Coevolution

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Coevolution produces amazing outcomes

one of these is the pupa of a black fly and the other something completely different
Summary: Coevolution

- defining coevolution

- plants and pollinators
  - mutualism with some twists

- fishes and unionid mussels
  - maybe initially mutualism, but sometimes getting nasty

- aggressive mimicry in reef fishes and beetles
  - abusing coevolved interactions

- Batesian mimicry in butterflies
  - latching onto a coevolved (or learned?) aversion reaction

- what constitutes evidence for coevolution?

Defining coevolution

- coevolution can occur if part of the environment experienced by a species is influenced by a specific set of genes of other species

- the intensity (strength of fitness effects) and frequency (spatial and temporal patterns) of the interactions affects coevolution
  - only if intensity and frequency are high, do we expect coevolution of highly specialised interactions
  - in other cases, the interactions can be quite diffuse, but they can sometimes still have very consequential effects

- an important concept is the extended phenotype, namely all the effects of a gene upon the world
  - the meaning of the word ‘gene’ is often rather vague, and it is often much clearer to talk about a (gene) locus and its alleles
  - the 'effect' of an allele is always in comparison with another allele at a given locus

- the ‘conventional’ phenotype is a special case, in which the effects seem confined to the individual body in which the gene resides
Defining coevolution

- coevolutionary interactions can be classified as:
  - mutualism (+/+)
  - parasite-host, predator-prey (+/-)
  - competition (-/-)
  - commensalism (0/+)
  - by-product (0/-)

narrow-sense coevolution: each partner evolves in response to the other

broad-sense coevolution
only one partner evolves in response to the other

(continues on next slide)
Defining coevolution

- costs and benefits of interactions between partners can be difficult to measure and depend on the environment
- interactions vary spatially and temporally
  - a species may coevolve with another over only part of its range and/or only some of the time
  - complete spatial and temporal overlap is unlikely at the origin of a coevolutionary interaction and it is not the most frequent case
  - similar life histories facilitate coevolution between partners, which may explain the highly unusual generation times of 13 and 17 years in some insects
- interactions vary in symmetry
- understanding the signs and strengths of interactions requires sampling across sites
  - and thus knowledge about the amount of gene flow between the different sites can be important

Defining coevolution

- levels of coevolution
  - genetic elements within organisms
  - ancient symbioses
  - males and females
  - parents and offspring
  - coevolving species
  - coevolving clades
  - coevolution of genes and culture
- coevolution can be both inter- or intra-specific
Plants and pollinators

- the star orchid (*Angraecum sesquipedale*) from Madagascar has an extremely long floral tube (28-32 cm)
- based on its examination, Darwin in 1862 hypothesised that this floral tube had evolved as a consequence of coevolution
- he predicted the existence of a moth with a similarly long proboscis
- but his suggestion was ridiculed by contemporary entomologists

From: A Very Victorian Passion: The Orchid Paintings of John Day.

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Plants and pollinators

- a candidate hawkmoth (*Xanthopan morganii praedicta*) was described already in 1903, but the first observations of the pollination behaviour were actually made only recently

from Stearns & Hoekstra 2005
Plants and pollinators

- the moth evolves a longer tongue than needed to forage efficiently
  - does pollen transfer carry costs for the pollinator?
  - does close contact to the flower lead to a higher predation on moths by ambush predators that sit on the flowers?
- the orchid evolves a floral tube longer than matching the tongues
  - does it pay for the orchid to cheat by economising on nectar production?
  - is pollen export improved if the moth has to try harder to reach the nectar?
Plants and pollinators

• in the orchid *Plathanthera bifolia* the floral tube length does affect the reproductive success
  
  • so tubes that accommodate the entire tongue are advantageous for the orchids, because they lead to more efficient pollen transfer

![Graph showing the relationship between floral tube length and reproductive success.](from Stearns & Hoekstra 2005)

**Figure 2.9** The sexual performance of a species of Swedish orchid, *Plathanthera bifolia*, as a function of the lengths of its floral tubes. The longer the tubes, the more pollinia were removed and more stigmas were pollinated. Experiments were performed on two different years, 1986 and 1987. (From Nilsson 1988, reproduced by kind permission of the authors and *Nature*.)

Plants and pollinators

• orchids are masters of deceptive pollination and strategies include
  
  • floral mimicry, where flowers mimic generic or specific rewarding model species
  
  • brood-site imitation, where plants mimic egg laying sites or shelters, both visually and olfactorily
  
  • sexual mimicry, where flowers mimic female mating signals, including body shape and also pheromones

![Flowers of Ophrys speculum, the Mirror Bee Orchid.](from Jersáková et al 2006)

![A male Neozeleboria cryptodes wasp on a scented bead.](from Jersáková et al 2006)
Fishes and Unionid mussels

• reproduction in the European bitterling (*Rhodeus sericeus*)
  • males defend territories with one or several mussels of the family Unionidae
  • females lay eggs into the exhalant syphon using their ovipositor
  • males deposit sperm into the inhalant syphon to fertilise the eggs (often both before and after the female deposits her eggs)
  • embryos and larvae develop for about 1 month in the gills of the mussel

![male and female bitterling](image)

![oviposition of female bitterling](image)

![fertilization by male bitterling](image)

from Smith et al 2004
Bitterling spawning

https://www.youtube.com/watch?v=4oq83fHDBPw

Fishes and Unionid mussels

• bitterling embryos and larvae are adapted to growing inside a mussel
  • the low-oxygen conditions in the mussel has favoured vascular adaptations in the developing embryos and larvae
  • the water flow through the gills has favoured morphological adaptations in the larvae to avoid being flushed out

Fig. 8. Embryonic vascularization in two species of freshwater fish at the same developmental stage: (a) Bitterling, Rhodeus sericeus at c. 8 mm; (b) rough sculpin, Cottus scorpius at c. 7.5 mm. Modified from Kryshmanovskii (1969).

Fig. 9. Bitterling (Rhodeus sericeus) larva during development in the mussel gill chamber: short, wing-like gill projections. Length c. 5 mm. Modified from Kryshmanovskii (1969).

from Smith et al 2004
Fishes and Unionid mussels

• unionid mussels have parasitic larvae
  • these glochidia are obligate ectoparasites on fishes, mostly on gills, but also on fins and other tissues
  • they are in part nourished by nutrients obtained from the fish host and obtain dispersal via the fish
  • they are first brooded in the gills of the mussel and then released into the water column, generally upon contact with a fish

[Images of glochidia on fish gills]

• the interactions between the bitterlings and the mussels have classically been viewed as mutualistic
  • the fish benefits from the protection of its brood, and the mussel achieves nourishment and dispersal for its glochidium larvae
  • the costs for the mussel and the fish have been thought to be small

• but recent evidence questions this view
  • bitterlings appear to be very poor hosts for glochidia, as they show low prevalence, low infection intensities and low retention of glochidia

<table>
<thead>
<tr>
<th></th>
<th>Rhodeus sericeus</th>
<th>Rutilus rutilus</th>
<th>Perca fluviatilis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence</td>
<td>1% (7 of 657)</td>
<td>12% (91 of 763)</td>
<td>39% (271 of 692)</td>
</tr>
<tr>
<td>Maximum intensity</td>
<td>2 Unio sp. glochidia</td>
<td>142 Unio sp. glochidia</td>
<td>1244 Anodonta sp. glochidia</td>
</tr>
</tbody>
</table>

• some evidence even suggests that mussels compete with the fish embryos for oxygen and maybe even nutrients

• moreover, other fish species clearly suffer from the glochidia, and so mussels need adaptations to attract the fish

[Images of glochidia on fish gills]

from Smith et al 2004 and Spence and Smith 2013
Fishes and Unionid mussels

• the fluted kidneyshell (*Ptychobranchus subtentum*) produces ovisacs that visually mimic black fly pupae
  • these ovisacs are filled with hundreds of glochidia

from http://unionid.missouristate.edu/

Fishes and Unionid mussels

• the North American Ouachita kidneyshell (*Ptychobranchus occidentalis*) produces ovisacs that mimic larval fish

from http://unionid.missouristate.edu/
Fishes and Unionid mussels

• the North American Ouachita kidneyshell (*Ptychobranchus occidentalis*) produces ovisacs that mimic larval fish

![Image](http://unionid.missouristate.edu/)

From the *Unio Gallery*

probably an orangethroat darter (*Etheostoma spectabile*)

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Fishes and Unionid mussels

• the North American orange-nacre mucket (*Lampsilis perovalis*) produces ovisacs in so-called "superconglutinates"

![Image](http://unionid.missouristate.edu/)
Fishes and Unionid mussels

• impressive adaptations on part of the mussels, but no clear evidence for a coevolutionary response in the host fishes
  • probably a fairly low specificity of the interaction for the fish (the interaction is highly asymmetrical)
  • it is costly for the fish to avoid feeding opportunities

from http://unionid.missouristate.edu/

Aggressive mimicry

• in aggressive mimicry a species (often a predator) disguises itself or part of itself as something harmless or even desirable
• examples include
  • all of those food-mimicking ovisac adaptations that I just showed
  • some reef fish species mimic a cleaner wrasse to get close to their hosts (note the different position of the mouth)
  • females of some firefly species imitate the blinking patterns of another firefly species and eat their males when they approach

False Cleanerfish (Aspidontus taeniatus)

Bluestreak cleaner wrasse (Labroides dimidiatus)

A female Photuris versicolor firefly that has captured a male Photinus tanytarsus firefly by mimicking female P. tanytarsus flash signals
Aggressive mimicry

• juvenile triungulin larvae of the blister beetle (*Meloe franciscanus*) need to reach a nest of the solitary bee *Habropoda pallida*, where they then feed on pollen, nectar and bee eggs

• the species lives in a highly arid habitat, the sand dunes of the southwestern United States, so for the tiny larvae (2mm) it would be difficult to move over large distances in search of host nests

![Triungulin](image)

Aggressive mimicry

• to find host nests the triungulin larvae form aggregations of up to 2000 individuals on vegetation

• these aggregations vaguely resemble female bees in shape and size

• the larvae release an odour that mimics the sex pheromones of female bees, attracting male bees to the aggregations

![Graph](image)

Fig. 2. Results of bioassays to characterize the nature of male bee attraction to triungulin aggregations of female bees. (A) Male bee inspection visits of triungulin aggregations. Visual models of aggregations, and models treated with an extract of triungulin (n = 31). *p* = 0.020. Visual models received no treatment were not included in the data analysis. (B) Inspection visits of male bees to caged female bees, caged male bees, and empty cage controls (n = 15). Two-way ANOVA: treatment, *F* = 27.46, *p* = 0.0001, df = 2, 17; sex, *F* = 1.83, *p* = 0.26, df = 1, 17. Bars marked by different letters are significantly different (Student-Newman-Keuls procedure; *p* < 0.05).

from Saul-Gershenz & Millar 2006
Aggressive mimicry

- when a male comes close and tries to copulate with an aggregation, the triungulins quickly transfer to the male
- males then transfer triungulins to the females during copulations or copulation attempts
- females carry triungulins into their nest during nest building and provisioning
- triungulins hop off in the nest and feed on the provisions deposited by the female and later also the female’s brood
Batesian mimicry

• in Batesian mimicry an edible species (the mimic) evolves to resemble a warningly coloured noxious species (the model)
• selection on Batesian mimicry is mediated by predators that avoid mimics, because they are trying to avoid the models
• the convergence of the mimic to the model is strongly linked to the sensory system of the predator
  • thus the fact that, at least to our senses, many mimics are quite accurate copies of their models, suggests that predators also have sophisticated sensory systems
• the cost of eating a model must be higher than the benefit of eating a mimic
• may lead to the evolution of learning in the predator
• the fitness advantages for the mimic are frequency-dependent
• Batesian mimicry has evolved many times independently

Figure 16.6 The moths swallowtails of Africa (Papilio dardanus) are one of the most remarkable cases of Batesian mimicry known. The females mimic different toxic models in different geographical regions, with the result that they look very different both from the males of their own species and from the males of their species in other geographical regions. The males are not mimics, and on Madagascar, where no toxic models are available, the females are not mimics and resemble the males. Top row: Left, male; right, female from Madagascar. In the remaining rows the mimicking female is on the left and the toxic model is on the right of each pair. Second row: Left, pair; left specimen, *P*. dardanus var. fumosus; female (mimic); right specimen, *A*mauris fumosus (model) from South Africa. Third row: left, pair; left specimen, *P*. dardanus var. multipuncta; female (mimic); right specimen, *Hypochrysops* fumosus (model) from South Africa. Fourth row: left, pair; left specimen, *P*. dardanus var. fumosus; female (mimic); right specimen, *A*mauris fumosus (model); right specimen, *Hypochrysops* fumosus (model) from Madagascar. Fourth pair: left, pair; left specimen, *P*. dardanus var. fumosus; female (mimic); right specimen, *A*mauris fumosus (model) from South Africa. The models are in the family Nymphalidae; the mimics are in the family Papilionidae. The papilionid mimics accurately reproduce the patterns that evolution elected from the nymphalid ground plan (Figure 7.21). Illustration photo credit to Terry DiGges; specimens courtesy of the Peabody Museum, Yale University, arranged by Raymond Pye, Curatorial Assistant in Entomology.)
What constitutes evidence for coevolution?

- **the selection criterion**
  - the evolution of the interaction is observed directly and the changes in reproductive success are documented for both partners

- **the perturbation criterion**
  - an experimental perturbation of the interaction leads to observable changes in the reproductive success of one or both of the partners

- **the functional criterion**
  - an interaction affects the reproductive success of both partners and is beneficial for at least one of the partners (if it is not beneficial, it does not occur)

- **the design criterion**
  - an interaction looks as if it were designed, i.e. it is complicated, unusual, and precise; many classical examples of coevolution are only ‘adaptive story-telling’

- in order show that an interaction has a coevolutionary origin one must show that it has resulted from reciprocal evolutionary change
  - may be possible by placing character states on molecular phylogenies

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- what constitutes evidence for coevolution?
Literature

- Mandatory Reading
  - none
- Suggested Reading
- Books
  - none
- Online Resources
  - http://unionid.missouristate.edu/
Literature

from Janzen et al. 2010

Literature

from Clarke et al. 2010