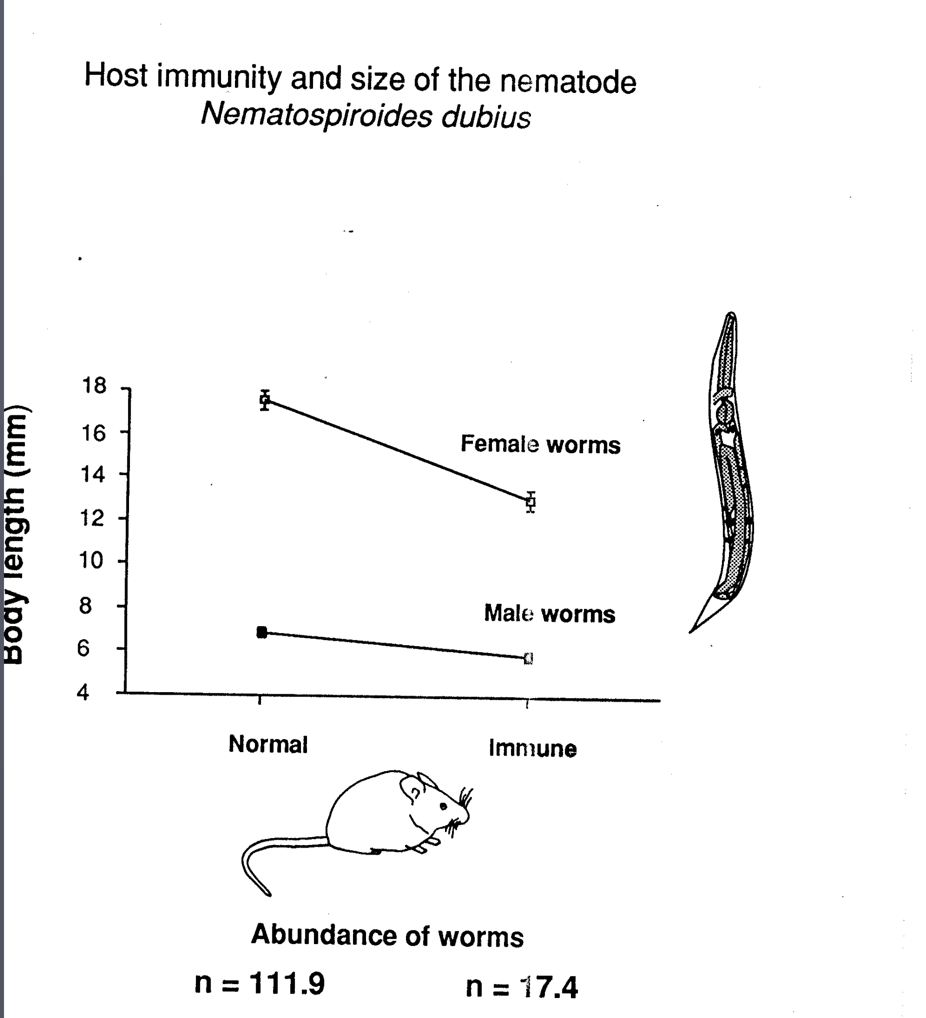
Effect of host body size on parasite body size





Oxyuride nematodes in primates

Effect of host immunity on parasite body size



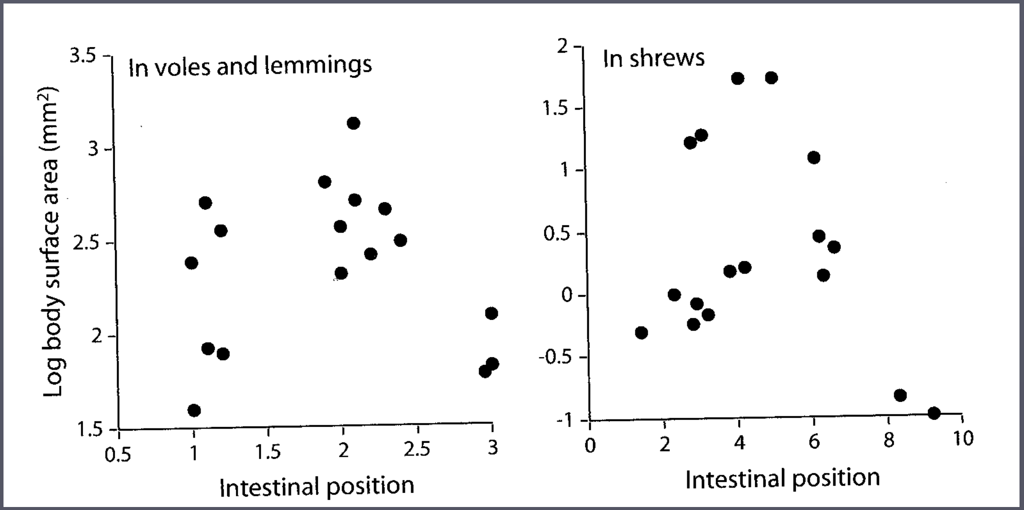
Host immunity and size of the nematode
Nematospiroides dubius

Abundance of worms

n = 111.9 **n = 17.4**

Effect of attachment position on parasite body size

- Ex. Tapeworm body size is linked with position in the intestine of its mammalian hosts



Position in the intestine = median position of attachment, the intestine was divided into 10 same parts for shrews or 3 parts for voles and lemmings

Effect of external factors on parasite body size

- Ectoparasites - the effect of external conditions on body size

  - Geographical trend (Bergman's rule)

  Ex. Monogenea and parasitic Crustacea in higher latitudes and deeper waters - a tendency for larger body size

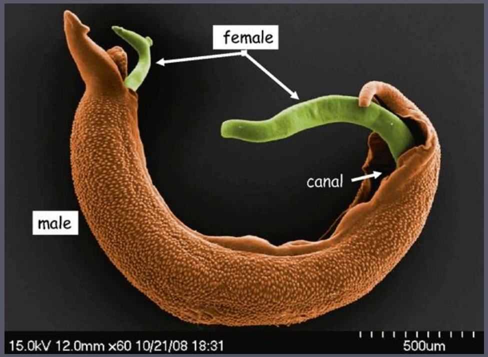
  - Seasonal variability in body size (*Gyrodactylus*)

Effect of sexual dimorphism on the evolution of parasite body size

- Sexual selection - controlling mechanism of evolution of sexually determined dimorphism (Nematoda, Acanthocephala)
- Ex. Nematoda (Oxyuridae) - smaller size in males than in females

  - strong competition for food

  - sexual selection - rapid maturation of males



!!! Schistosomes - gonochorists, hermaphrodite ancestor, male > female

- evolution for „distribution of tasks" – females for reproduction, males for movement and obtaining food

Age of parasites at the time of sexual maturity

- General relationship between body size and age of sexual maturity
- Helminths - the prepatent period, i.e. the time between infection of the definitive host and the onset of egg production
- Early maturation = early egg production, late maturation = larger size and faster egg production
- Intraspecific plasticity in reaching the age of the first reproduction

Ex. Tapeworm *Schistocephalus solidus*

- infection by one individual = displacement onset of the first reproduction

Age of parasites at the time of sexual maturity

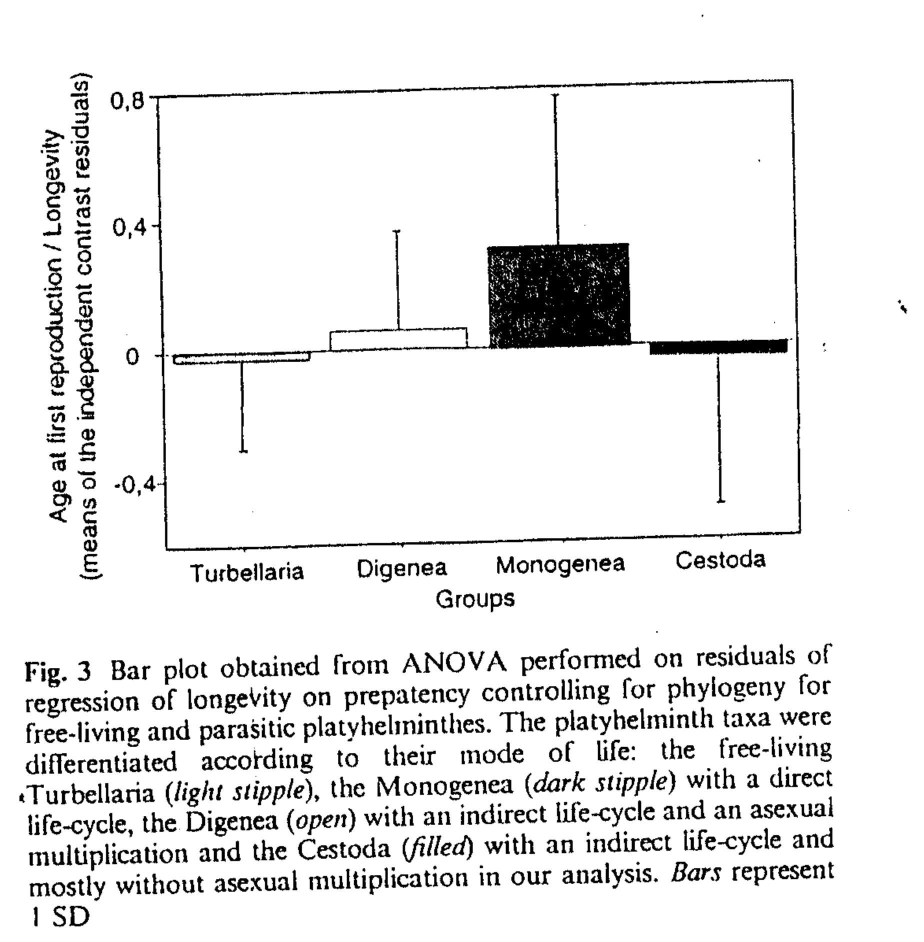


Fig. 3 Bar plot obtained from ANOVA performed on residuals of regression of longevity on prepatency controlling for phylogeny for free-living and parasitic platyhelminthes. The platyhelminth taxa were differentiated according to their mode of life: the free-living Turbellaria (*light stipple*), the Monogenea (*dark stipple*) with a direct life-cycle, the Digenea (*open*) with an indirect life-cycle and an asexual multiplication and the Cestoda (*filled*) with an indirect life-cycle and mostly without asexual multiplication in our analysis. *Bars* represent 1 SD

Age of parasites at the time of sexual maturity

- Optimal age of sexual maturity

  - to maximize reproductive success during the life of the parasite

  - it depends on age-related mortality and the relationship between body size and fecundity

  - studied mainly in nematodes - the period of sexual maturity determines the body size of parasites, which is related to fecundity

  - mathematical models supported empirically - a compromise between higher fecundity (with increasing body length) and the risk of death before reaching this length → parasitic nematodes mature earlier if the mortality of their larval stages is high

Effect of host mortality on the age of parasites at the time of sexual maturity

- High host mortality → shortened time to sexual maturity
- Low host mortality (longer-lived hosts) → delayed onset of sexual maturity

Production of eggs and offspring of parasites

- 2 general strategies in animals (K- or r- strategists)
- Parasites - r-strategists (short-lived, early sexual maturity, small body size, high egg production)
- Evolution of parasite fecundity leads to higher egg production
- !! Variability in egg production among parasites (some monogeneas < 100)

- Does the transition to parasitism direct fecundity?

  - comparison of wild and parasitic sister taxa

  Ex. Copepoda and Isopoda parasitizing in fish - higher fecundity

Production of parasite eggs

	The number of eggs during an individual's life	Multiplication of larval stages
Turbellaria (wild)	10	x1
Monogenea (ectoparasite)	1000	x1
Digenea (endoparasite)	10 million	x≥1000
Cestoda (endoparasite)	10 million	x(1-1000)

Production of parasite eggs

- Fecundity estimates
  - egg production
  - larval multiplication

  - generation time (from egg formation to adult stage)

  - small number of eggs/individuals + short generation time (*Gyrodactylus*)
  - large number of eggs + long generation time

Production of parasite eggs

- Selection pressure from the host and/or environment
- Ex. Copepoda - transition from invertebrate hosts to fish hosts → tendency to higher eggs production
- Ex. Copepoda - latitude gradient on egg number independent of body size

Compromises and strategies for egg production in parasites

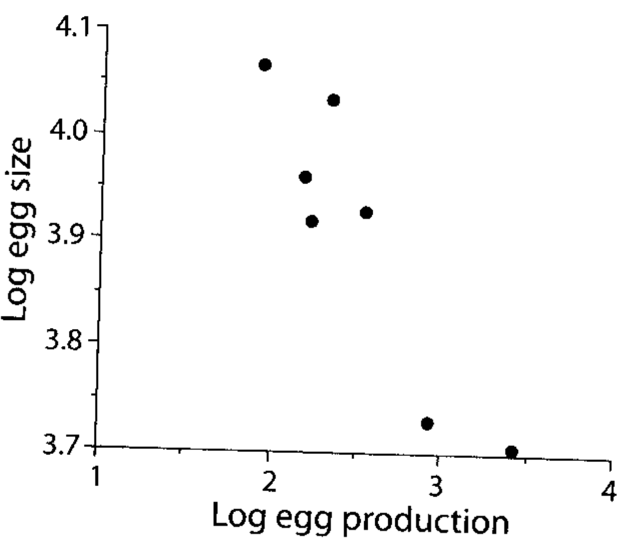
- Larger parasites tend to produce more eggs and/or larger eggs (Ascothoracida, Digenea)
- In some parasites, intraspecific and interspecific variability in egg size (Nematoda)
- Selection does not maximize both number and size → compromise between the number of eggs (fecundity) and the size of the eggs (schistosomes, Copepoda)

  → two parasite strategies

    1. production of a large number of small eggs
    2. production of a small number of large eggs

the probability of transmission determines the strategy

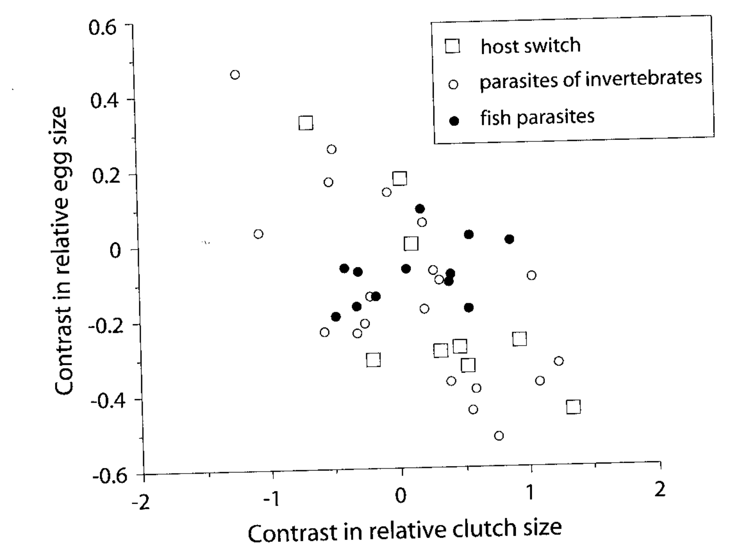
Compromises and strategies for egg production in parasites



Ex. Negative correlation between the number of eggs (fecundity) and the size of eggs in schistosomes parasitizing mammals

Compromises and strategies for egg production in parasites

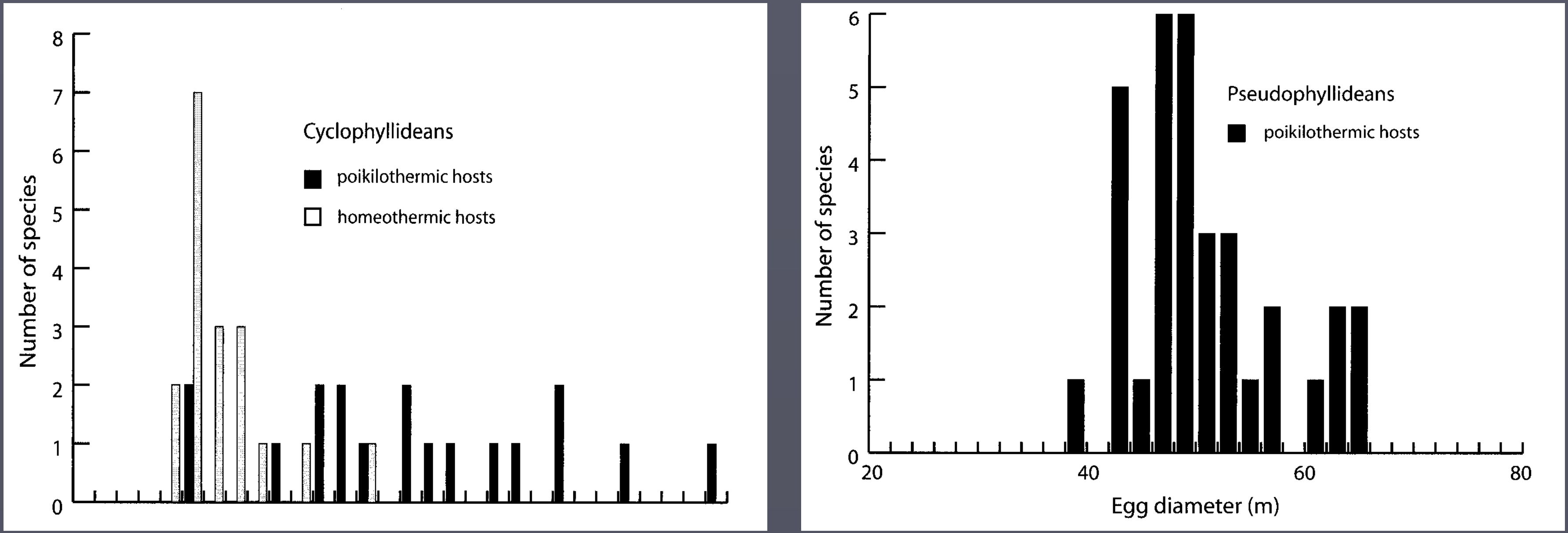
- Compromise - negative relationship between size and number of eggs, e.g. parasitic Copepoda



Ex. host switch – a situation where one taxon is parasitic in invertebrates, the sister taxon is parasitic in fish

Compromises and strategies for egg production in parasites

- Homeothermic vs. poikilothermic hosts
- - homeothermic host - better growth conditions for endoparasites → small eggs and rapid growth of larvae



Ex. Frequency distribution of egg size in two groups of tapeworms

Compromises and strategies for egg production in parasites

- Environmental impact

Latitude gradient on reproductive strategy of monogeneans

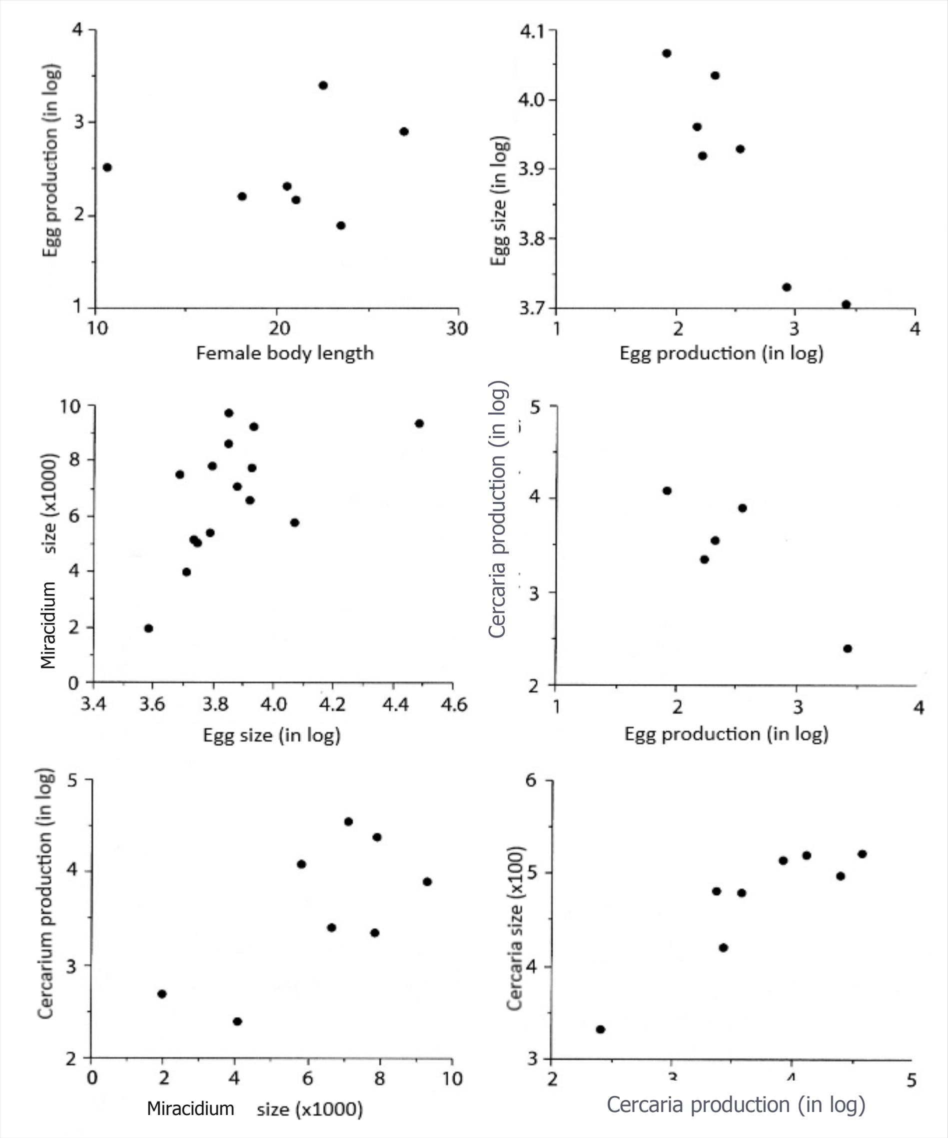
e.g. *Gyrodactylus*

- warm waters, tropics - small diversity, few larger ones descendants
- waters of the northern hemisphere - extremely diversified, worthy of small offspring

Compromises and strategies for egg production in parasites

- Endoparasites with complex developmental cycles

  \- compromise between egg production in the final host and asexual multiplication of larval stages in the intermediate host



Comparison of life-history traits between wild and parasitic organisms

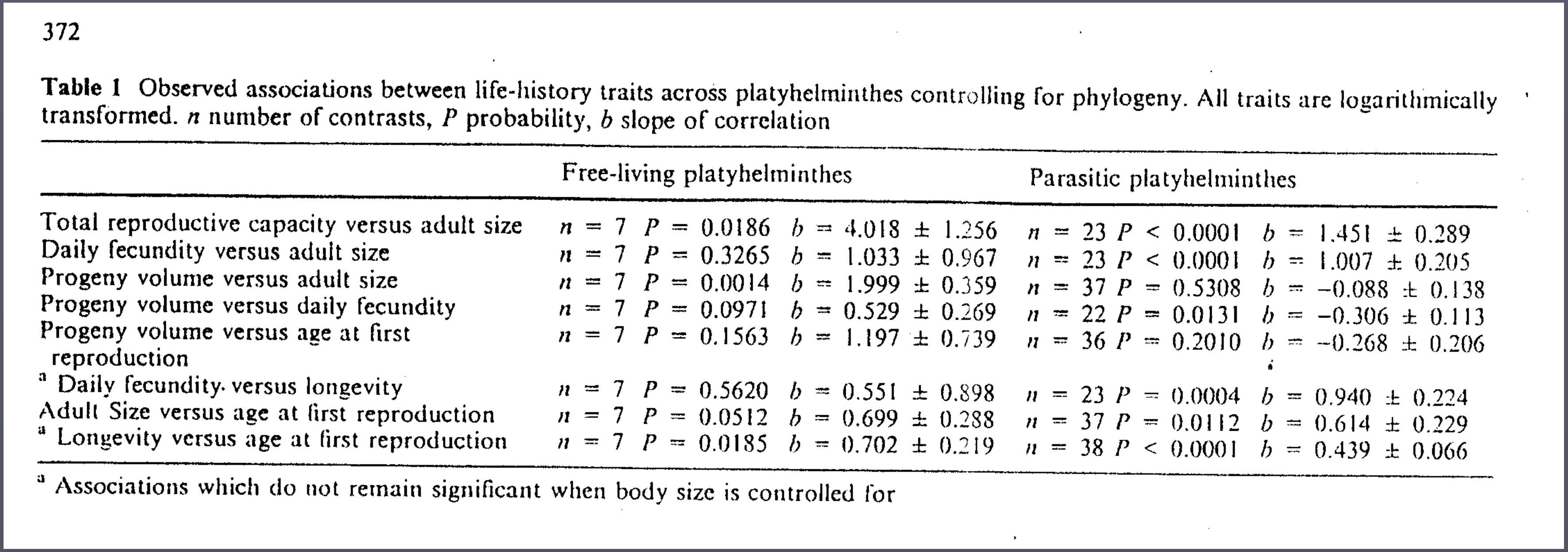


Table 1 Observed associations between life-history traits across platyhelminthes controlling for phylogeny. All traits are logarithmically transformed. *n* number of contrasts, *P* probability, *b* slope of correlation

	Free-living platyhelminthes			Parasitic platyhelminthes		
Total reproductive capacity versus adult size	$n = 7$	$P = 0.0186$	$b = 4.018 \pm 1.256$	$n = 23$	$P < 0.0001$	$b = 1.451 \pm 0.289$
Daily fecundity versus adult size	$n = 7$	$P = 0.3265$	$b = 1.033 \pm 0.967$	$n = 23$	$P < 0.0001$	$b = 1.007 \pm 0.205$
Progeny volume versus adult size	$n = 7$	$P = 0.0014$	$b = 1.999 \pm 0.359$	$n = 37$	$P = 0.5308$	$b = -0.088 \pm 0.138$
Progeny volume versus daily fecundity	$n = 7$	$P = 0.0971$	$b = 0.529 \pm 0.269$	$n = 22$	$P = 0.0131$	$b = -0.306 \pm 0.113$
Progeny volume versus age at first reproduction	$n = 7$	$P = 0.1563$	$b = 1.197 \pm 0.739$	$n = 36$	$P = 0.2010$	$b = -0.268 \pm 0.206$
[a] Daily fecundity versus longevity	$n = 7$	$P = 0.5620$	$b = 0.551 \pm 0.898$	$n = 23$	$P = 0.0004$	$b = 0.940 \pm 0.224$
Adult Size versus age at first reproduction	$n = 7$	$P = 0.0512$	$b = 0.699 \pm 0.288$	$n = 37$	$P = 0.0112$	$b = 0.614 \pm 0.229$
[a] Longevity versus age at first reproduction	$n = 7$	$P = 0.0185$	$b = 0.702 \pm 0.219$	$n = 38$	$P < 0.0001$	$b = 0.439 \pm 0.066$

[a] Associations which do not remain significant when body size is controlled for