Parasitic strategies of host utilization

Evolution of virulence

- Virulence

- the ability of the parasite to reduce the biological fitness of the host

- individual property

- the degree of virulence of individual populations of the parasite is variable

- parasite-induced host mortality

- in some host-parasitic systems, manifestations of virulence beneficial to parasites

Evolution of virulence

- Evolution of virulence associated with the fecundity and rate of transmission of the parasite

- a compromise between parasite reproduction rate and host survival

- prevents uncontrollable fluctuations in virulence
- does not prevent high virulence values
- is analyzed using mathematical models
- for each host-parasite system - optimal strategies of host utilization = maximization of parasite fecundity
- optimal value of virulence at the local level

Evolution of virulence

Epidemiological model (Anderson & May, 1982, 1991)

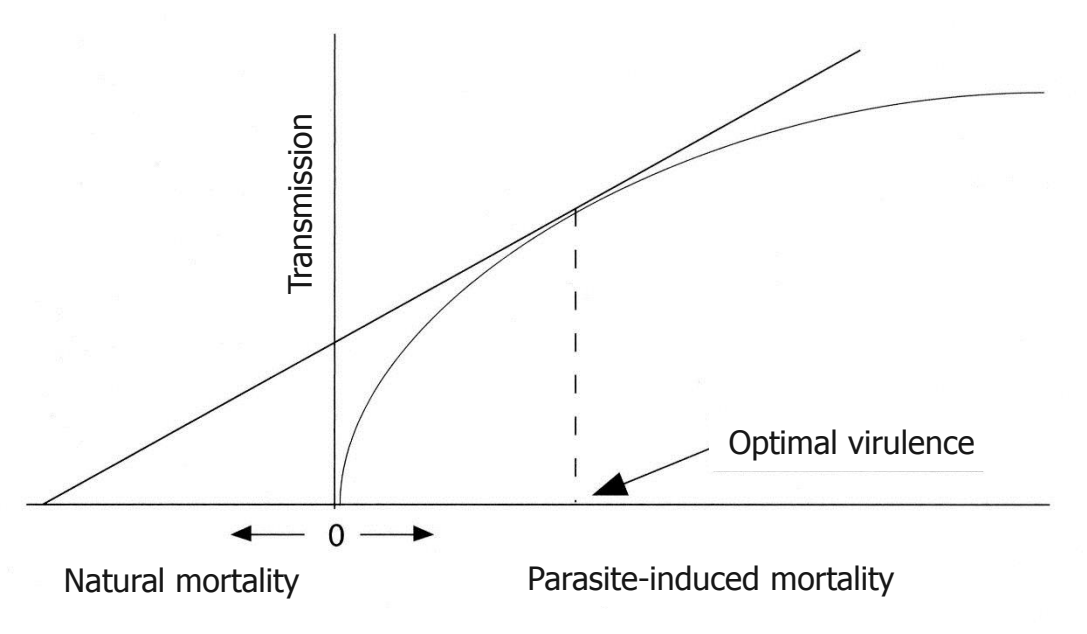
$$R_0 = \frac{\beta(N)}{\mu + \alpha + \nu}$$

Fitness parasite = reproductive success during life

β is the rate at which infected hosts transmit parasites to susceptible ones
μ is the natural mortality
α is the parasite-induced rate of host mortality
ν is the time of host recovering

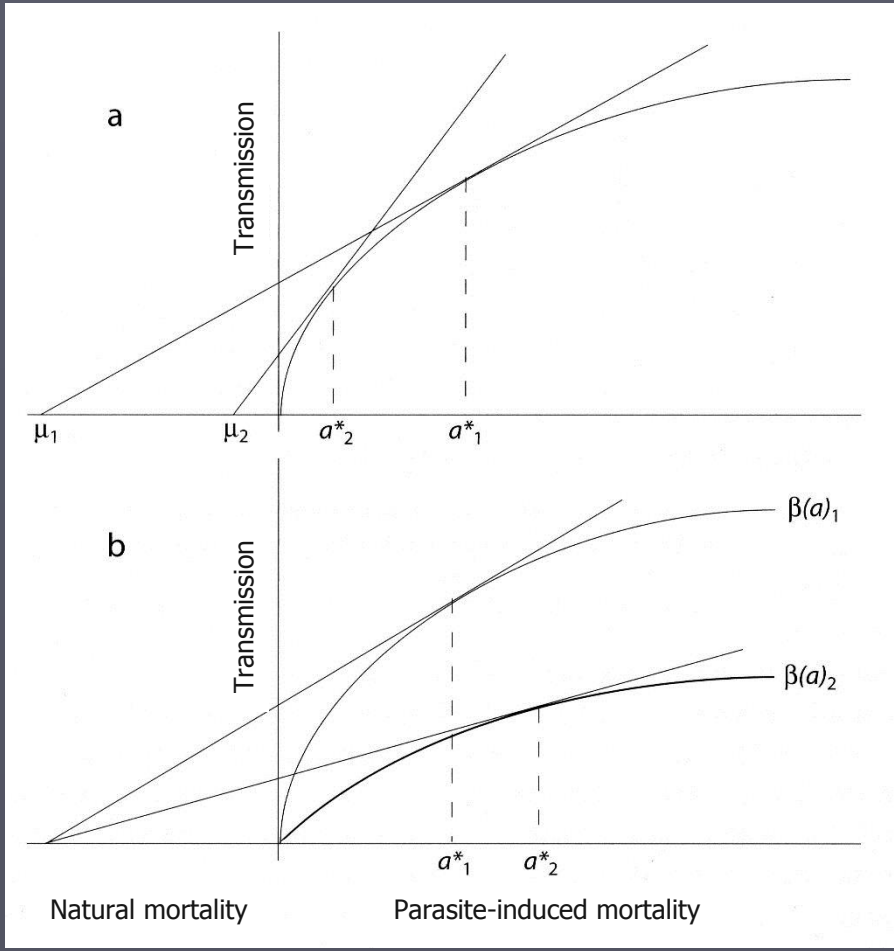
Evolution of virulence

- Optimal virulence of the parasite derived from the application of the marginal value theorem for the functional relationship between the rate of transmission (β) and parasite-induced mortality (α)



Models of virulence evolution

- Prediction of virulence evolution in different conditions



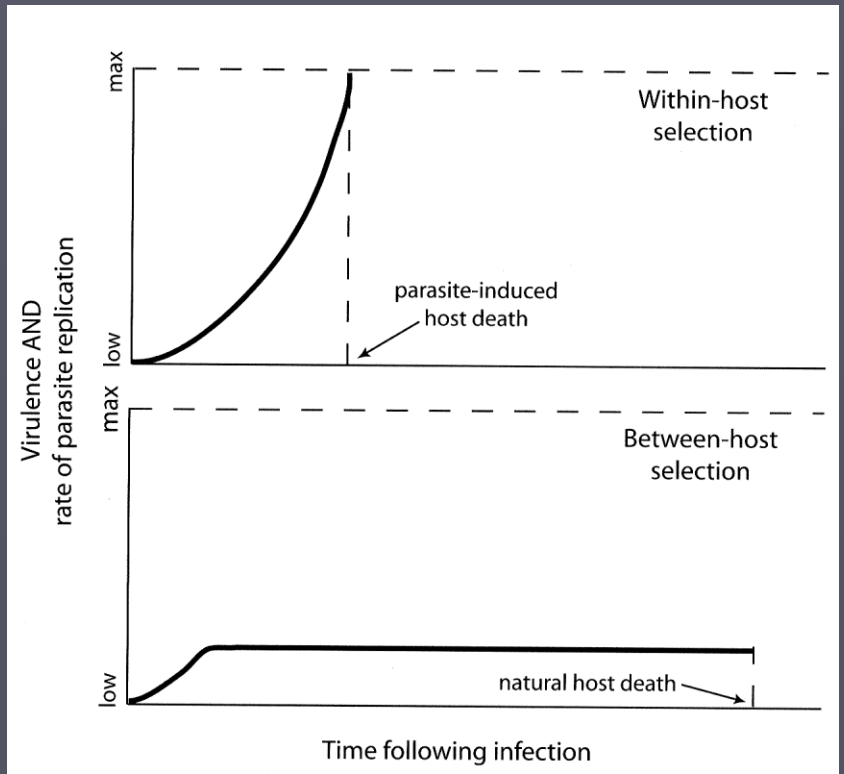
Evolution of virulence in the case of multispecies infection

- Competition of two types → selection for higher host utilization and higher virulence within the host

the virulent parasite kills the host quickly

- The coexistence of two species → selection between hosts favours a lower rate of host utilization and a lower degree of virulence

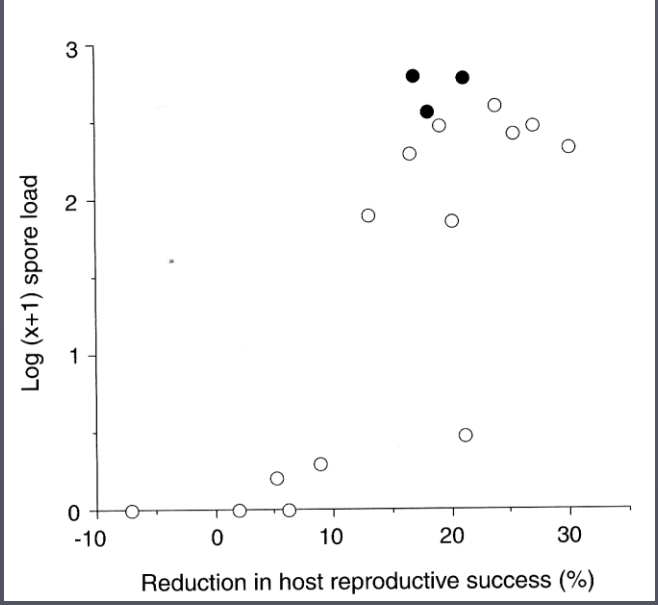
parasites allow the host a longer life, have a higher reproductive potential



Evolution of virulence: empirical support of theoretical models

- 2 assumptions of the virulence model empirically supported:

- 1. evolution of high virulence limited by a compromise between the rate of host utilization by the parasite and host survival
- 2. high virulence leads to higher replication of the parasite



Relationship between virulence (measured as a reduction in host reproductive success) and spore production of *Pleistophora intestinalis* (Microsporidia) infecting planktonic crustacean *Daphnia magna*

Evolution of virulence: empirical support of theoretical models

- Influence of transmission on the evolution of parasite virulence

- Ex. Study of virulence of protozoa, bacteria and viruses - pathogens in humans (Ewald 1983, 1994)
  virulence = the probability of infection leading to the death of the host

empirical support of theoretical models:

- pathogen virulence using aquatic systems for transmission > pathogen virulence using host contacts

- virulence of vector-borne pathogens > virulence of pathogens using host contacts

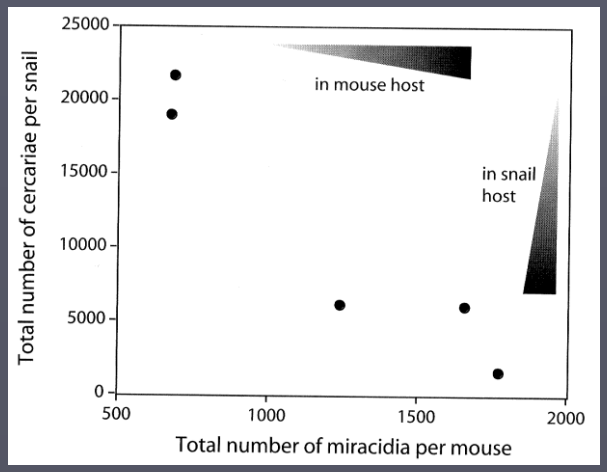
- virulence of pathogens surviving for a long time in the external environment > virulence of short-living pathogens in the external environment

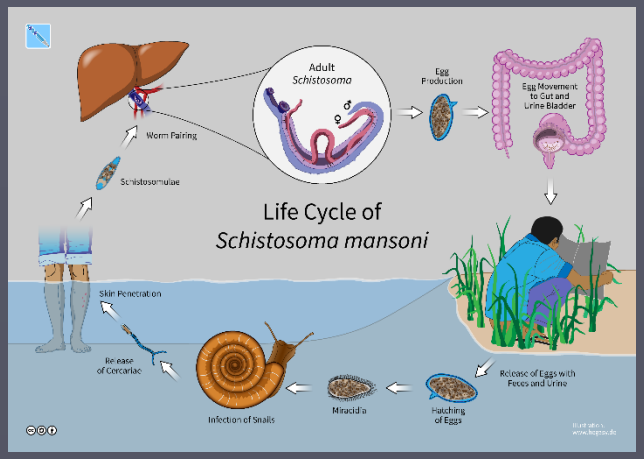
Evolution of virulence in parasites with a complex life cycle

- high degree of virulence in one host, low degree of virulence in the other host
- Helminths with predation to the DH - high virulence in IH (source, specialization) - aggressive strategy of the parasite using IH, low virulence in DH (dispersion)
- Helminths - without predation to the DH - virulent (inflammatory reaction caused by eggs in the host tissue)

Evolution of virulence in parasites with a complex life cycle

- Schistosomes eg *Schistosoma mansoni* - virulent in IH and DH
- parasite virulence in DH (mouse) positively correlates with egg production rate
- parasite virulence in IH (snail) negatively correlates with the rate of cercariae production





negative genetic correlation between parasite success in IH and DH

- Multiple strains at the same IH → strain with low virulence competitively favoured
- Parasite success in both hosts - genetic compromise = selection of intermediate virulence's in both hosts

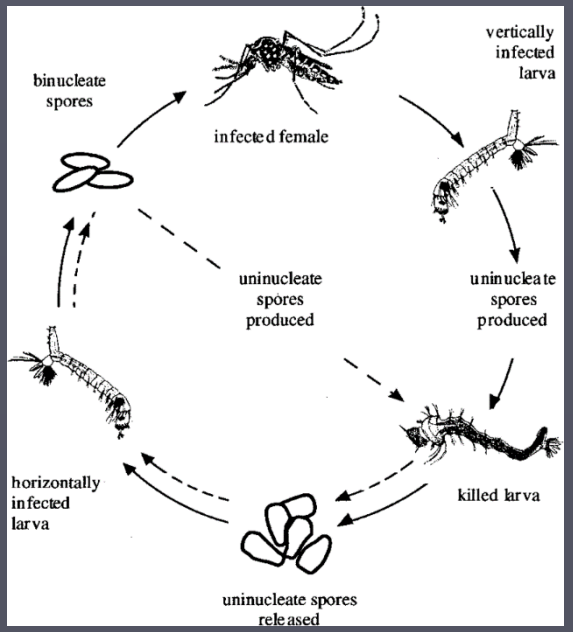
Influence of horizontal and vertical transmission on the evolution of virulence

- Horizontal transmission - high virulence
- Vertical transmission - low virulence
- Ex. Comparison of ectoparasitic arthropods in birds with different types of transmission

- Ex. Parasites with stages of horizontal and vertical transmission
- *Edhazardia eadis* (Microsporidia):

  - horizontally transmitted spores - high virulence in mosquitoes

  - vertically transmitted spores - low virulence



Manipulating host behaviour

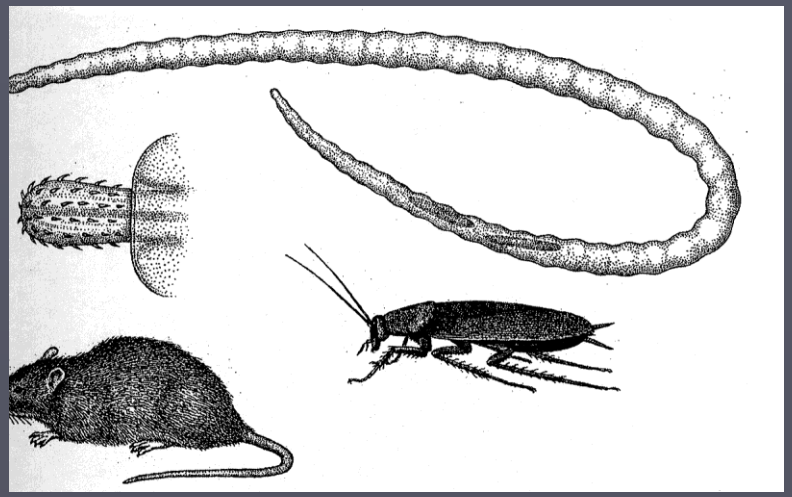
- targeted intervention in the functioning of the host organism
- modification of host properties - morphology, regulation of metabolism, specific interventions in the nervous system → changes in the behaviour of the infected host
- Virulent parasites, i.e. behavioural changes often maximize the transmission of parasites and increase the probability of host death

Adaptive vs. non-adaptive manipulation of hosts

- Parasites induced changes in host behaviour
- 1. the result of adaptation - higher rate of transmission to DH and/or an increase in the fitness parasite
- 2. non-adaptive accidental effects of parasitic infection
  - accidental changes or side effects of parasite pathology
  - parasitism in IH does not increase the predation rate of DH
  - increasing the host susceptibility to predation, which is not necessary for the life cycle

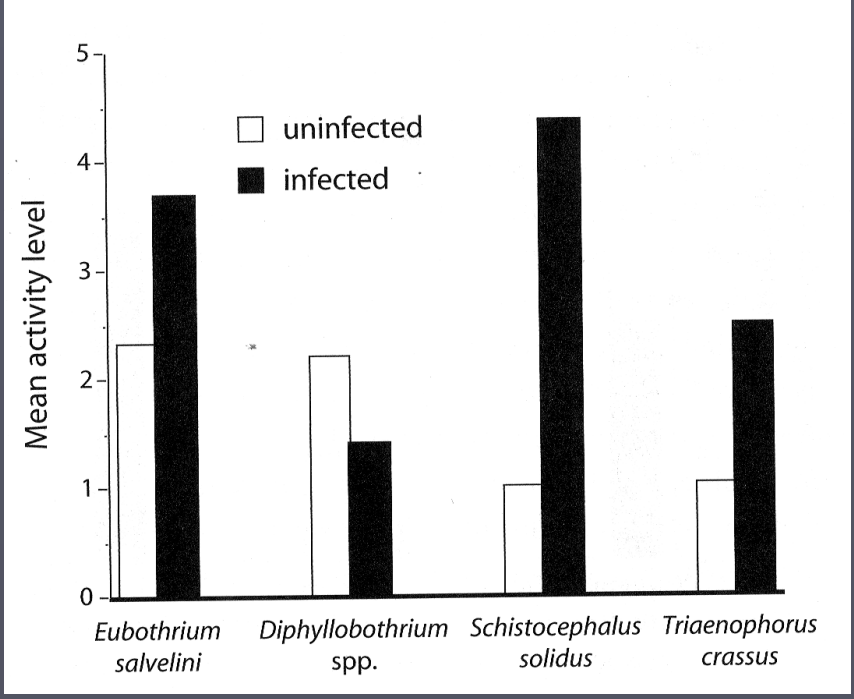
Adaptive vs. non-adaptive manipulation of hosts

- 3. benefits (?) for both the host and the parasite
- e.g. *Moniliformis moniliformis* (Acanthocephala) influences the behaviour of intermediate cockroach hosts



Non-adaptive effects of parasitic infection

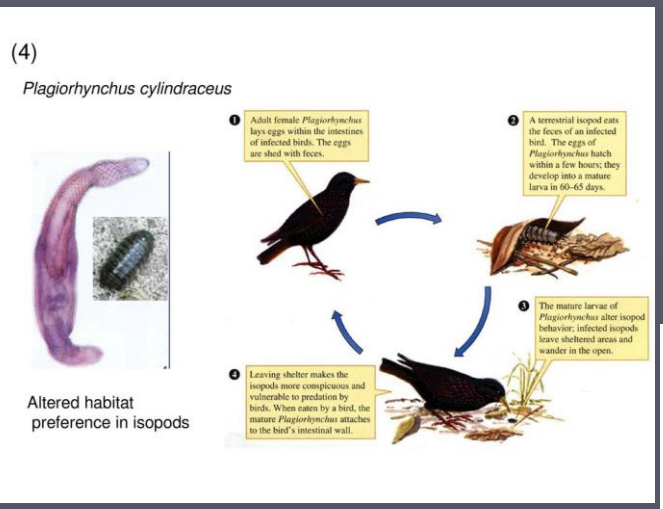
- Changes in host activity caused by the parasite in the opposite direction and have different effects on parasite transmission (in similar host-parasite systems)

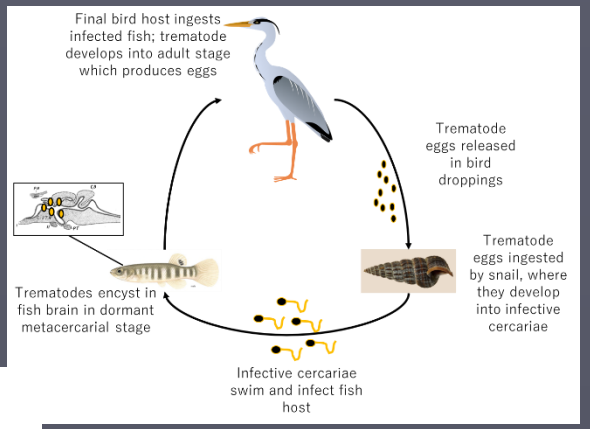


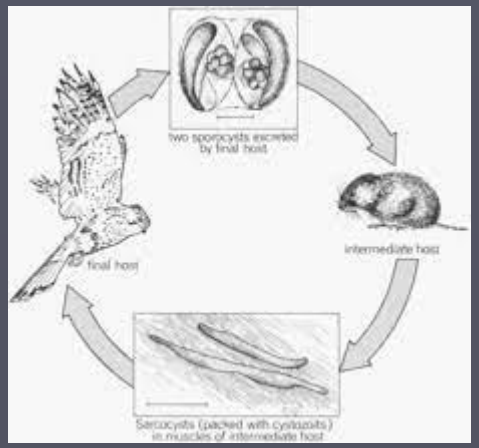
Effect of infection of 4 cestodean species on the activity of *Cyclops* spp.

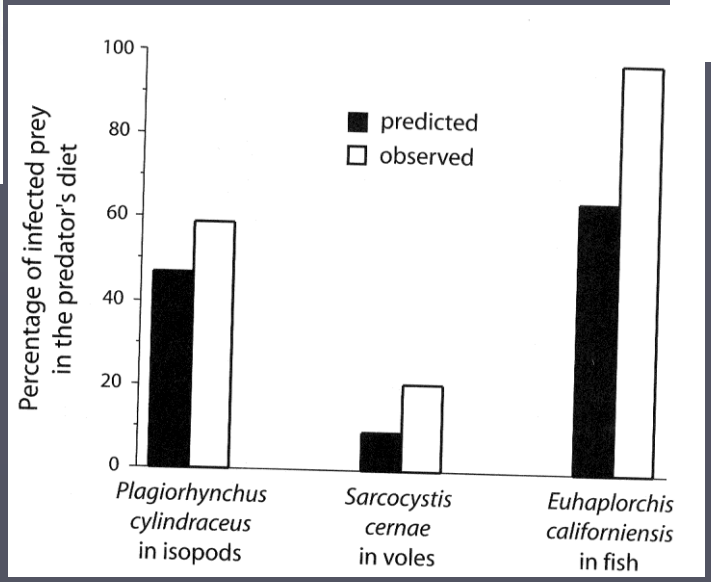
Adaptive host manipulation

- parasites manipulate IH behaviour → higher tranmission rate to DH
  - infected IH is more susceptible to predation by DH than uninfected IH









DH starlings DH kestrels DH piscivorous birds

Adaptive host manipulation

- parasite-induced changes in hosts affect the fitness of parasites
- When is it an adaptation?

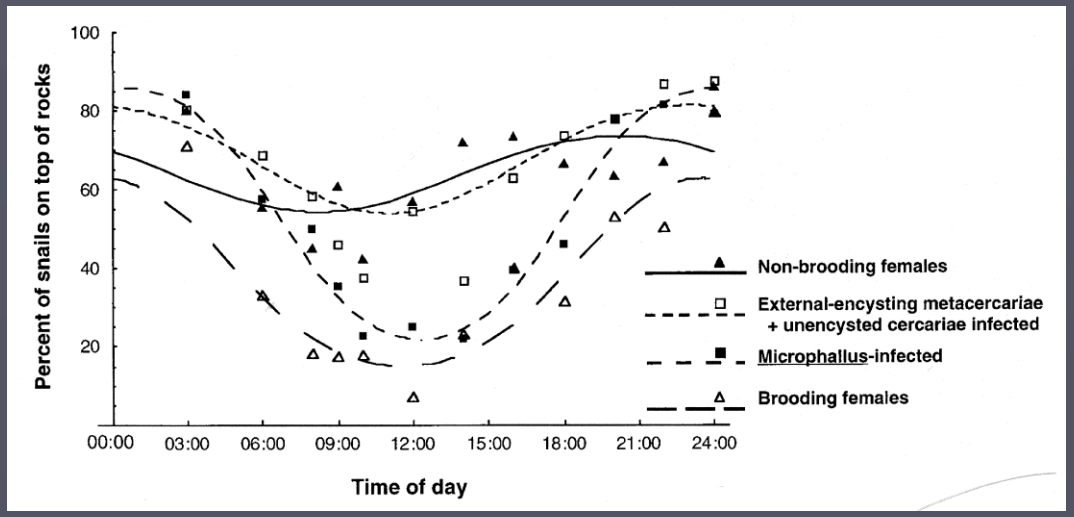
1. time synchronization between parasite infection and behavioural change expression in hosts

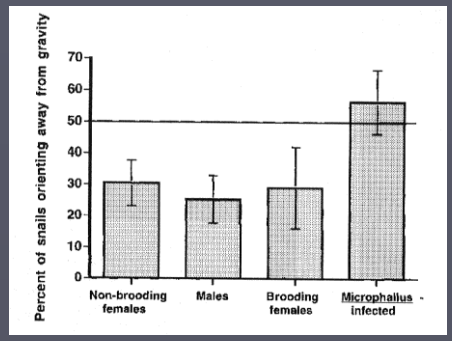
2. a certain degree of host specificity of adaptive manipulation of host behaviour

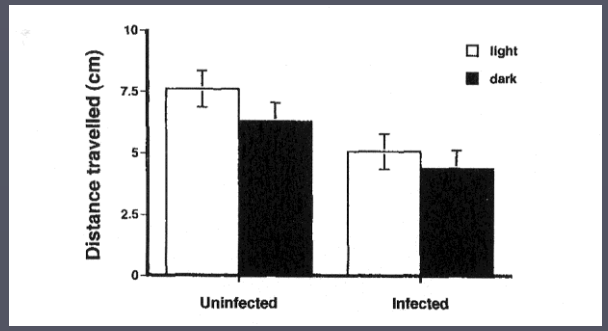
Adaptive host manipulation

- Ex. Freshwater snail *Potamopyrgus antipodarum* infected with the parasite *Microphallus* sp. (Digenea)

  - modified behaviour to increase predation by waterfowl (DH) and reduce predation by fish







Parasites induced changes in host behaviour

- Changes positively affect the transmission of the parasite

1. Direct, e.g. infection of the host neuroendocrine system

2. Indirect, e.g. change in the host physiology, which evokes a specific response in the behaviour of the infected host

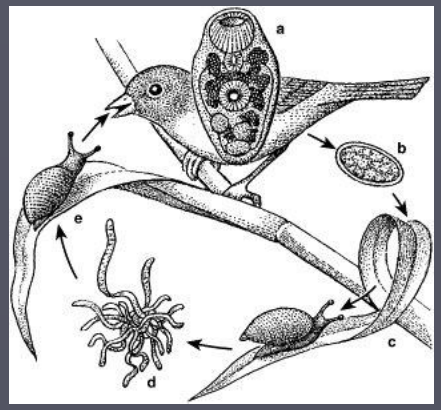
Parasites induced changes in host behaviour

- Host visibility (aggressive mimicry)

  - parasite-induced color changes in the intermediate host, formation of white or dark spots or swelling

  - increase the predation success of the final host

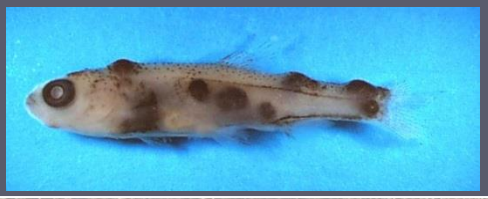
e.g. colored sporocysts of *Leucochloridium macrostomum* pulsating in tentacles of the terrestrial snail of the genus *Succinela*

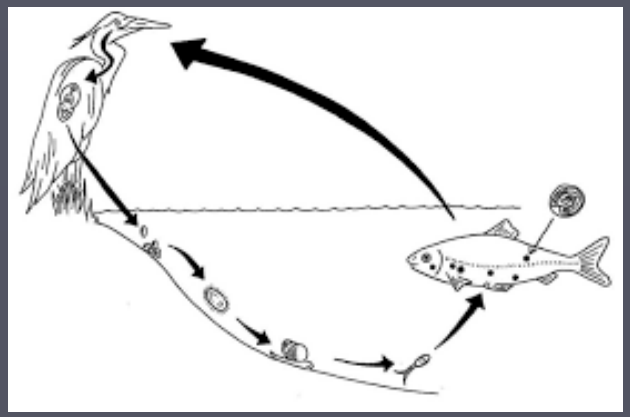


http://www.youtube.com/watch?v=EWB_COSUXMw

Parasites induced changes in host behaviour

- E.g. black spots on the skin of freshwater fish ("black spot disease") caused by some digenean species
- *Posthodiplostomum cuticola*



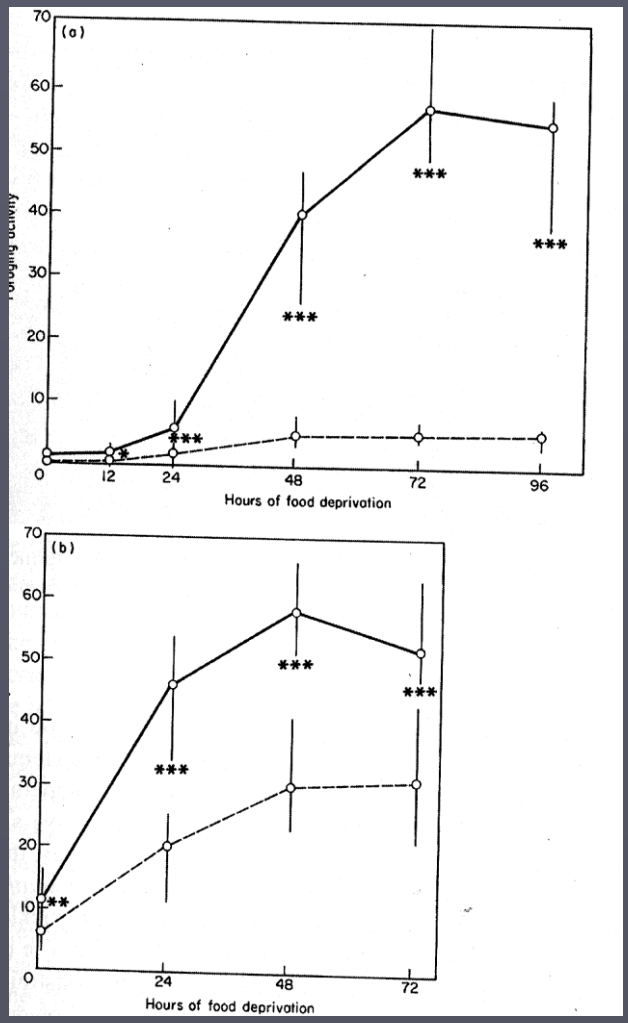


Parasites induced changes in host behaviour

- Altered feeding behaviour

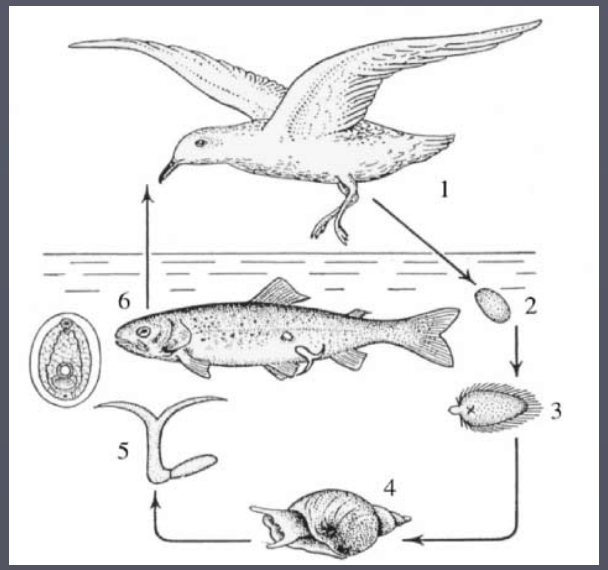
  - parasite-induced change of host feeding behaviour - long search for food near the predator

  - e.g. plerocercoids of the tapeworm *Schistocephalus solidus* in three-spined stickleback (*Gasterosteus aculeatus*)



Parasites induced changes in host behaviour

- Altered ability to move -> disorientation of the host
  - the parasitized host shows an atypical movement
  - e.g. metacercariae of *Diplostomum spathaceum* in freshwater fish (intermediate host) - localization in the lens of the eye



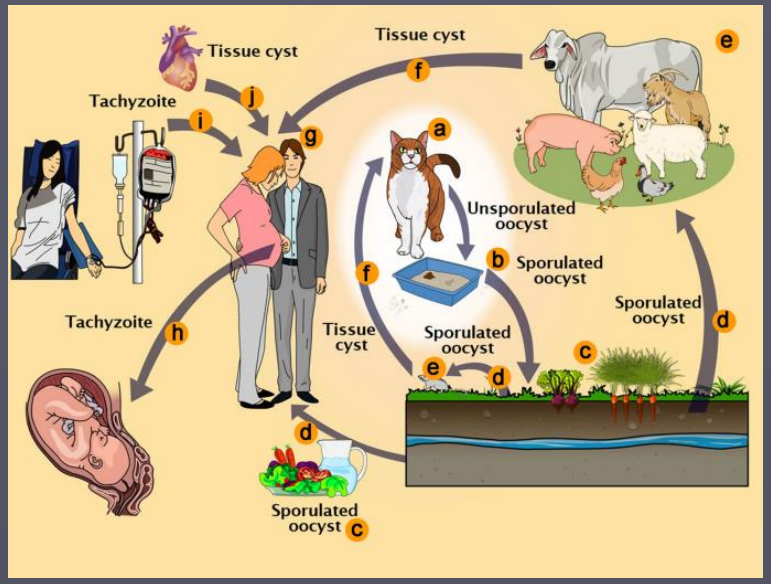
Parasites induced changes in host behaviour

- Altered behaviour in the presence of a predator

- the parasitized host has a reduced susceptibility to the presence of a predator
- the escape distance between the predator and the infected host is shortened
- the reaction of the infected host to the predator's attack is stiffness
- Ex. plerocercoids of tapeworm *Schistocephalus solidus* in *Gasterosteus aculeatus*

Parasites induced changes in host behaviour

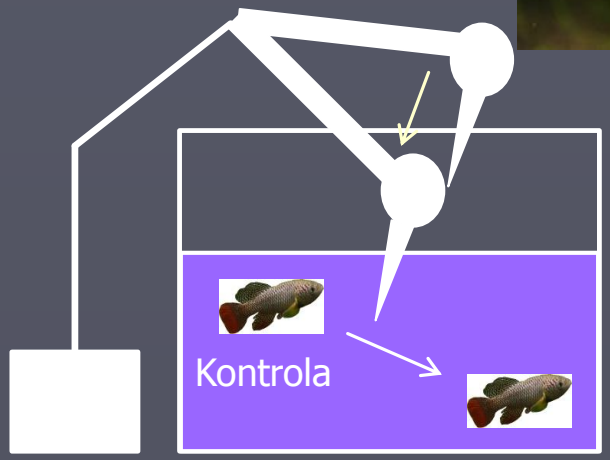
- *Toxoplasma gondii* in rodents (intermediate hosts)
  - affects transmission to the final host (cats)
  - congenital aversion of rats to cats
  - parasite modification of host behavior - cat odour is an attractant to rats



http://www.youtube.com/watch?v=__K104jSGzs

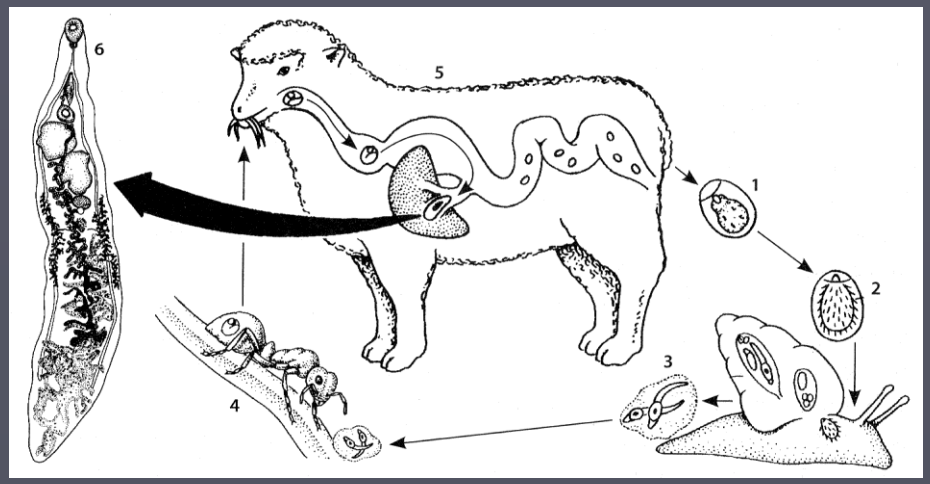
Parasites induced changes in host behaviour

- metacercariae of *Apatemon* (<15) in the fish brain
  Nothobranchius furzeri
  - "jumps" above the surface - the probability of catching an infected fish with a heron 30 times higher than in the case of a healthy fish



Parasites induced changes in host behaviour

- Habitat preferences
- The parasitized host moves to an environment where DH is more conspicuous and easier to reach
- Ex. Metacercariae of *Dicrocoelium dendriticum* in ants (*Formica praetensis*)



http://www.youtube.com/watch?v=lGSUU3E9ZoM

Parasites induced changes affecting host reproduction

- Modification of sexual behaviour

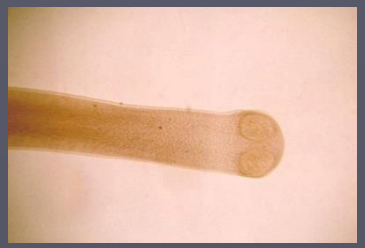
1. parasites directly use reproductive organs (feed on gonads)

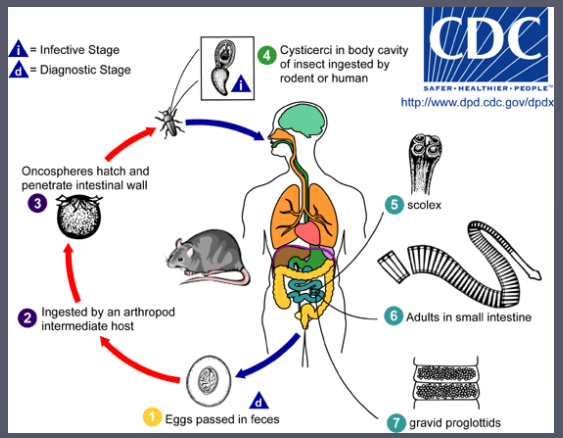
2. indirect use of the host - the host's reproductive effort to its advantage (host energy to reproduce or prevent sexual maturation of the host - castration)

Parasites induced changes affecting host reproduction

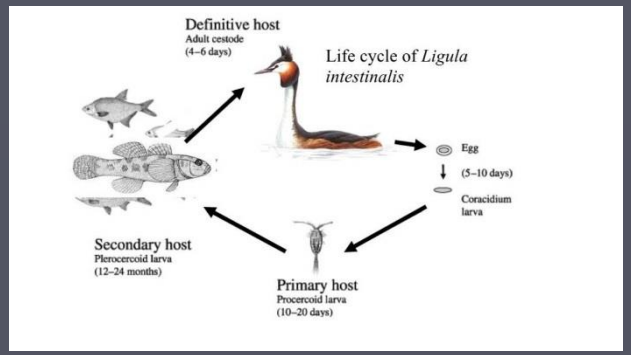
- production of hormones that prevent sexual maturity of the host

Ex. the tapeworm *Hymenolepis diminuta* suppresses vitelogenesis in the insect intermediate host (*Tribolium confusum* and *Tenebrio molitor*) - smaller size and viability of eggs





Ex. Plerocercoids of tapeworm *Ligula intestinalis* prevents the development of gonads and reaching sexual maturity of fish IH



Parasites induced changes affecting host reproduction

- the parasite uses the energy intended for host reproduction to benefit its own growth through castration of the host

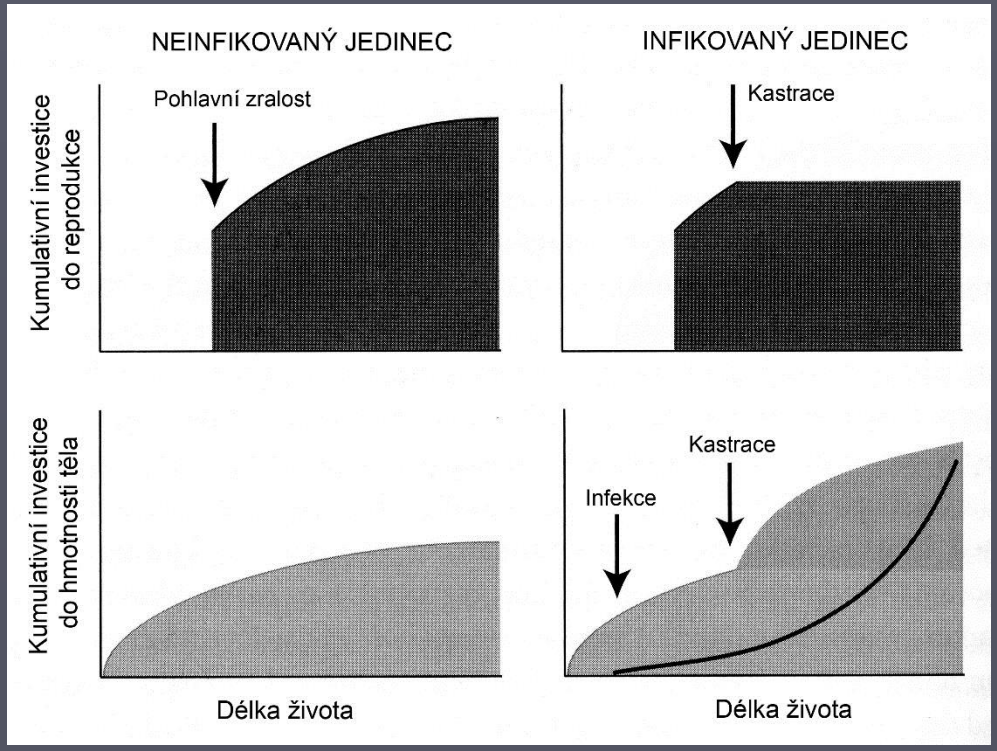
  Ex. Digenea castrating snails

  Ex. *Sacculina carcini* (Cirripedia) parasitizing crabs - castration of males and females + hormonal interference - feminisation of males

http://www.youtube.com/watch?v=LFaqeTauVhA

Parasites induced changes affecting host reproduction

- Castration of hosts - ideal parasite strategies for host utilization
  - the parasite does not reduce the lifespan of the host
  - energy not used for reproduction, the host invests energy in somatic growth

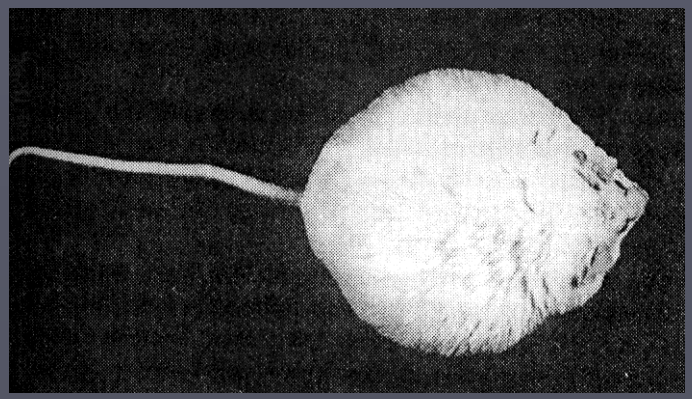


Cumulative host investment in reproduction and body weight in the case of an uninfected and infected individual by a parasitic castrator

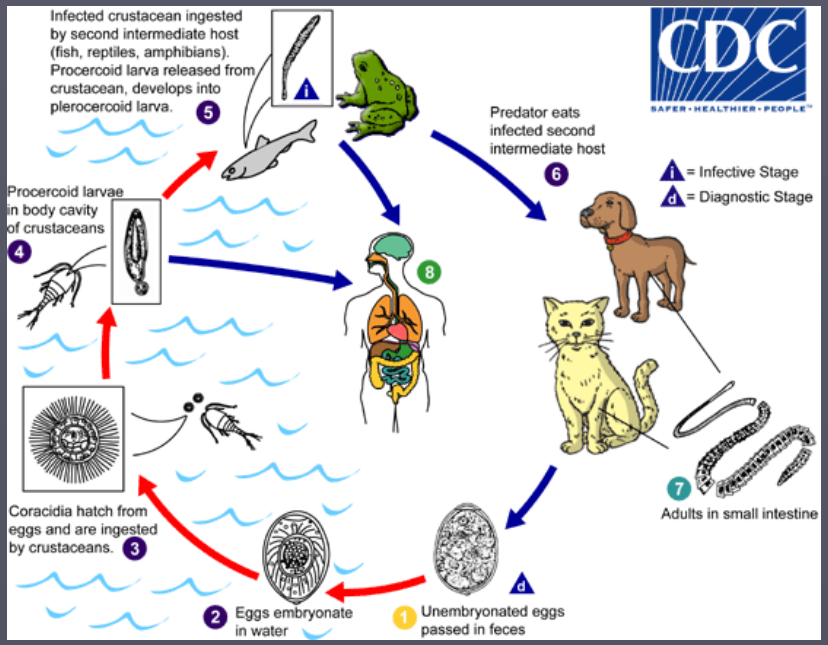
Parasites induced change - host gigantism

- Host gigantism

- growth factor secretion, excessive food intake, inability to metamorphosis
- secretion of analogues by parasites which mimic the growth factor host



Plerocercoids of *Spirometra mansonoides* in rodents produce a growth factor which mimics mammalian growth hormone



Parasites induced change - host gigantism

- Hypotheses

1. Parasite strategies to exploit the host

- later benefit for longer-lived parasites with intermediate growth rate (e.g. for larval stages of digeneans parasitizing snails)

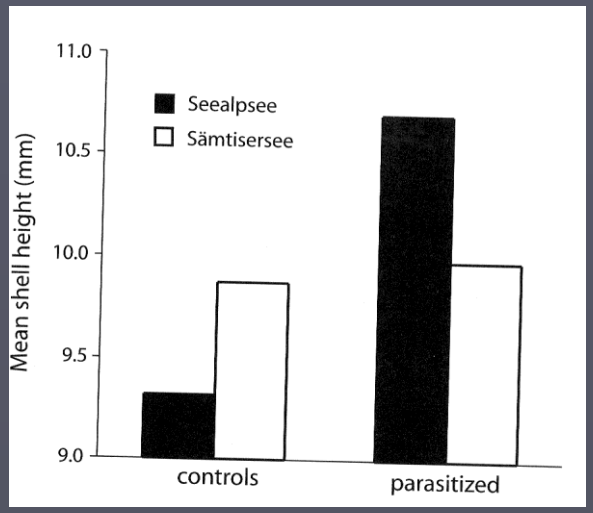
- resources released by castration are invested in the body weight of the host for later use of the parasite, the parasite induces very low or no host mortality

2. Adaptive response of the infected host

- compensation of the parasite effect

Parasites induced change - host gigantism

- Host gigantism
- Experiment: gigantism as a strategy of a parasite using a host or gigantism as a host adaptation to compensate for the effect of parasitism?



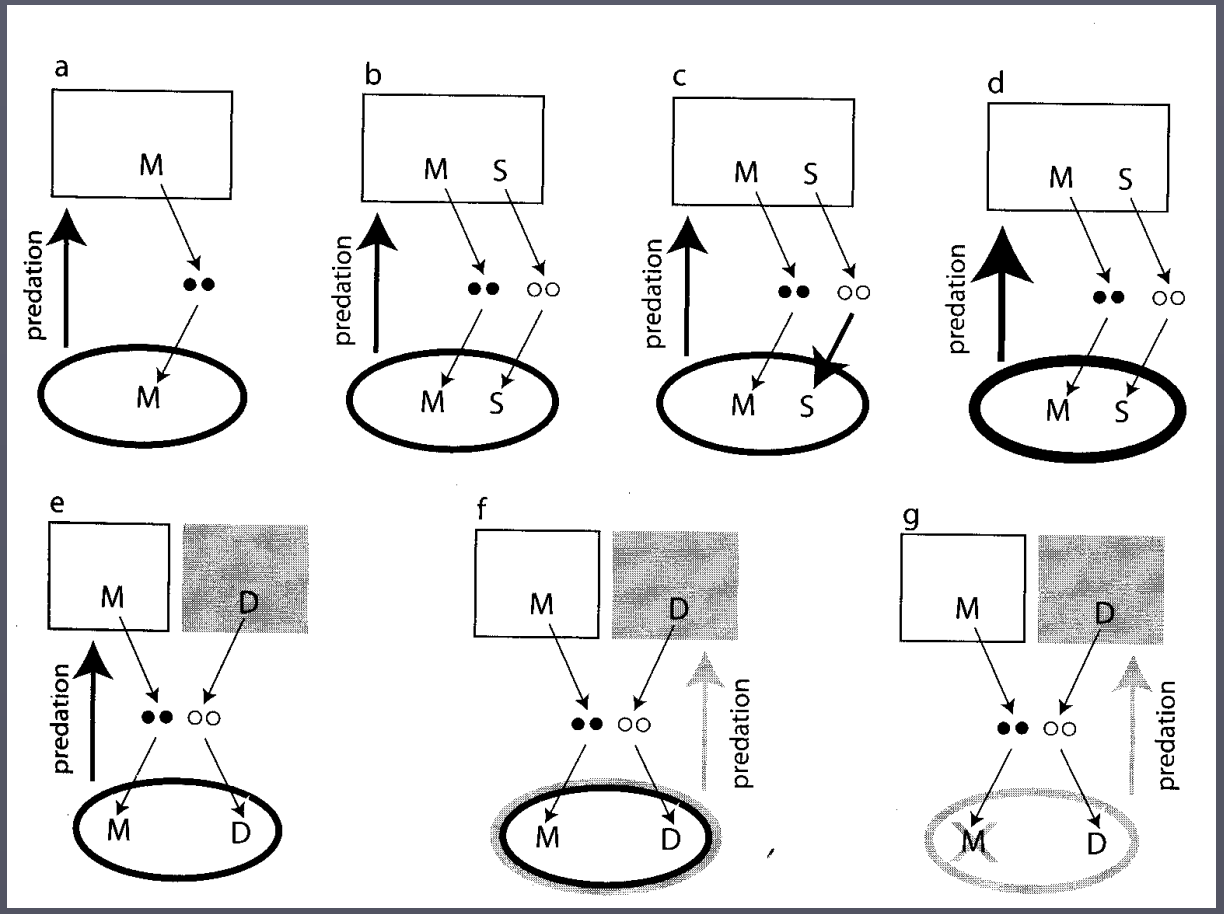
Effect of castration by the parasite *Diplostomum phoxini* (Digenea) on the growth of the intermediate host *Lymnaea peregra*

Host manipulation from the perspective of the concept of multispecies parasite infection

- Many larval helminths share intermediate hosts with other parasite species

- some manipulate host behaviour, others do not manipulate
- some have the same, others have different life cycles
- same definitive host = cooperation of parasite species
- different definitive host = conflict between parasite species

Host manipulation from the perspective of the concept of multispecies parasite infection



Host manipulation from the perspective of the concept of multispecies parasitic infection

- "Hitchhiking" tracking strategy - a larva of a non-manipulating parasite actively searches for and infects a manipulated host
- Active "hitchhiking" is only beneficial in case of low manipulator prevalence's

- Ex. Digenea in Amphipoda (IH)

Microphallus papillorobustus - manipulative species - the host swims at the surface of the water, where it is exposed to predation by a definitive host - the bird

Maritrema subdolum - a non-manipulative species, actively swims at the surface of the water

Host manipulation from the perspective of the concept of multispecies parasitic infection

- double manipulators - copilot strategy at the same IH

  - each affects the host phenotype differently

  - the effect of both on the rate of transmission is additive (selection favors synergisme)

Ex. Acanthocephala (*Pomphorhynchus laevis* and *Acanthocephalus clavula*) in Amphipoda (IH), definitive host fish

Ex. Echinostom Digenea (*Curtuteria australis* and *Acanthoparyphium* sp.) Cerastoderma (bivalves) (IH), the definitive host bird

Host manipulation from the perspective of the concept of multispecies parasitic infection

- "Hijack" strategy - a competitive process to take control on IH

  - both parasite species manipulate

  - one is stronger (affecting the host phenotype) – with manipulation mechanisms or which was first in the host

  - "arms races" between manipulators (costs associated with loss are large)

  - Ex. Acanthocephala (*Pomphorhynchus laevis* and *Polymorphus minutus*) in Amphipoda (IH), different DH: fish for PL), bird for PM

  - stronger PL

Host manipulation from the perspective of the concept of multispecies parasite infection

- "Co-pilot shooting" strategy

Ex. Cestoda parasitizing beetles (IH) - *Hymenolepis diminuta* (DH rat) and *Raillietina cesticillus* (DH chicken) - both manipulate

- Infection of beetles with *R. cesticillus* prevents *H. diminuta* infection

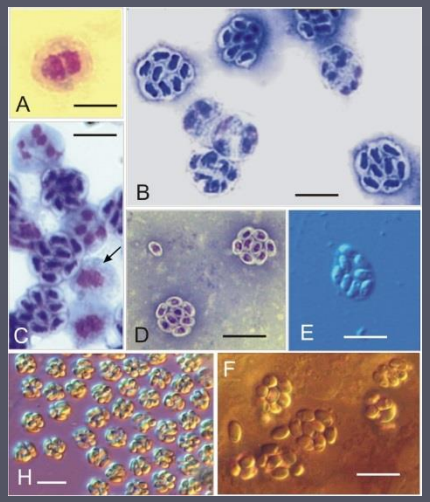
Ex. Acanthocephala in Amphipoda (IH) - *Pomphorhynchus bulbocolli* and *Leptorhynchoides thecatus* (DH for two parasites are different freshwater fish species)

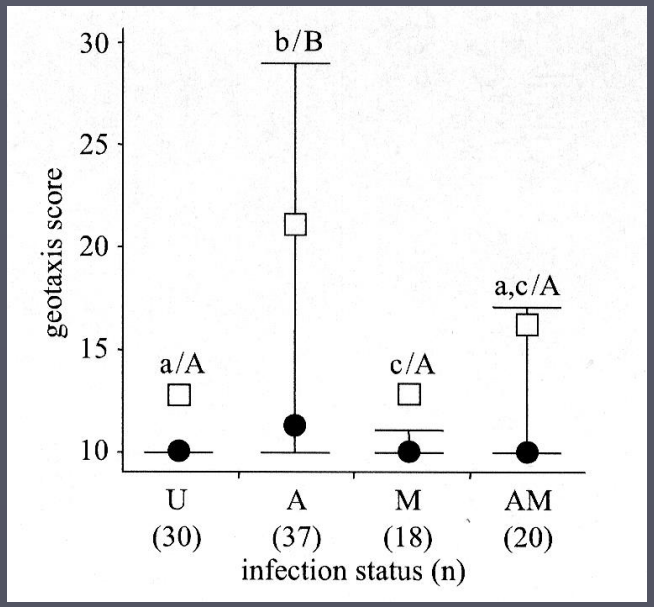
- The presence of one species negatively affects the growth of the other (both are host-manipulating species)

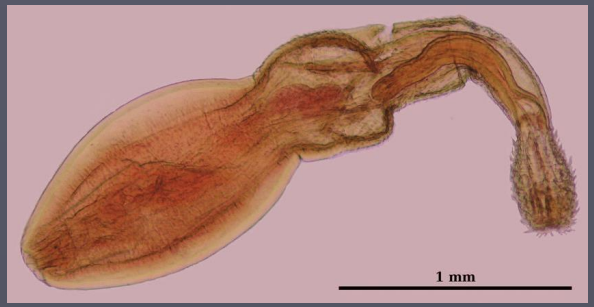
Host manipulation from the perspective of the concept of multispecies parasite infection

- Sabotage hypothesis - neutralization of manipulation

Vertically transmitted parasite *Dictyocoela* sp. (Microsporidia) and the horizontally transmitted parasite *Polymorphus minutus* (Acanthocephala) in IH *Gammarus roeseli* (PM modifies IH behaviour)







Manipulation of the sex ratio of the host

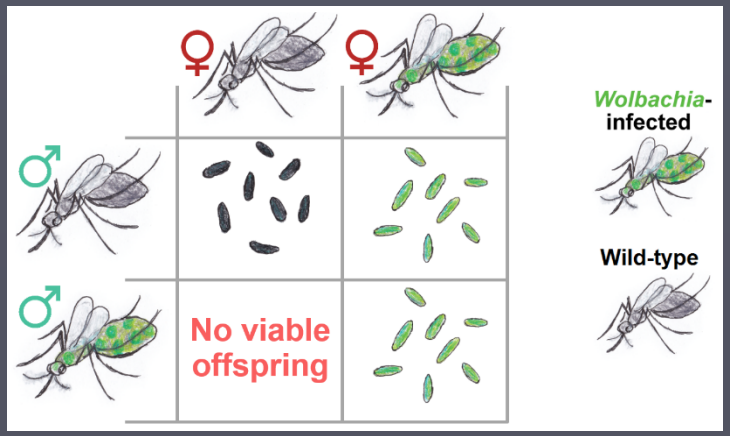
- Parasites transmitted vertically: microsporidia, viruses, bacteria
- *Wolbachia* bacteria - live in the cytoplasm of host gametes, female infections - transmission for offspring, male infections - evolutionary end

- parasite manipulation = effect on investment in female offspring

1. kill the male offspring of the host

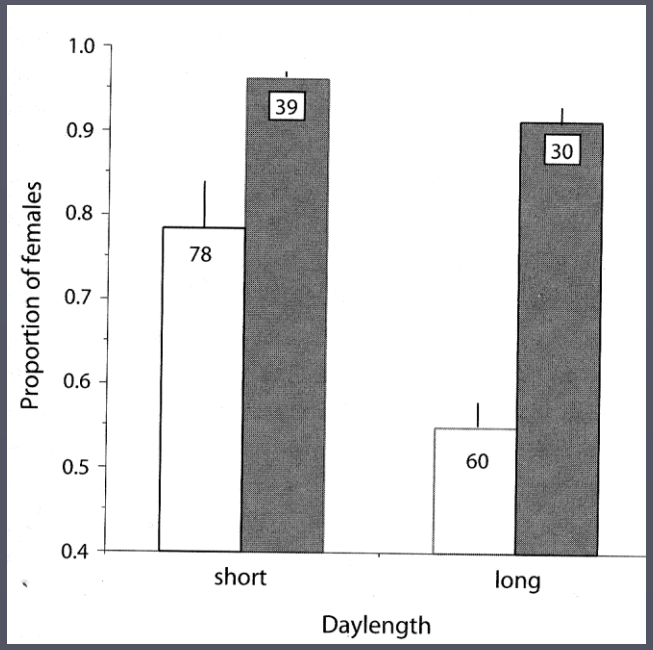
2. deform the primary sex ratio by changing the expression of host genes (convert the genotype of males into the genotype of females)

3. feminize male offspring (change of genotypic males to functional phenotypic females)



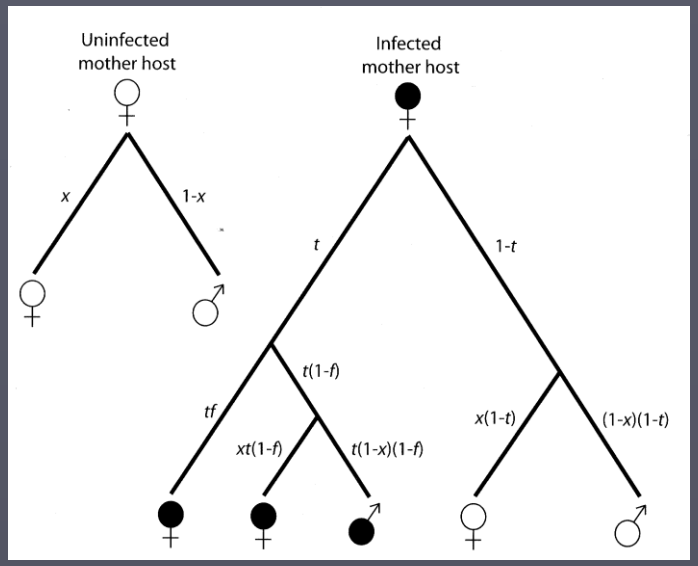
Manipulation of the sex ratio of the host

- Ex. Representation of female offspring in the clutch of female *Gammarus duebeni* uninfected and infected with the transovarian transmitted parasite *Octosporea effeminas* (Microsporidia)



Manipulation of the sex ratio of the host

- The effect of the parasite on the sex ratio depends on:
  1. the primary sex ratio of the host
  2. the ability to transmit the parasite from mother to offspring
  3. on the feminizing effect of the parasite



Risk strategy of using the host !!!
Maximization of transmission and feminization
→ extinction of the host population (elimination of males)
and extinction of the parasite