Evolution of host-parasite interactions

Coevolution

- Mode (1958) – mathematical model for host-parasite coevolution
- Janzen (1980) - process between interacting species, where each of the interacting species changes its genetic structure in response to a genetic change in its partner
- Thomspon (1994) - process of reciprocal evolutionary changes of interacting species

- coevolutionary processes at the level of molecules, cells, genes, males-females, parents-offspring, species

- Its importance depends on the frequency of interactions between partners and the impact on their reproductive success

Coevolution

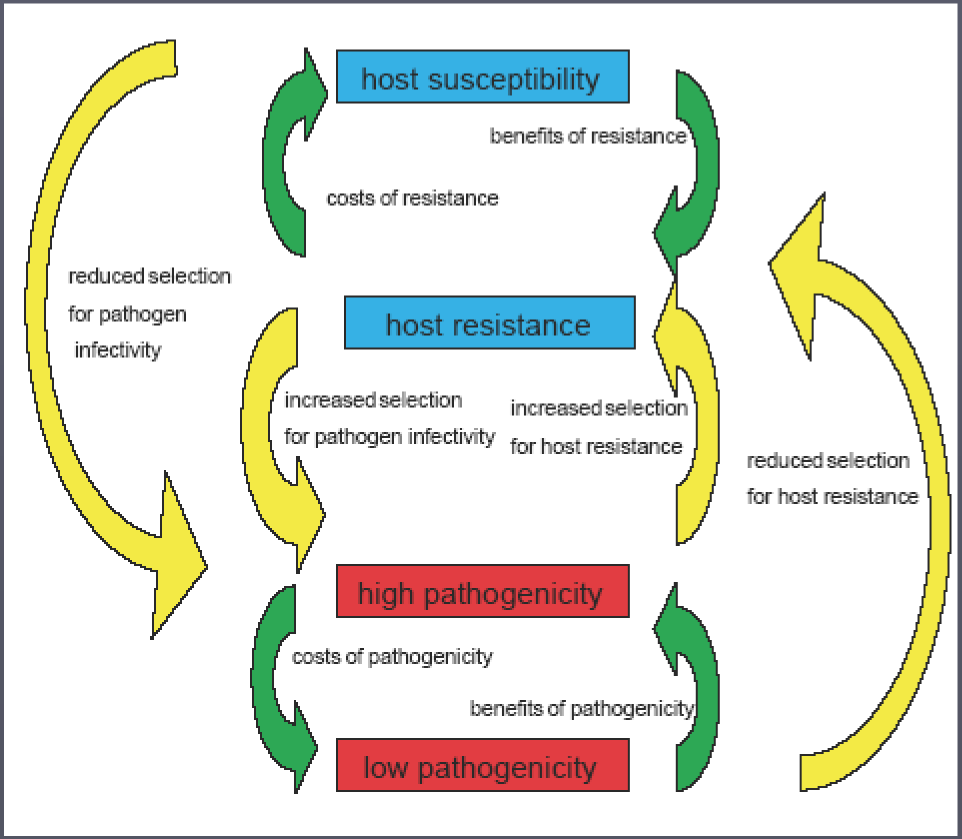
- Woolhouse et al. (2002). Nature Genetics 32: 569–577

  Reciprocal, adaptive genetic changes between interacting species

  Host-parasite coevolution can be studied from the following perspectives:

  - mutual phenotypic characteristics (resistance and infectivity)
  - interacting parasite and host molecules
  - genes or nucleotide sequences

Coevolution of host-parasite interactions



Schematic representation of coevolution with emphasis on reciprocity:
Changes in allele frequency due to selection in one species have a selective effect on the other species - changes in allele frequency in another species

Coevolution

- From the point of view of evolutionary parasitology coevolution = common evolution of parasites and their host species, during which they interact

- In the strict sense - the evolution of associated groups, expressed as reciprocal adaptations

- Association with macroevolutionary (cospeciation) and microevolutionary (coadaptation) components

Macroevolution versus microevolution

- Macroevolution - the origin and evolution of higher taxa than the species
  - rules that determine the origin of a certain form and adaptive changes
  - changes in species diversity within and between evolutionary groups, rate of speciation and extinction in the long term (historical, unrepeatable, unique)
- Microevolution - evolutionary processes within a species
  - short-term, recent, ongoing changes, experimentally studyable
  - population genetics, ecology, ethology

Cospeciation and coadaptation

- Cospeciation
  - macroevolutionary process
  - may reflect the degree of congruence or incongruence between the phylogenies of hosts and parasites

- In the strict sense: topological congruence and the same rate of molecular divergence (same branch lengths) in the associated groups
- Known examples: Figs and their wasps, *Buchnera aphidicola* (symbiont) and aphids, Australian mistletoe and pine, pocket gophers (Geomyidae) and their lice

Coadaptation

- originally co-accommodation
- microevolutionary processes
- includes anagenesis and reciprocal adaptation (arms race scenario)
- associated with host specificity

Coevolution models in host-parasite systems

1. model of allopatric cospeciation

- parasites and hosts share common space and energy
- disruption of gene flow between host populations → allopatric speciation of hosts and parasites

- synchronous cospeciation - speciation of parasites and hosts takes place simultaneously
- delayed cospeciation - a host or parasite speciation is delayed after speciation of the other

Coevolution models in host-parasite systems

2. Resource tracking model

- based on the ecological concept
- parasites track resources over evolutionary time
- the evolution of a parasite is a response to a change in the resources provided by the host
- the host changes the resources that the parasite is looking for → the parasite undergoes evolutionary changes that allow it to use new resources
- changes in the parasite occur after changes that have taken place in the resources provided by the host

Coevolution models in host-parasite systems

3. Model of an evolutionary arms race

- the most strict view of coevolution - mutual adaptive responses between hosts and parasites
- permanent evolution between parasites and hosts - aggressive targeting of each other
- parasite selection - higher host utilization, host selection - more successful parasite elimination
- This model is part of the concept of the hypothesis gene for the gene

Coevolutionary models in host-parasite systems - gene for gene

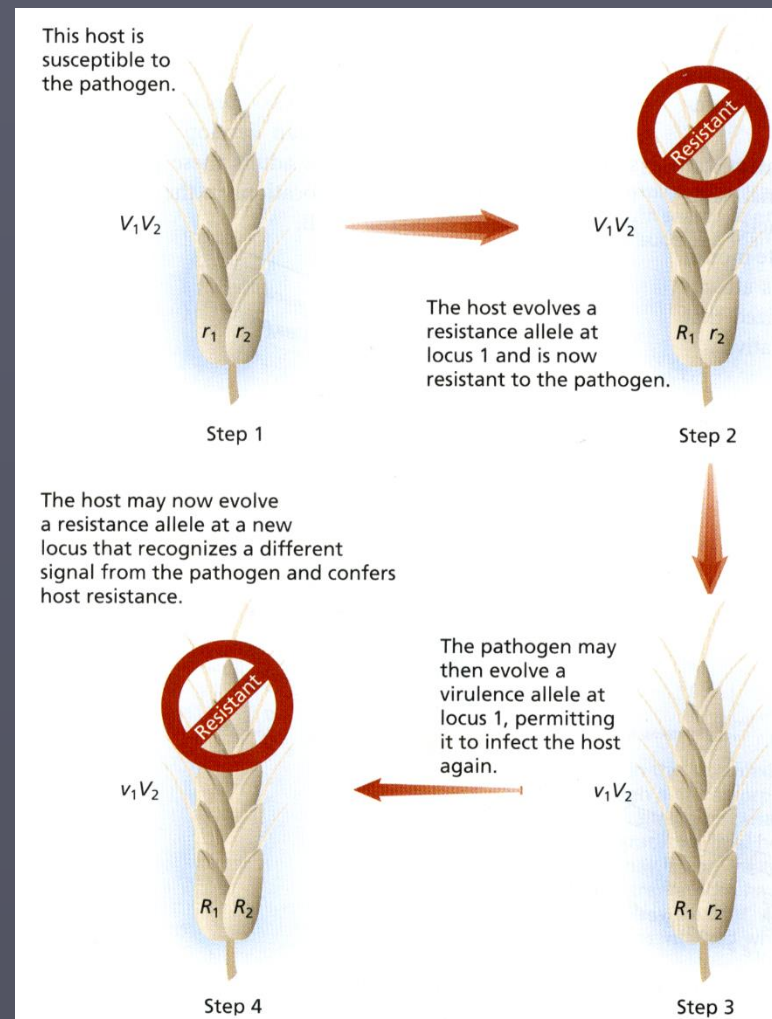
- for each gene conferring resistance in a host, there is a corresponding suitable gene for avirulence in the parasite
- host resistance is dependent on the presence of the resistance gene and the corresponding avirulence gene in the parasite
- resistance genes and avirulence genes = dominant genes

	Host genotype		
Parasite genotype	RR	Rr	rr
AA	Resistant	Resistant	Susceptible
Aa	Resistant	Resistant	Susceptible
aa	Susceptible	Susceptible	Susceptible

Coevolutionary models in host-parasite systems - arms race

- 1. parasites reduce a host's fitness
- 2. the host creates defense mechanisms against parasites = mutations or gene recombinations
- 3. the host with a new defense mechanism increases fitness and expands in the population
- 4. a new mutant or recombinant appears in the parasite population - it resists the host's defense mechanisms
- 5. a new mutant spreads in a population of parasite, it is able to enter the host
- 6. cycle is repeated

Coevolutionary models in host-parasite systems - arms race



Coevolution

- 4 rules
- Fahrenholz's rule (Stammer 1957, Dogiel 1964) - the phylogeny of parasites is a mirror of the phylogeny of hosts
- Szidat's rule (Szidat 1956, 1960) - the more "primitive" the host is - the more "primitive" are its parasites
- Eichler's rule (Eichler 1941, 1948) - species-rich group of hosts - a larger number of parasite species

Coevolution

- Manter's rule (Manter 1955, 1966)

  a) parasites evolve more slowly than their hosts

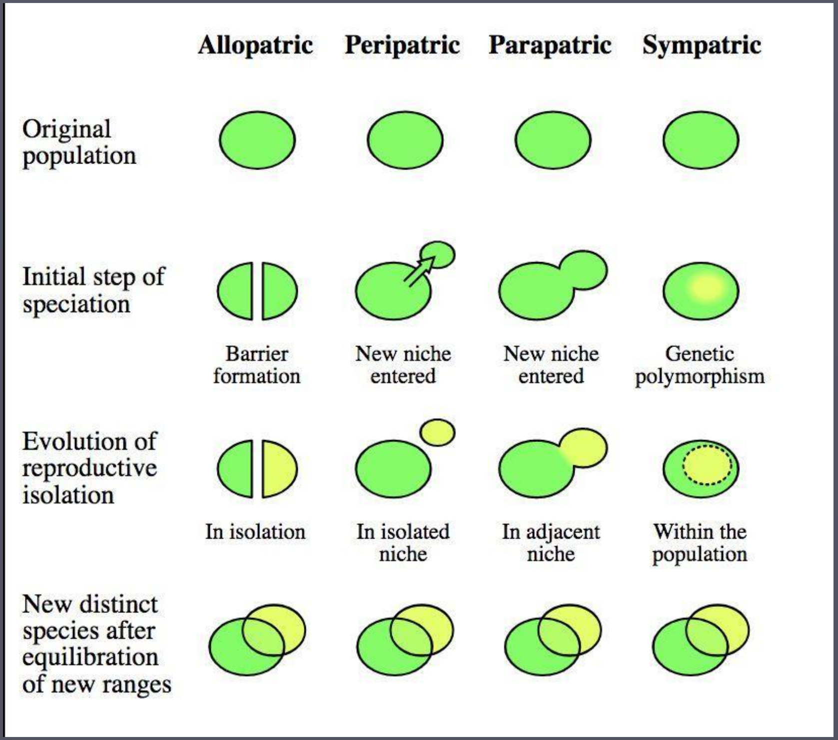
  b) longer association to a certain host group → higher specificity of parasites

  c) the host species are parasitized by the higher number of parasite species in the area where they have resided for the longest time.

  If the distribution of one or two closely related host species is disjunctive and yet the same parasites are found in these hosts, then the range of their distribution was overlapped in the past.

Speciation of parasite species

- Speciation - the evolutionary process of the origin of one or more species from an ancestral species
- 2 types of geographical speciation in parasites
- Allopatric speciation - in conditions of non-overlapping host areas
- Sympatric speciation - in conditions of overlapping host areas



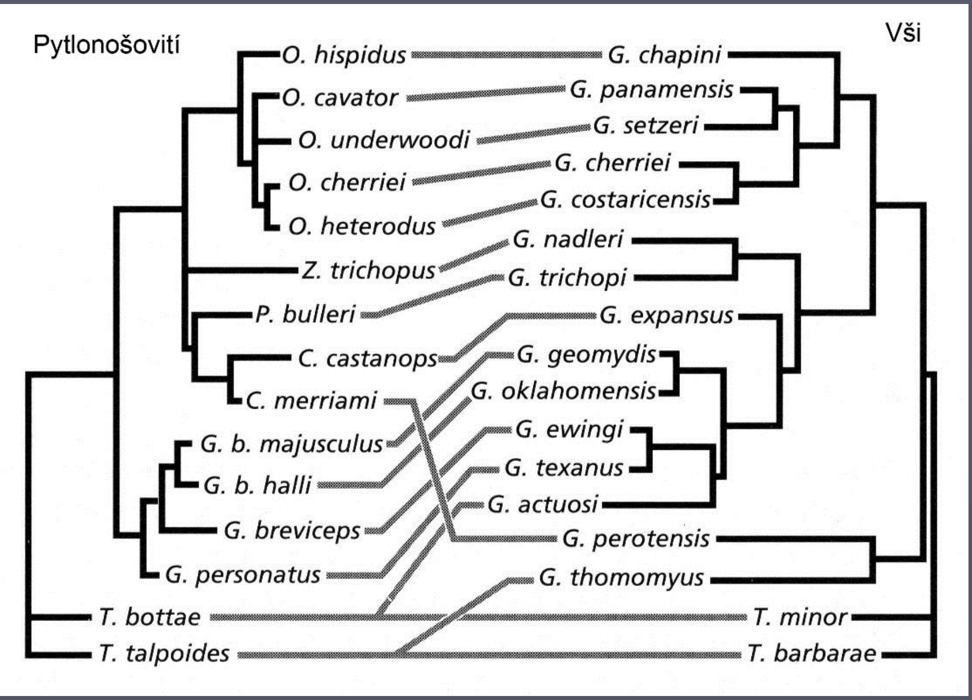
Allopatric speciation of parasites

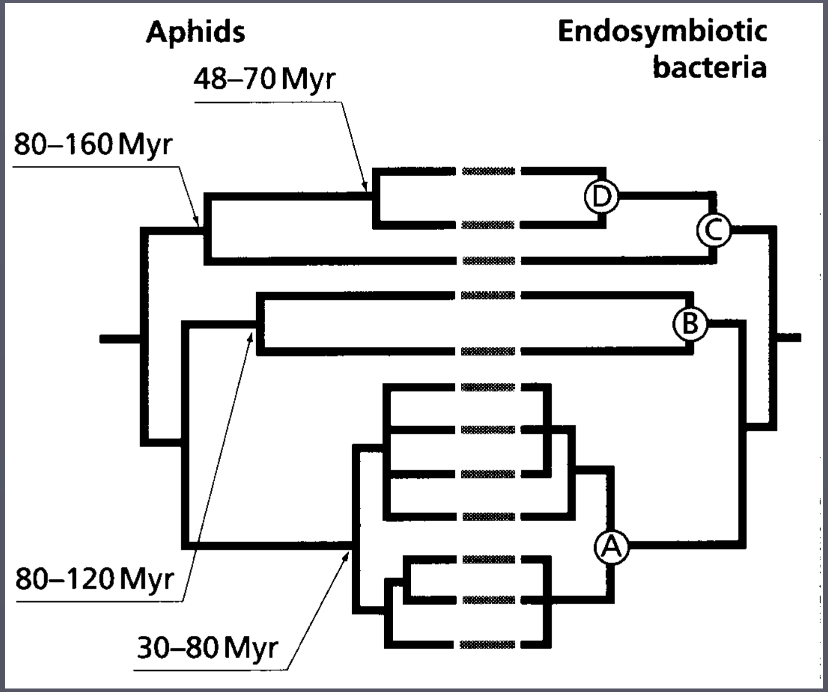
- Cospeciation - parasite speciation follows host speciation
- geographical isolation, reproductive isolation, genetic divergence of host populations

- Identical topology of phylogenetic reconstructions of hosts and parasites (Fahrenholz's rule)

Cospeciation

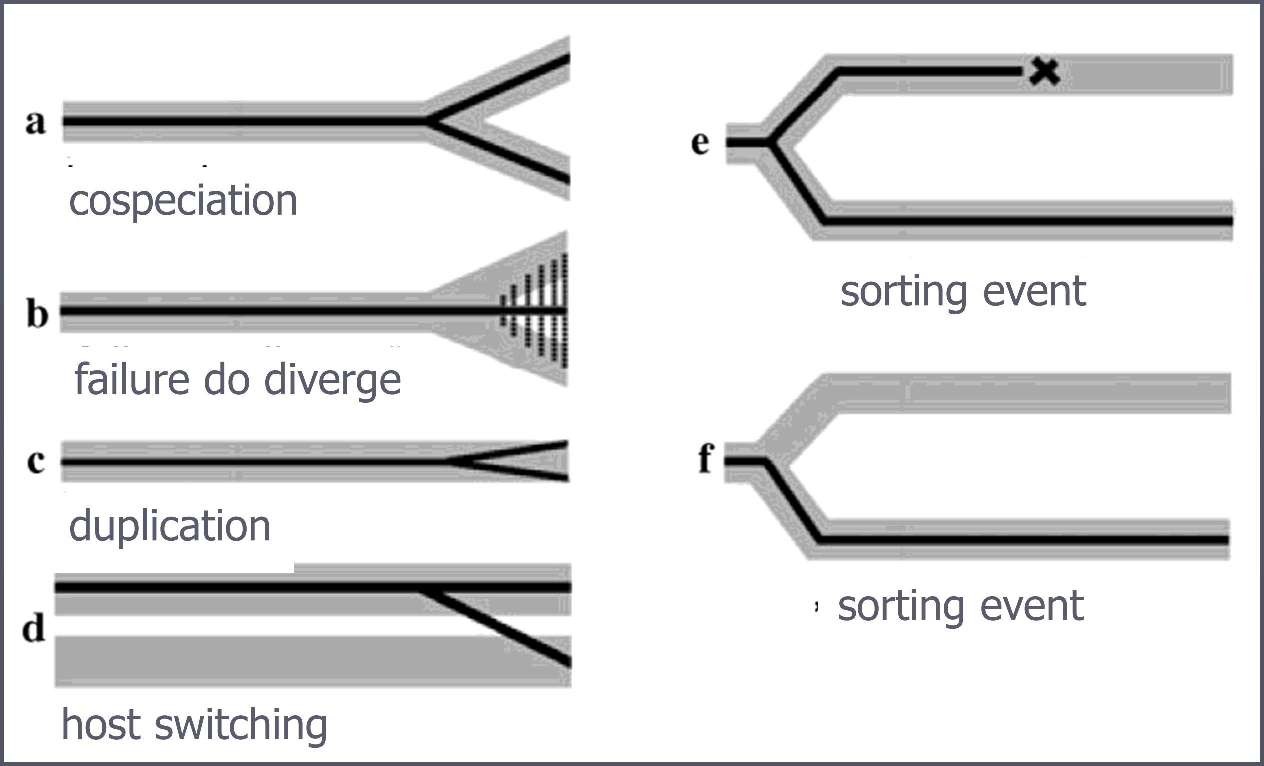
- pocket gophers (Geomyidae) and ectoparasitic lice
- Aphids and endosymbiotic bacteria





Sympatric speciation of parasites

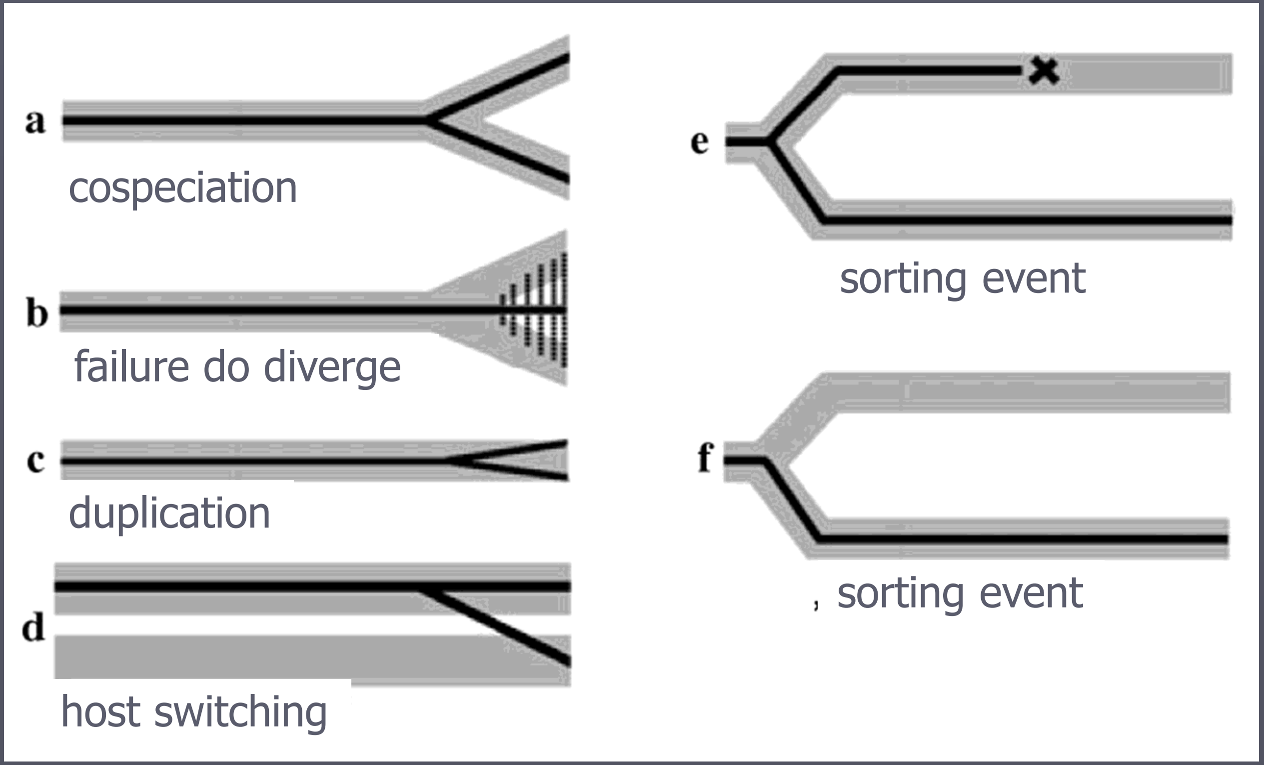
- host switching = colonization of different host species, evolution of multihost parasite species
- intrahost speciation = parasite duplication



Other coevolution events in host-parasite systems

Host speciation without corresponding parasite speciation:

- Failture to diverge
- Sorting event - extinction of the parasite following cospeciation
  - „missing the boat"



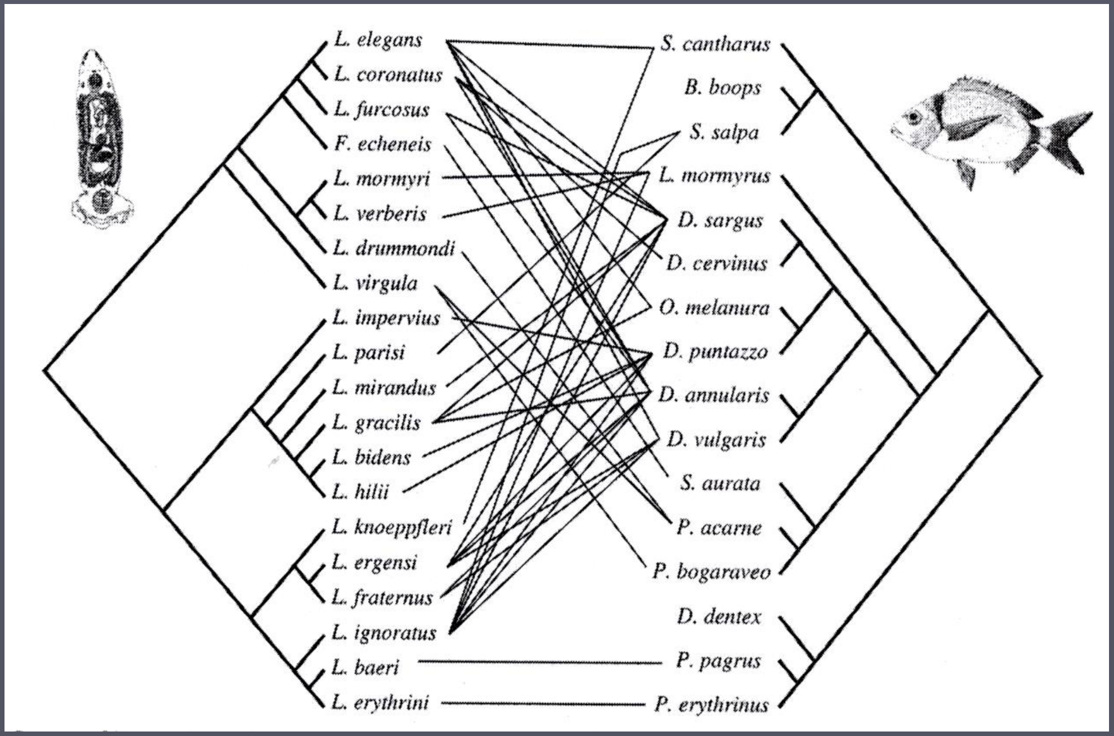
Speciation of congeneric parasites

- Speciation of monogeneans
  - highly host-specific
  - direct life cycle
  - high morphological diversity
  - high species diversity
  - adaptation
  - high number of congeneric species (within some genera)
  - high number of congeneric species per host

Speciation of congeneric parasites

- Ex. *Lamellodiscus (Monogenea)* parasitizing marine fish of the Sparidae
  - old genus
  - high intraspecific morphological variability of the sclerotized parts of the attachment apparatus
  - high dispersibility of host species

fast speciation by
host switch

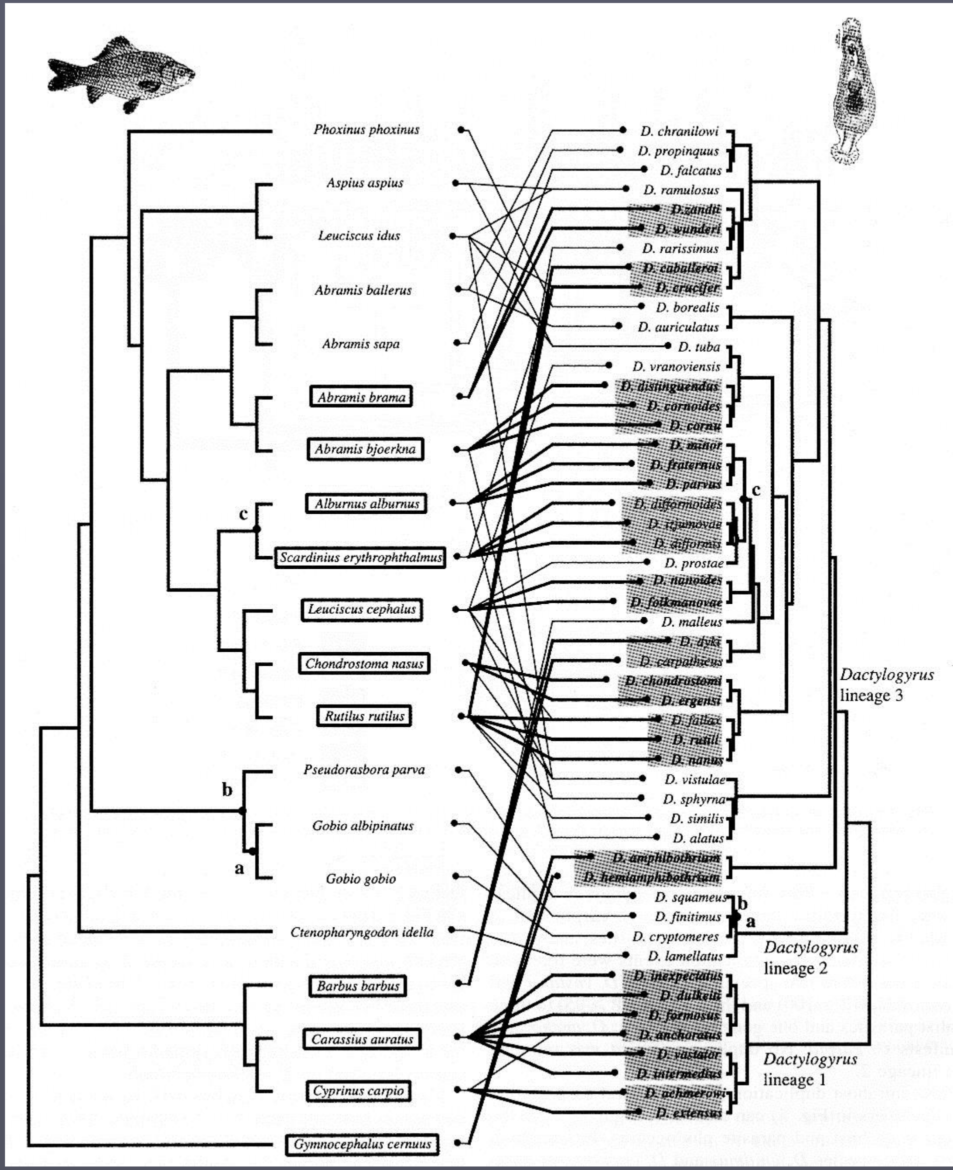


Speciation of congeneric parasites

- Ex. *Dactylogyrus* (Monogenea)
  - freshwater fish of Cyprinidae
  - high number of host-specific parasites
  - high number of species coexisting on 1 host species

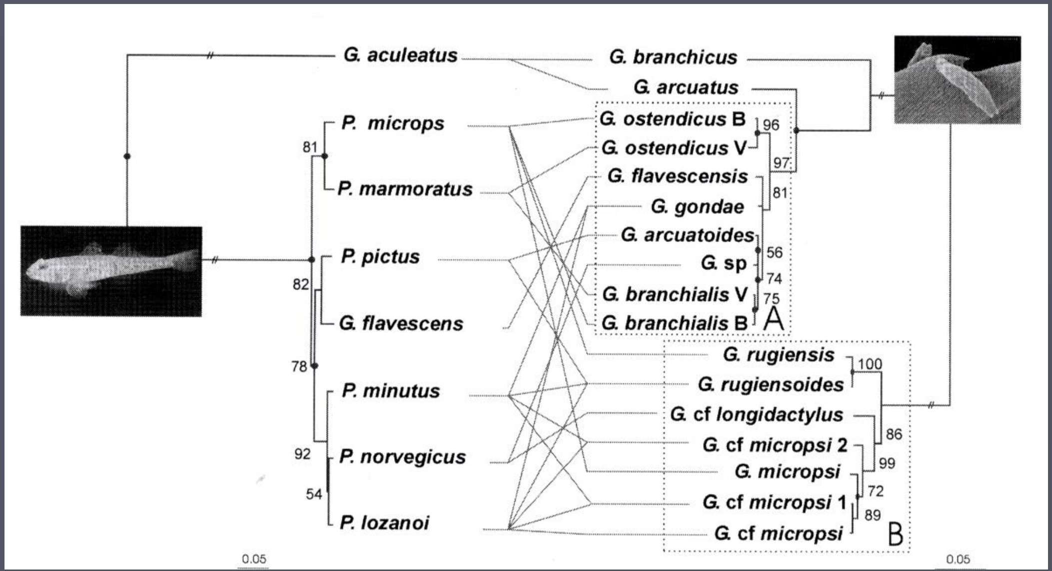
intrahost speciation

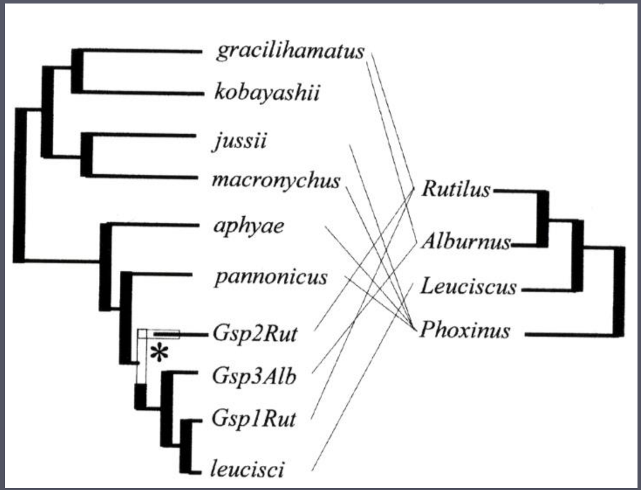
- evolution of different positions of preferred niches



Speciation of congeneric parasites

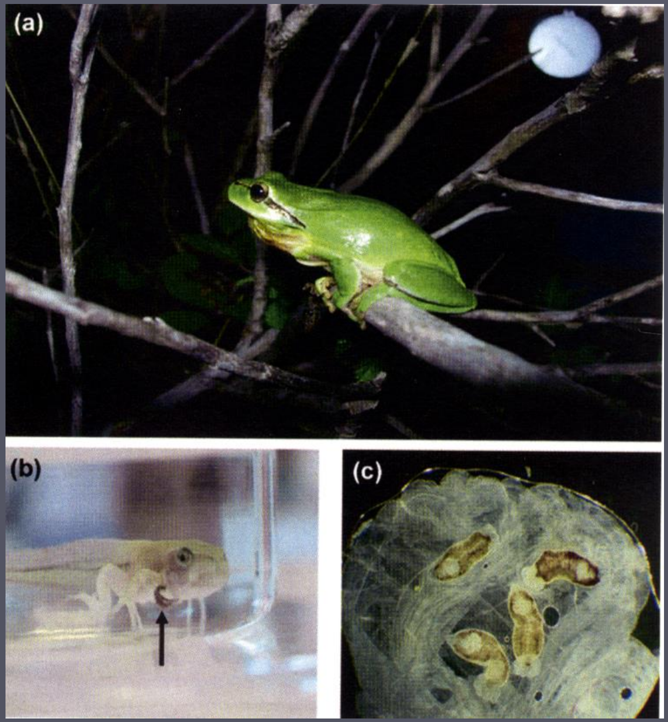
- *Gyrodactylus* (Monogenea)
  - viviparous, capable to colonize a wide range of freshwater and some marine fish species
  - speciation by host switch, adaptive radiation

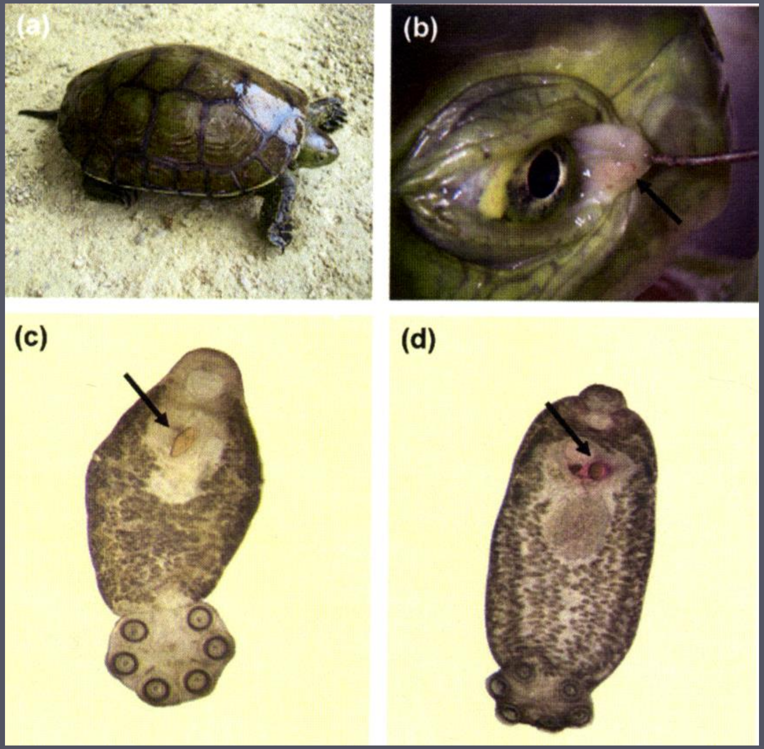




Speciation of congeneric parasites

- Ex. Polystomes (Monogenea)
  - a special group of endoparasitic monogeneans
  - infect mainly amphibians and freshwater turtles

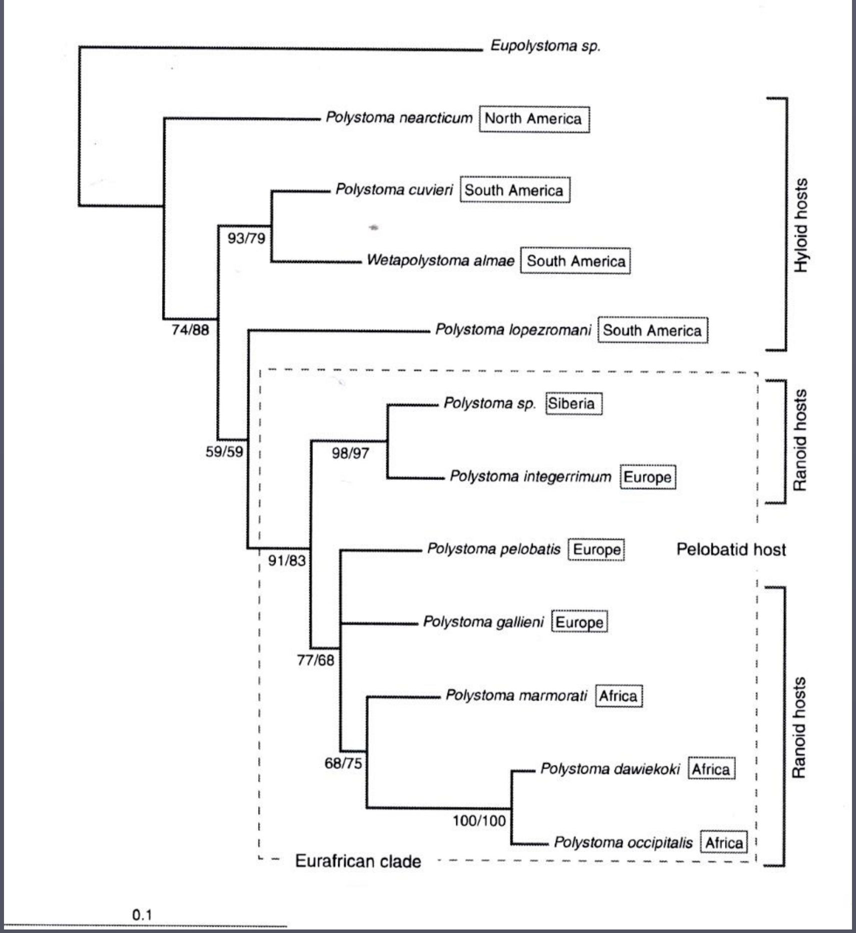




Speciation of congeneric parasites

- Ex. Polystomes (Monogenea)
  - high morphological similarity
  - highly host specific
  - preferences for different niches within the host

Host switch and cospeciation



Parasites affecting the evolutionary biology of hosts

- Evolution of interactions between hosts and parasites from a perspective other than coevolution

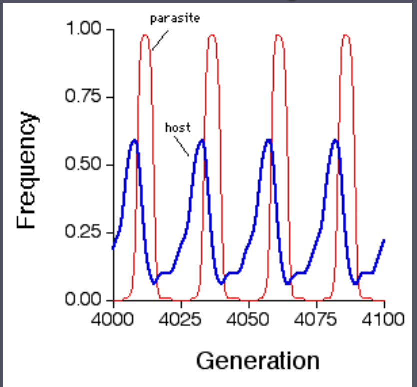
- Role of parasites in:
  1. the evolution of sexual reproduction of the host
  2. the sexual selection of the host
  3. the evolution of host genetic polymorphism

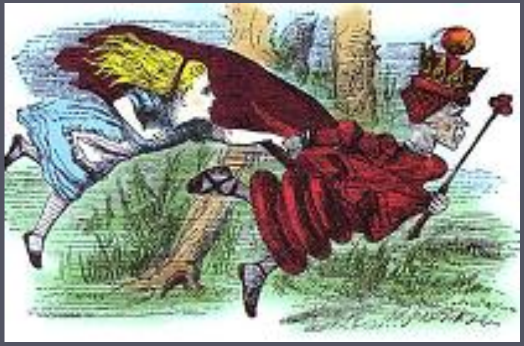
The role of the parasites in the evolution of sexual reproduction of the host

- Red Queen hypothesis

- „Now you run to stay in the same place." (Lewis Carroll, 1872. Through the Looking-Glass, and What Alice Found There)

- "In the beginning, it was a fragile plant that someone sometimes ate; at the end there is a thorny and poisonous monster, which is also sometimes eaten by someone." (Jan Zrzavý et al. 2004. How evolution is done: from the selfish gene to the diversity of life)





The role of the parasites in the evolution of sexual reproduction of the host

- The Red Queen Hypothesis - a specific type of evolutionary arms race hypothesis
- the benefit of sexual reproduction by frequency-dependent selection directed against a common host genotype
- sexual reproduction and recombination → rare genotypes capable to escape parasites
- selection favors hosts with rare genotypes
- rare genotypes become common, parasites are able to trace these genotypes due to frequency-dependent selection

The role of the parasites in the evolution of sexual reproduction of the host

- Sexual reproduction produces offspring with new genotypes - resistance to parasites
- Asexual reproduction produces offspring with the same combination of resistance genes as in parents - the target of increased parasitism

- Ex. *Poeciliopsis monacha* - parthenogenetic form accumulated parasites much faster than sexually reproducing forms
- Ex. The most common genotypes of the triploid form of *Carassius gibelio* - a higher number of parasite species than in sexually reproducing form

The role of the parasites in the sexual selection of the host

Sexual selection

- natural selection affecting the expression of certain phenotypes in one sex (most often in males), which determine the success in selecting a partner by the other sex (mostly by females) -> sexual dimorphism

e. g. body size, tail size, color, antlers, vocal expressions

The role of the parasites in the sexual selection of the host

Sexual selection leads to the evolution of secondary sexual traits (sexual ornamentation) Darwin (1971)

Two causes of sexual selection:

1. competition between males (at the level of individuals, at the level of sperm)

2. female preferences (females invest more in reproduction)

The role of the parasite in the sexual selection of the host

- Handicap hypothesis (Zahavi, 1975)
- Expression of a secondary sexual trait
  - represents a handicap for males
  - a male with a good genetic predisposition can cope with a handicap
  - indicates the quality of the male
  - expression of a trait is expensive (energetically, predation)
  - males with higher genetic quality have lower costs and greater benefits associated with the expression of a trait

The role of the parasite in the sexual selection of the host

- Hamilton-Zuk hypothesis (1982)
- Secondary sexual trait - an indicator of the effectiveness of resistance genes against parasites
- Females prefer resistant males - selection of suitable genes for offspring (hypothesis of good genes)

- 3 assumptions of the hypothesis:

1. expression of secondary sexual characteristics in males is associated with overall good health and vitality
2. inherited parasite resistance in hosts (consequence of coevolution)
3. negative effect of parasites on host viability (selection of resistant males)

The role of the parasites in sexual selection of the host

Intraspecific test of the Hamilton-Zuk hypothesis

Poecilia reticulata
Infection with the parasite *Gyrodactylus turbulli* decreases with the intense ornamentation of males - more attractive for females

Females select colored males (resistance or prevention of parasite transmission)

Females infected with the parasite show a lower tendency toward male preferences

The role of the parasites in sexual selection of the host

Intraspecific test of the Hamilton-Zuk hypothesis

Barn swallow (*Hirundo rustica*) and mites

1. The expression of ornamentation is associated with the parasite intensity
Males with a long tail have fewer mites
Females prefer males with a long tail

2. The parasite affects the fitness of the host
Offspring with high parasite intensity are smaller and have lower survival

3. Heredity in parasite resistance
The offspring of long-tailed males showed hereditary resistance to mites

Intraspecific tests of the Hamilton-Zuk hypothesis

Reference	Organism	Parasite Costly	Heritable variation	Ornament depends on parasite	Females choose males with fewer parasites	Unique prediction tested	Parasite aggregation known
Zuk 1987, 1988	cricket	YES	NO	NO	NO	NO	
Jaenike 1988	octomilka	YES			YES	NO	NO
Kennedy et al 1987	živorodka	YES		YES	YES	NO	
McMinn 1990	živorodka					YES	NO
Milinski and Baker 1990	koljuška	YES		YES	YES	NO	NO
Hausfater et al. 1990	tree frog			YES	YES	NO	NO
Tinsley 1990	toad	YES			NO	NO	NO
Ressel and Schall 1989	iguana	YES		YES		NO	NO
Hilgarth 1990	pheasant	YES	YES	YES	YES	NO	NO
Zuk et al . 1990	hen	YES	YES	YES	YES	NO	NO
Johnson and Boyce 1990	capercailli e	MAYBE		YES	YES	NO	NO
Gibson 1990	capercailli e	NO		NO	NO	NO	NO
Clayton 1990	pigeon				YES	NO	NO
Moller1990	swallow	YES	YES	YES	YES	NO	NO
Borgia1986; Borgia and Collis 1989	Silk hem		YES	YES	YES	NO	NO
Pruett-Jones et al. 1990	paradise			YES	YES	NO	NO

Interspecific tests of the Hamilton-Zuk hypothesis

		Correlation Observed Between Brightness And					
Reference	**Organism**	**Prevalence**	**Intensity**	**Diversity**	**Phylogenetic Effects Contolled**	**Alternative Factors Considered**	**Info On H-p Interaction**
Hamilton and Zuk 1982	North American passerines (plumage bright.and song complexity)	YES			NO	NO	NO
Read 1987	European passerines (plumage bright.)	YES			NO	NO	NO
Read and Harvey 1989	North American passerines (plumage bright.)	NO			YES	NO	NO
Read and Weary 1990	North American passerines (song complexity)	NO			YES	NO	NO
Zuk 1990	Neotropical birds (plumage characters)	YES				NO	NO
Pruett- Jones et al. 1991	New Guinea birds (plumage characters)	YES	NO	YES	YES	YES	NO
Weathe rhead et al.	Wood warblers	NO	NO	NO	YES		NO
Ward 1988	British fish (degree dimorph)			YES			
Cabana and Chandler 1991	British + NA fish						
Lefcort and Blaustein 1991	Lizards (brightness)	NO (neg correl)		NO	YES	YES	NO

Hamilton-Zuk hypothesis in interspecific studies

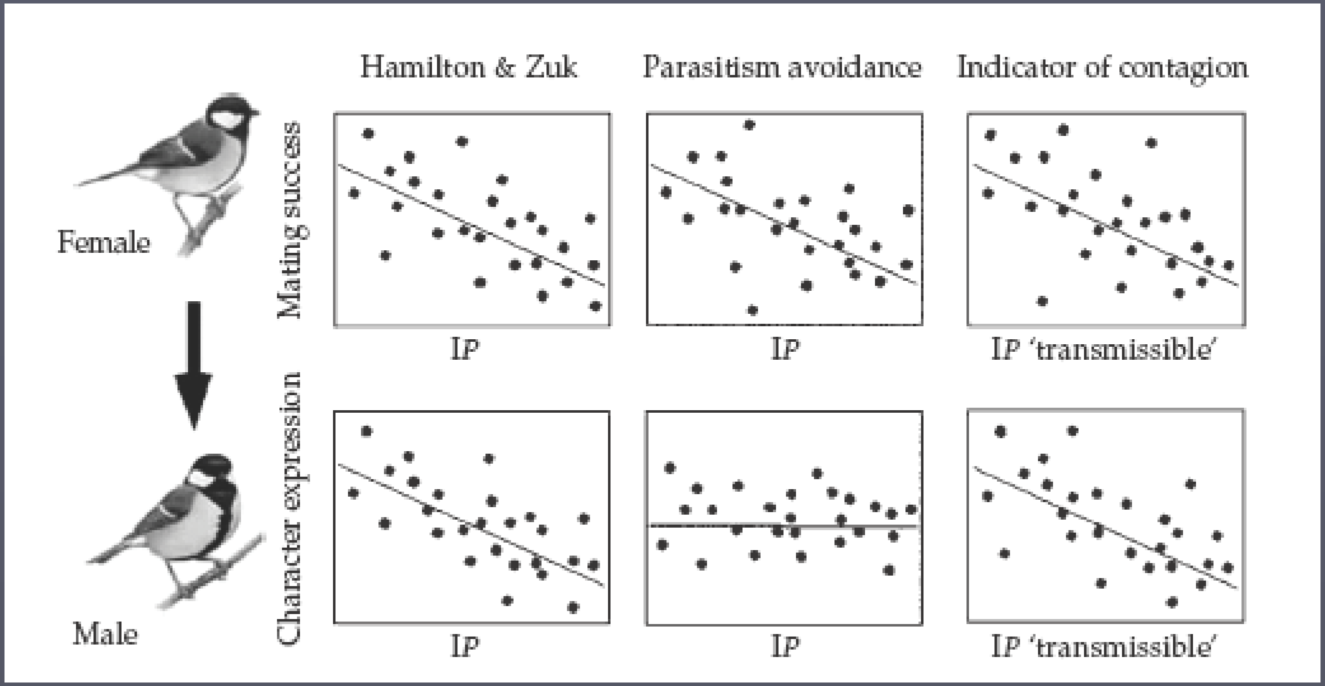
- Problem with hypothesis testing in interspecific studies
- Reverse causality: host ornamentation may attract parasites (more colored species may attract more ectoparasites, or species that invest more in orgnamentation invest less in parasitism resistance)
- Ecological correlation: coloration and parasitism may be associated with another factor (polygyny, type of nests)
- Falsification: if no correlation is recorded, is the data sufficient to reject the hypothesis?
- The need of control for phylogenetic relationships

The role of the parasites in the sexual selection of the host

3 models of parasite-mediated sexual selection

- 1. females do not select partners infected by parasites transmitted by direct contacts
- 2. the female selects a healthy and viable male to help her take care of the offspring
- 3. the female selects a resistant male to obtain resistance genes for offspring (= higher offspring viability) - a model of "good genes"

Why are non-parasitic males better?



The success of males in mating decreases with increasing intensity of parasitism

1. Hamilton & Zuk hypothesis - hereditary resistance to parasites for offspring

2. Hypothesis of parasitism avoidance - no effect of parasites on the expression of ornamentation, female detects parasites and avoids contact with the parasitized male

3. Hypothesis of indicator of contagion - females avoid contact with parasitized males to protect themselves and their offspring from infection (infection is transmissible to offspring)

The role of the parasites in the sexual selection of the host

- Immunocompetence handicap hypothesis (Fostad and Kartet, 1992)

  - a mechanism for explaining sexual selection

  - a trade-off between costs and benefits of high testosterone level

  - the dualistic nature of testosterone

    1. increase in the expression of secondary sexual traits

    2. reduction in resistance and suppresssion of the immune defense (induction of immunosuppressive effect)

The role of the parasites in the sexual selection of the host

- Handicap imunocompetence

- Females select males with remarkable secondary sexual traits, indicating quality of the immune system despite of testosterone immunosuppression

- Trade-off between expression of secondary sexual traits and immunity, but strong males are still viable and resistant to parasitism

Studies on associations between immune response and sexual selection

Table 3. Examples of studies of immune defence and sexual selection.

study question	organism	finding	references
Does testes size variation fit the expectations of the immuno-handicap hypothesis?	greenfinch (*Carduelis chloris*)	males with larger testes have higher parasite loads and brighter plumage (as expected from hypothesis)	Merila & Sheldon (1999)
Does testosterone reduce immune response?	house sparrow (*Passer domesticus*)	testosterone implants lead to dominance, higher ectoparasite loads and a larger status badge. Testosterone reduces (immuno-suppression) but also increases (status badge) success	Poiani *et al.* (2000)
Does testosterone reduce immune response?	wild and captive house finch males (*Carpodacus mexicanus*)	in captive males it increases infection by coccidia, but opposite relationship is observed in free-living males, perhaps owing to condition-dependence	Duckworth *et al.* (2001)
Does testosterone reduce immune response? (Over prolonged times?)	wild and captive dark-eyed junco males (*Junco hyemalis*)	long-lasting testosterone implant reduces antibody production in captive males, but cell-mediated immunity in free-living males	Casto *et al.* (2001)
Does sexual activity reduce immune response?	damselfly (*Matrona basilaris*)	encapsulation response is lower shortly after courtship and copulation activities	Siva-Jothy *et al.* (1998)
Does sexual activity reduce immune response?	fruitfly (*Drosophila melanogaster*)	males exposed to many females have lower antibacterial activity in haemolymph	McKean & Nunney (2001)
Does testosterone reduce immune response? (Over prolonged times?)	sand lizard (*Psammodromus*)	long-lasting testosterone implant lowers immune haematological parameters and leads to higher tick loads and lower survival	Salvador *et al.* (1996)