Coevolution

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Coevolution

Summary: Coevolution

- defining coevolution
- plants and pollinators
- bitterlings and unionid mussels
- aggressive mimicry
- Batesian mimicry
- what constitutes evidence for coevolution?

Defining coevolution

- coevolution can occur if part of the environment of a species is shaped by a specific set of genes of one or several other species
- the intensity (i.e. the fitness effects) and frequency (i.e. the spatial and temporal patterns) of the interaction are important parameters for coevolution
- only if both parameters are high do we expect highly specialised interactions to coevolve
    - otherwise the interactions can be quite diffuse (but they may nevertheless sometimes also lead to big effects)
- extended phenotype
    - all effects of a gene upon the world. As always, 'effect' of a gene is understood as meaning in comparison with the other alleles
    - the conventional phenotype is a special case in which the effects are regarded as being confined to the individual body in which the gene sits

Defining coevolution

- coevolutionary interactions can be classified in the following types:

- mutualism (+/+)
- parasite-host, predator-prey (+/-)
- competition (-/-)
- commensalism (0/+)
- by-product (0/-)

narrow-sense coevolution:
both partners evolve in response to the other

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

Defining coevolution

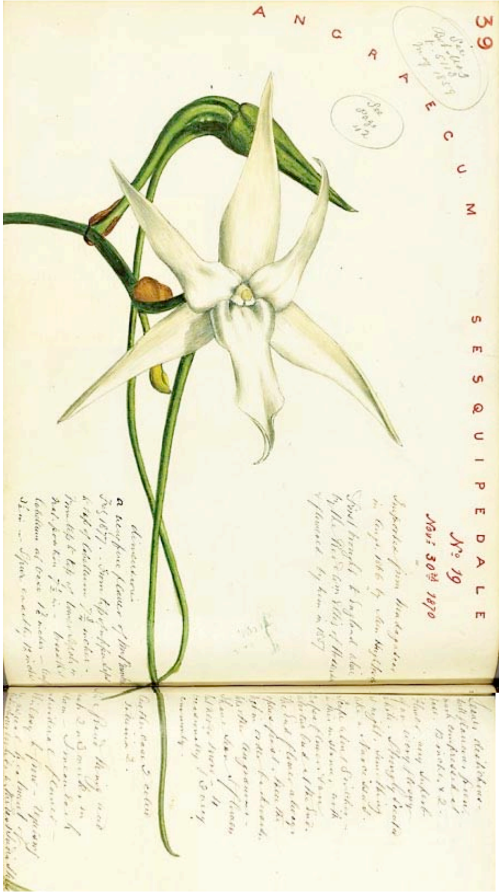
- the costs and benefits of the interactions between the partners can be difficult to measure and they may depend on the environment
- the interactions may vary spatially and temporally
    - a species may coevolve with another species over only part of its range and/or only part of the time
    - complete spatial and temporal overlap is unlikely the condition at the origin of an interaction and not the most frequent case
    - similar life histories facilitate coevolution between partners
- the interactions may vary in symmetry
- understanding the signs and strengths of coevolutionary interactions may require sampling over several populations
    - and thus gene flow between these populations is 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 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 and predicted that there must exist a moth with similarly long proboscis
- his suggestion was ridiculed by entomologists



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

Plants and pollinators

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

Figure 2.8 The Madagascar star orchid (*Angraecum sesquepedale*) is pollinated by a hawkmoth (*Xanthopan morgani praedicta*) whose existence and long proboscis were predicted by Darwin from the morphology of the orchid. The length of the orchid's nectary has evolved to fit the length of the hawk's proboscis. (Photo courtesy of L. T. Wasserthal.)

Plants and pollinators

Plants and pollinators

- in another orchid species (*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

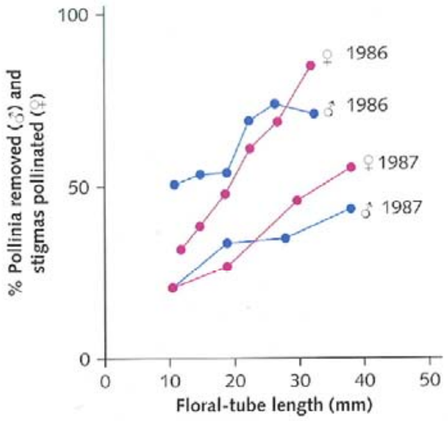


Figure 2.9 The sexual performance of a species of Swedish orchid, *Platanthera bifolia*, as a function of the lengths of its floral tubes. The longer the tubes, the more pollinia were removed and more stigmas were pollinated. Experiments were performed on two different years, 1986 and 1987. (From Nilsson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

Plants and pollinators

- so why should an exaggerated floral tube length evolve?
  - the moths may evolve a longer tongue than needed to forage efficiently
    - pollen transfer could carry costs
    - close contact to the flower due to a matching tongue length could lead to higher predation on moths by ambush predators that sit on the flowers
  - there must be a benefit for the orchid if the moth has a too short tongue
    - does it pay for the orchid to cheat by economising on nectar?

Plants and pollinators

- deceptive pollination in orchids
  - generalised food deception (non-model mimicry)
    - flowers mimic rewarding flowers, but not a specific model
  - ‘Batesian’ floral mimicry
    - flowers mimic a particular rewarding model
  - brood-site imitation
    - plants mimic egg laying sites, both visually and olfactorily
  - shelter imitation
    - plants provide shelter (may not necessarily be deceptive)
  - pseudoantagonism
    - plants invoke defence mechanisms
  - rendezvous attraction
    - flowers mimic flowers attractive to female pollinators
  - sexual response
    - flowers mimic female mating signals (e.g. shape and pheromones)

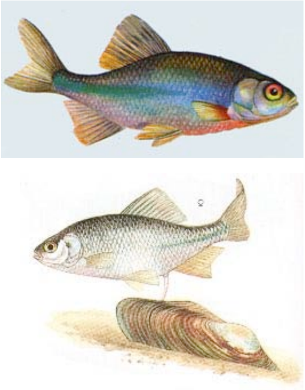
a female *Zapilothynnus trilobatus* and the orchid *Drakaea glyptodon*

Neozeleboria cryptoides on a scented bead

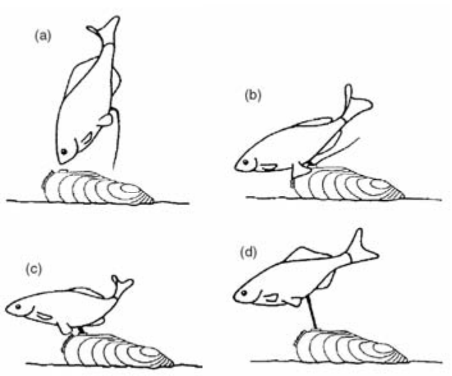
from Jersáková & al 2006

Bitterlings and Unionid mussels

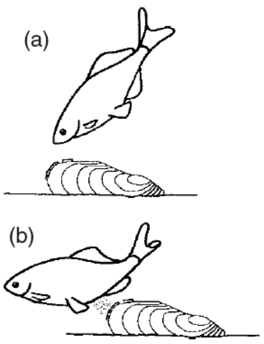
- reproduction in European bitterling (*Rhodeus sericeus*)
  - males defend territories with one or several mussels of the family Unionidae
  - females lay eggs into the exhalant syphon using their ovipositor
  - males deposit sperm into the inhalant syphon to fertilise the eggs (both before and after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



male and female bitterling



oviposition of female bitterling

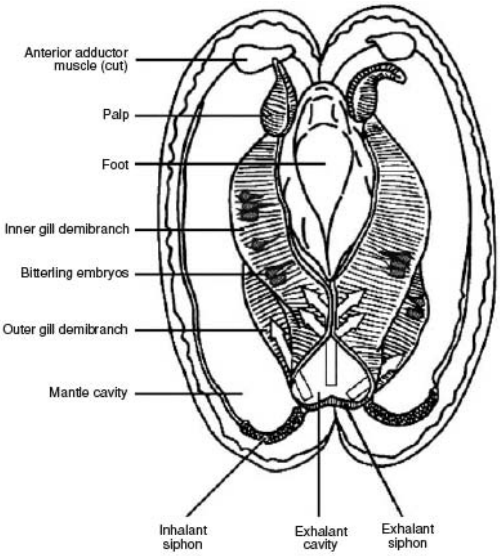


fertilization by male bitterling

from Smith & al 2004

Bitterlings and Unionid mussels

- juvenile bitterling are adapted to growing in a mussel
  - low-oxygen conditions in mussel
    - vascular adaptations in the embryo
  - water flow through gills
    - morphological adaptations of hatchling to avoid being flushed out



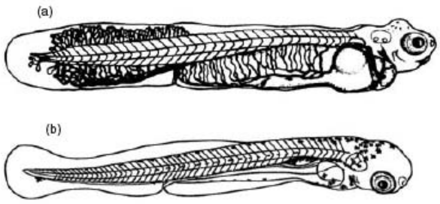


Fig. 8. Embryonic vascularization in two species of freshwater fish at the same developmental stage: (a) bitterling *Rhodeus sericeus* at *c.* 8 mm; (b) roach *Rutilus rutilus* at *c.* 7.2 mm. Modified from Kryzhanovskii (1949).

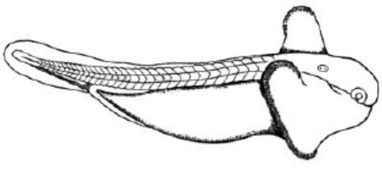
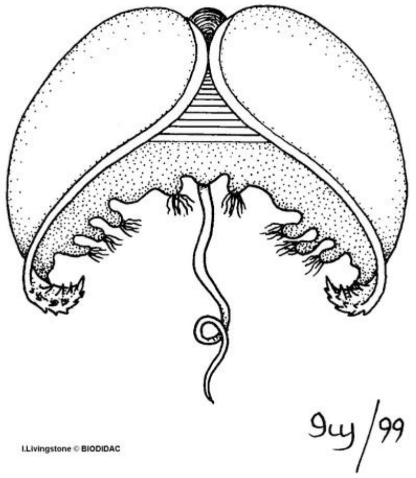


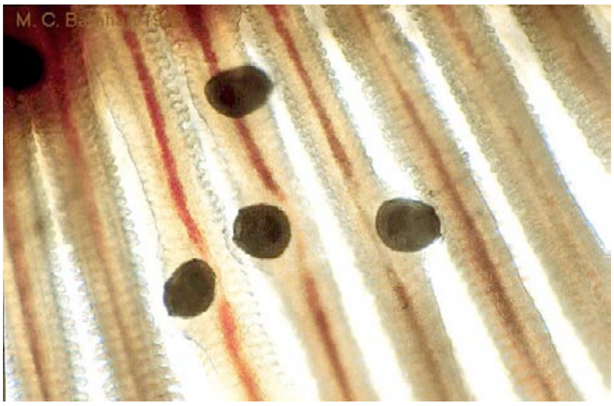
Fig. 9. Bitterling *Rhodeus sericeus* larvae during development in the mussel gill chamber, showing wing-like yolk projections. Length *c.* 5 mm. Modified from Kryzhanovskii (1949).

from Smith & al 2004

Bitterlings and Unionid mussels

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


I.Livingstone © BIODIDAC


M. C. Barnhart


© M. C. Barnhart 2005

Bitterlings and Unionid mussels

- the interactions between bitterling and the mussels has classically been viewed as mutualistic
  - the fish benefits from the protection of its brood and the mussel achieves nourishment and dispersal of its larvae
  - the costs to 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
    - low prevalence, low infection intensities and low retention of glochidia

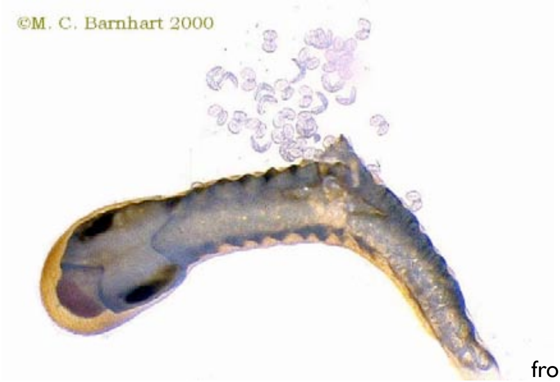
	Rhodeus sericeus	*Rutilus rutilus*	*Perca fluviatilis*
Prevalence	1% (7 of 657)	12% (91 of 763)	39% (271 of 692)
Maximum intensity	2 *Unio* sp. glochidia	142 *Unio* sp. glochidia	1244 *Anodonta* sp. glochidia

  - some evidence suggests that mussels compete with embryos for oxygen
- but other fish species clearly suffer from the glochidia, and so mussels need adaptations to attract the fish

from Smith & al 2004

Bitterlings and Unionid mussels

- The Ouachita kidneyshell (*Ptychobranchus occidentalis*) is a North American freshwater mussel and produces ovisacs that imitate fish



from http://unionid.missouristate.edu/

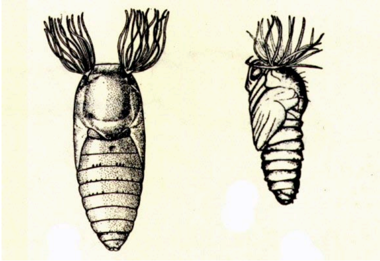
Bitterlings and Unionid mussels

from http://unionid.missouristate.edu/

Bitterlings and Unionid mussels

- impressive adaptations on part of the mussels, but no clear evidence for a coevolutionary response in the host fishes
  - probably not very high specificity
  - costly to avoid feeding opportinities
  - asymmetrical interaction

Ovisacs of fluted kidneyshell (*Ptychobranchus subtentum*)



blackfly pupae

from http://unionid.missouristate.edu/

Bitterlings and Unionid mussels

- The orange-nacre mucket (*Lampsilis perovalis*) is a North American species which produces "superconglutinates"

from http://unionid.missouristate.edu/

Aggressive mimicry

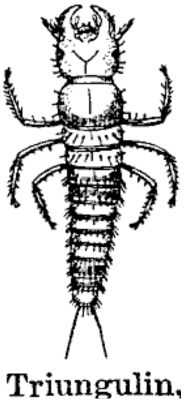
- in aggressive mimicry a species (often a predator) disguises itself as something harmless or even desirable
  - some fish species mimic a cleaner
  - females of some firefly species imitate the blinking patterns of another firefly species and eat the males when they approach

False Cleanerfish (*Aspidontus taeniatus*)

Bluestreak cleaner wrasse (*Labroides dimidiatus*)

Aggressive mimicry

- juvenile triungulin larvae of the blister beetle (*Meloe franciscanus*) need to reach a nest of the solitary bee *Habropoda pallida*, where they feed on pollen nectar and bee eggs
- both species live in a highly arid habitat, the sand dues of the southwestern United States
  - for the tiny larvae (2mm) it would be difficult to move over large distances



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 female sex pheromones, attracting males to aggregations

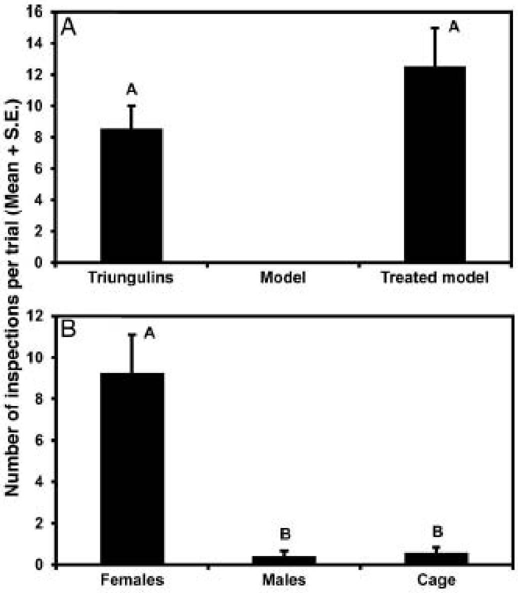


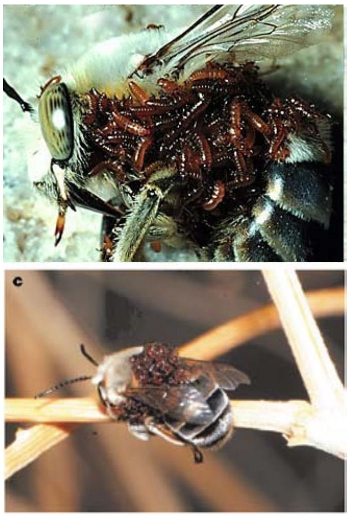
Fig. 2. Results of bioassays to characterize the nature of male bee attraction to triungulin aggregations or female bees. (*A*) Male bee inspection visits of triungulin aggregations, visual models of aggregations, and models treated with extracts of triungulins ($n = 3$) ($\chi^2 = 1.53$, $P = 0.22$). Visual models received no visits and were not included in the data analysis. (*B*) Inspection visits of male bees to caged female bees, caged male bees, and empty cage controls ($n = 9$). Two-way ANOVA: treatment, $F = 27.45$, $P = 0.0001$, $df = 2,17$; trial, $F = 1.63$, $P = 0.024$, $df = 5,17$. Bars marked by different letters are significantly different (Student–Newman–Keuls procedure, $P < 0.05$).

a male *Habropoda pallida* inspecting a triungiulin aggregation

from Saul-Gershenz & Millar 2006

Aggressive mimicry

- when a male comes close and tries to copulate with an aggregation almost all triungulins transfer to the male
- the males then transfer the triungulins to the females during copulation (attempts)
- and females carry the triungulins into their nest during nest building and provisioning



a male and a female *Habropoda pallida* with triungulins

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 limited by the sensory system of the predator
  - thus the fact that many mimics are quite accurate copies of their models suggests that predators have sophisticated sensory systems
- the cost of eating a model must be higher than be benefit of eating a mimic
- may lead to the evolution of learning in the predator
- the fitness advantages for the mimic are frequency-dependent
- has evolved many times independently

Batesian mimicry

Figure 18.6 The mocker 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 females 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. *planemoides* female (mimic); right specimen, *Bematistes poggei* (model) from Kenya; right pair, left specimen, *P. dardanus* var. *trophonius* female (mimic); right specimen, *Danaus chrysippus* (model) from South Africa. Third row: left pair, left specimen, *P. dardanus* var. *niobe* female (mimic); right specimen, *Bematistes tellus* (model) from Sudan; right pair, left specimen, *P. dardanus* var. *hippocoonides* female (mimic); right specimen, *Amauris albimaculata* (model) from Mozambique. Fourth row: left pair, left specimen, *P. dardanus* var. *hippocoon* female (mimic); right specimen, *Amauris naivius naivius* (model) from Great Lakes region; right pair, left specimen, *P. dardanus* var. *cenea* female (mimic); right specimen, *Amauris echeria* (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 elicits from the nymphalid ground plan (Figure 7.2). (Butterfly photos credit to Terry Dagradi; specimens courtesy of the Peabody Museum, Yale University, arranged by Raymond Pupedis, Curatorial Assistant in Entomology.)

from Stearns & Hoekstra 2005

What constitutes evidence for coevolution?

- four criteria (in decreasing order of stringency)
  - the selection criterion
    - the evolution of the interaction is observed (or reciprocal trait evolution reconstructed for a phylogeny)
  - the perturbation criterion
    - an experimental perturbation leads to observable changes in the reproductive success of the partners
  - the functional criterion
    - an interaction affects the reproductive success of both partners and is beneficial for at least one (if not, it does not occur)
  - the design criterion
    - an interaction looks as if it were designed
- many classical examples of coevolution only represent 'adaptive story-telling'
  - in order show convincingly that an interaction has a coevolutionary origin one must show that it has resulted from reciprocal evolutionary change

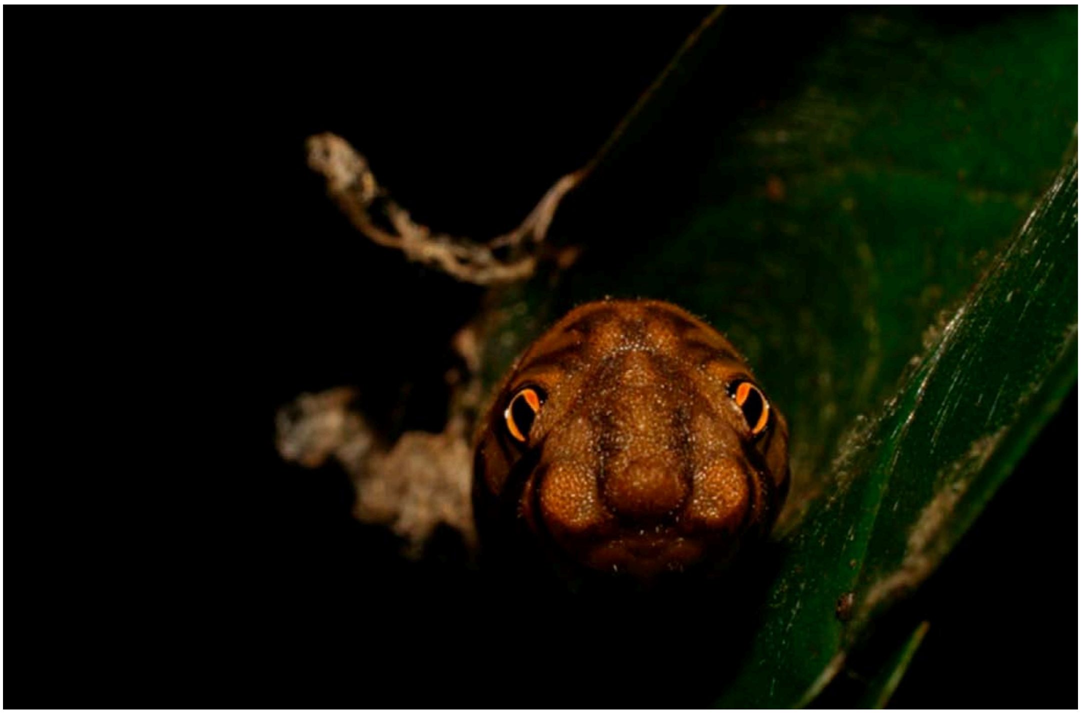
Summary: Coevolution

- defining coevolution
- plants and pollinators
- bitterlings and unionid mussels
- aggressive mimicry
- Batesian mimicry
- what constitutes evidence for coevolution?

Literature

- Mandatory Reading
  - none
- Suggested Reading
  - Chapter 18 on Coevolution of Stearns & Hoekstra (2005). Evolution: An Introduction. 2nd Edition. Oxford University Press
  - Janzen, Hallwachs & Burns (2010). A tropical horde of counterfeit predator eyes. Proc. Natl. Acad. Sci. USA 107:11659-11665.
- Books
  - none
- Online Resources
  - http://unionid.missouristate.edu/

Literature



from Janzen et al. 2010

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