Evolution part II:
co-evolution,
co-adaptation,
and why it takes all the running you can do just to stay in place

Overview

- What is co-evolution, how does it work, what does it produce?
- Evolution of insect-feeding in plants: *why you don't need a brain to be very clever*

Evolution: mechanisms, causes, and consequences

Relevant Standards:

8.3.5 Identify and describe the difference between inherited traits and physical and behavioral traits that are acquired or learned.

8.3.7 Recognize and explain that small genetic differences between parents and offspring can accumulate in successive generations so that descendants may be different from their ancestors.

8.3.8 Examine traits of individuals within a population of organisms that may give them an advantage in survival and reproduction in a given environments or when the environment changes.

8.3.9 Describe the effect of environmental changes on populations of organisms when their adaptive characteristics put them at a disadvantage for survival. Describe how extinction of a species can ultimately result.

Evolution: mechanisms, causes, and consequences

Review: How does natural selection cause evolution?

- organisms differ from each other

  Where does the variation come from?

- some of these differences are advantageous and heritable

  What determines whether a variant is advantageous?

  Why does it need to be heritable?

- more "fit" individuals reproduce more effectively

- subsequent generations show an increase in the frequency of traits that confer an advantage; less fit varieties become less frequent and are eventually lost

The environment as an agent of selection

- natural selection adapts a given species not just to its abiotic environment (e.g. climate) but also its biotic environment (e.g. other species such as prey, predators, symbionts)

- species that are part of the biotic environment of an organism may *themselves* evolve over time

- this in turn may force subsequent evolutionary changes in the first species, which in turn may bring about a second round of compensatory changes ("co-adaptations") in the other species

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- this in turn may force subsequent evolutionary changes in the first species, which in turn may bring about a second round of compensatory changes (“co-adaptations”) in the other species

- this back-and-forth of co-adapting between different species is called “co-evolution” or “reciprocal evolution”

- it can have many outcomes, typically resulting in extreme specialization and “fine tuning” or organisms and their parts

- *Examples!*

Examples of the mechanisms and consequences of co-evolution

Crypsis
Mimicry
Phytophagy
Pollination

CRYPSIS

1) Definition

- any mechanism that makes it harder to distinguish organisms from their environment

2) Mechanisms

a) morphological:
- match background in color and pattern
- disrupt shape/outline through adoption of a bizarre shape
- resemble certain features of the environment that are of no interest to a predator (masquerade/mimesis)

b) behavioral:
- active seeking of matching environment
- posture and/or motion to add in disguise

3) Examples...

Examples of crypsis

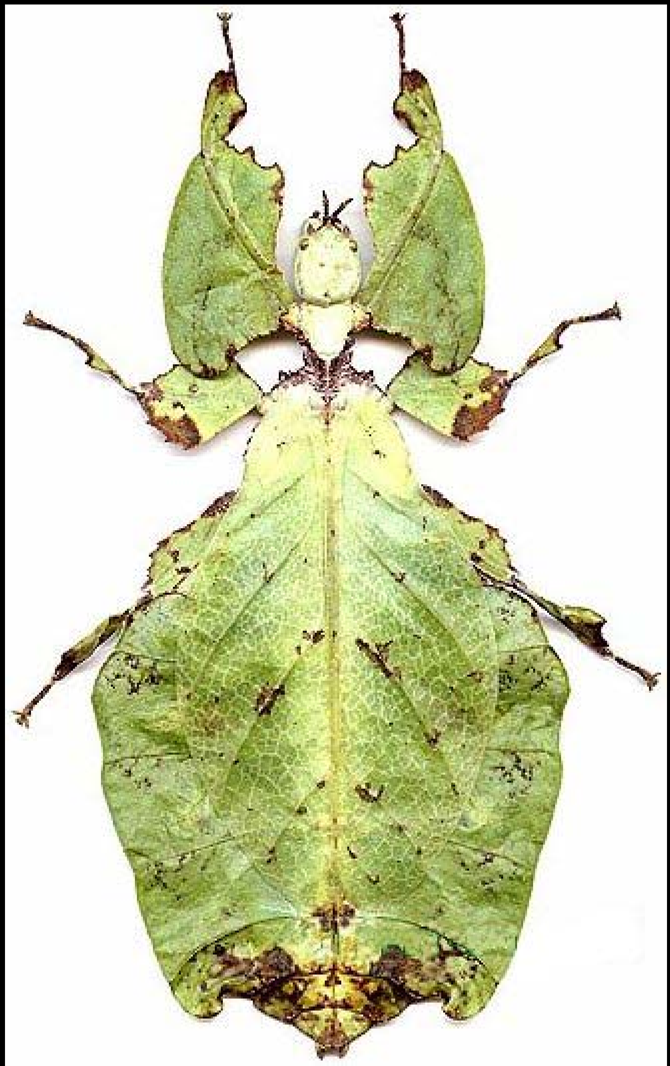
resembling objects in the environment of no interest to a predator
example: leaf imitations in katydids

Examples of crypsis

resembling objects in the environment of no interest to a predator
example: leaf imitations in katydids

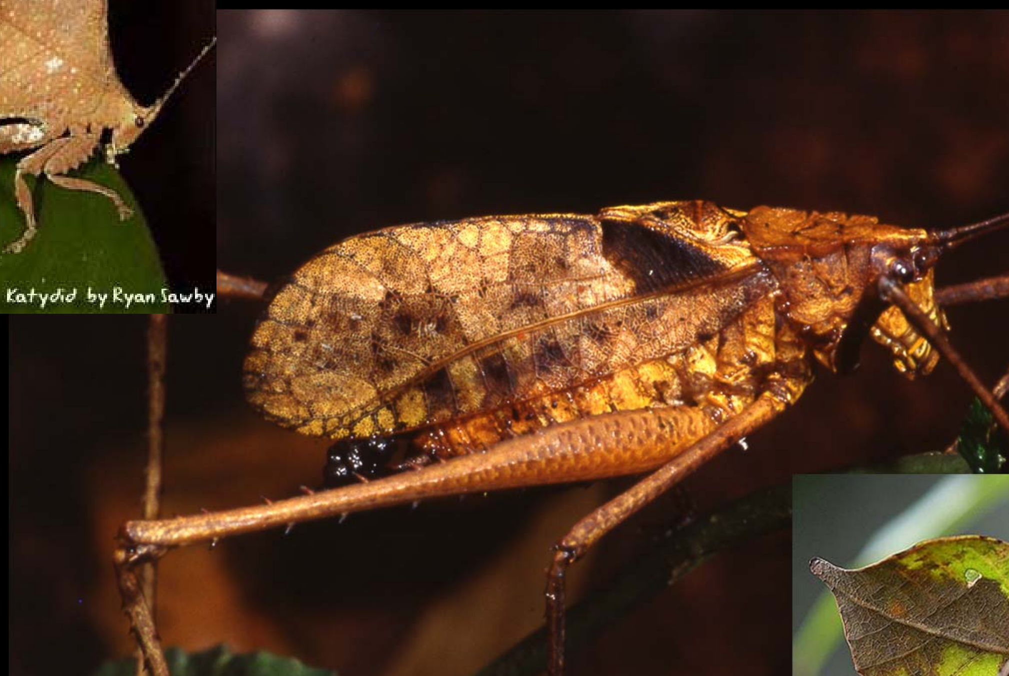
Examples of crypsis

resembling objects in the environment of no interest to a predator
example: leaf imitations in phasmids



Examples of crypsis

resembling objects in the environment of no interest to a predator
example: DEAD leaf imitations in orthopterans

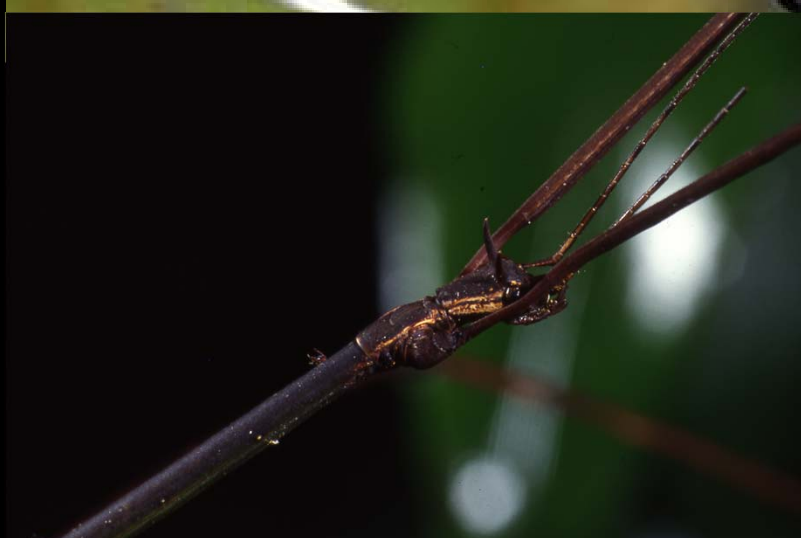


Examples of crypsis

resembling objects in the environment of no interest to a predator
example: DEAD leaf imitations in Lepidoptera

Examples of crypsis

resembling objects in the environment of no interest to a predator
example: stick imitations in catterpillars and stick insects



Examples of crypsis

resembling objects in the environment of no interest to a predator
example: imitations of bird droppings

Examples of crypsis

resembling objects in the environment of ~~no interest to a predator~~ **of interest to prey!**
example: flower imitations in orchid mantids

Examples of crypsis

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Examples of crypsis

resembling objects in the environment of ~~no interest to a predator~~ **<u>of interest to prey!</u>**
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Examples of crypsis

resembling objects in the environment of no interest to a predator
example: “backpack bugs” (Reduviidae, Assassin bugs))

This strategy also includes chemical crypsis as bug smells like dirt and dead ants!

CRYPSIS

Summary

- diverse mechanisms enable insects to be cryptic
- crypsis often works ONLY in particular context
- opportunity for co-evolution between insects' ability to hide and predators' ability to detect

Crypsis is by no means restricted to insects!

Crypsis in human defenses – examples of recent crime prevention measures in Japan

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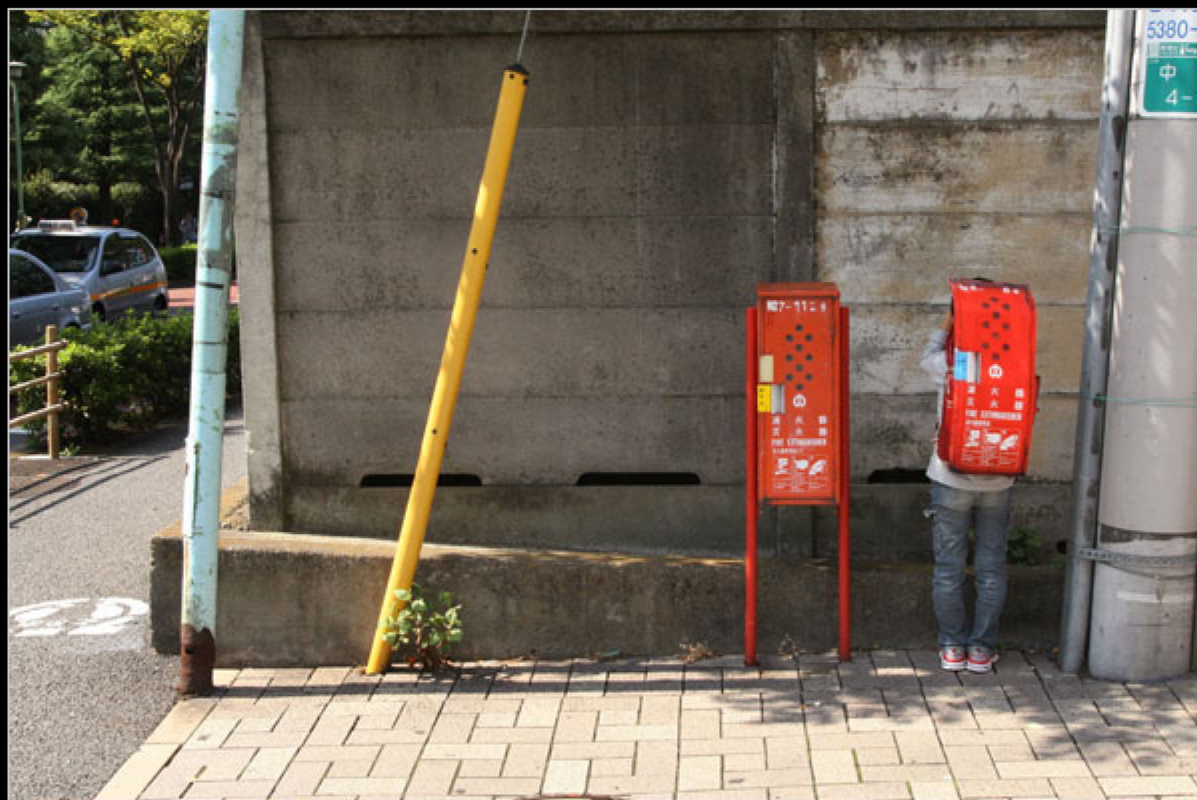

Crypsis in human defenses – examples of recent crime prevention measures in Japan

Crypsis in human defenses – examples of recent crime prevention measures in Japan

Examples of the mechanisms and consequences of co-evolution

Crypsis
Mimicry
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MIMICRY

1) Definition

- the resemblance of a mimic to a model by which the mimic gains protection from predators due to unpalatability of the model;
- model commonly advertises its unpalatability through conspicuous warning coloration (aposematism)

2) Two basic types of mimicry

A) Batesian mimicry

model: toxic

mimic: palatable

mechanism: predator forms association between model's appearance and its unpalatability; mimic is protected by disguising itself as model

implications:

- only works if mimic is relatively rare ***WHY?***
- otherwise predator less likely to form association
- the more frequent the mimic the more detrimental it is to the model
- if mimic is common, model may be forced to "evolve away" from it's mimic!

MIMICRY

B) Muellerian mimicry

model(s): toxic

mimic(s): toxic

mechanism: models and mimics are all distasteful and benefit from looking like each other as predators learn from tasting a single individual

implications:

- distinction between mimic and model becomes ambiguous (“co-mimics”)
- works even if mimics are common
- evolution favors convergence of appearances onto one type
- often involves many species in so-called mimicry rings

A) Batesian mimicry
Example 1: ant mimicry in insects and spiders

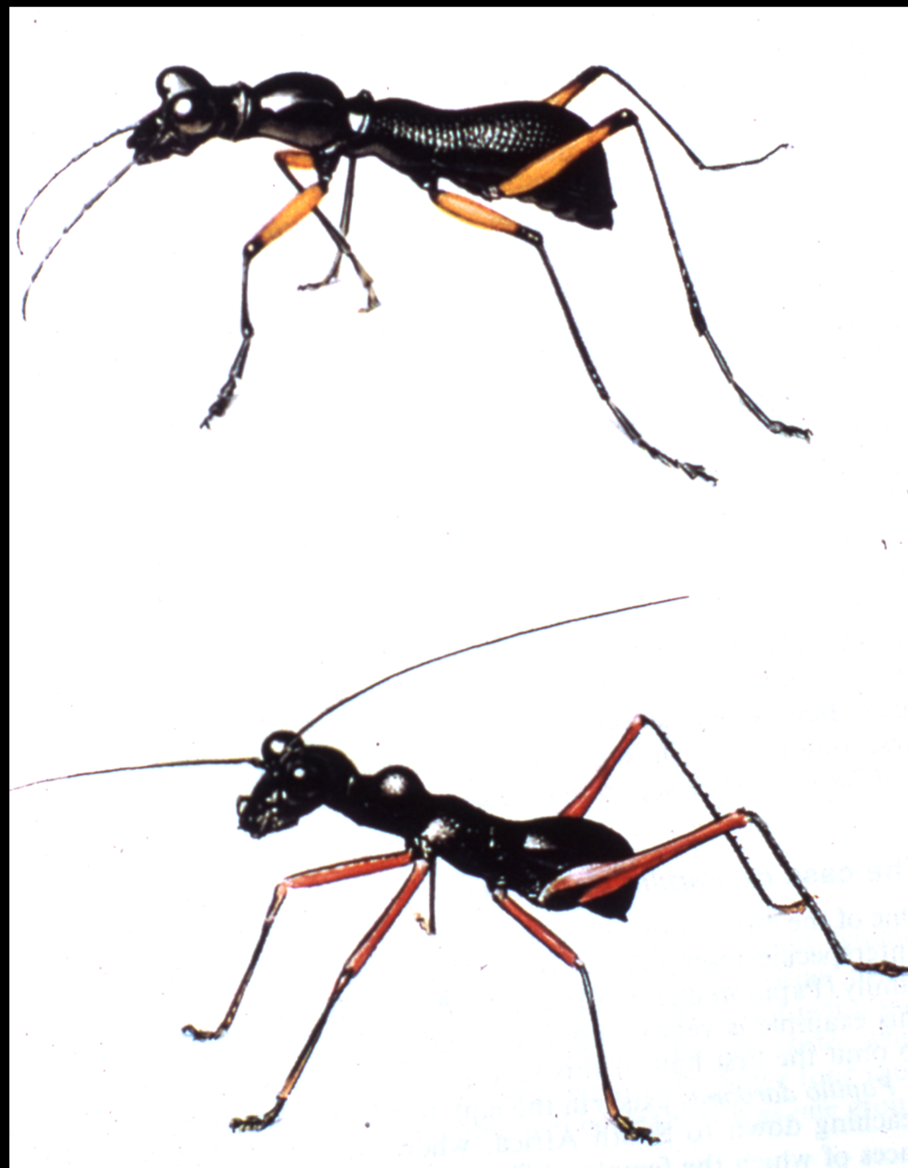
Model:

- ant appearance in general, sometimes species-specific
- protection mainly against birds
- ants are good models because
  - generally unpalatable except to specialists
  - often chemically well defended

Examples of ant- mimicry



Examples of ant- mimicry



Examples of ant- mimicry

A) Batesian mimicry
Example 2: wasp/bee mimicry in various insect orders

Model:

- wasp appearance in general
- protection mainly against birds
- often yellow/black banding and/or wasp waist sufficient to aquire some protection
- hymenoptera are good models because
  - generally extremely well defended

Examples of wasp/bee - mimicry

Examples of wasp/bee - mimicry

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Examples of wasp/bee - mimicry

A) Batesian mimicry

Example 3: butterflies

MODEL: *Battus philenor* (pipevine swallowtail, Papilionidae)

MIMIC: *Limenitis arthemis* (red-spotted purple, Nymphalidae)

MIMICRY

B) Muellerian mimicry

model(s): toxic

mimic(s): toxic

mechanism: models and mimics are all distasteful and benefit from looking like each other as predators learn from tasting a single individual

implications:

- distinction between mimic and model becomes ambiguous (“co-mimics”)
- works even if mimics are common
- evolution favors convergence of appearances onto one type
- often involves many species in so-called mimicry rings

B) Muellerian mimicry

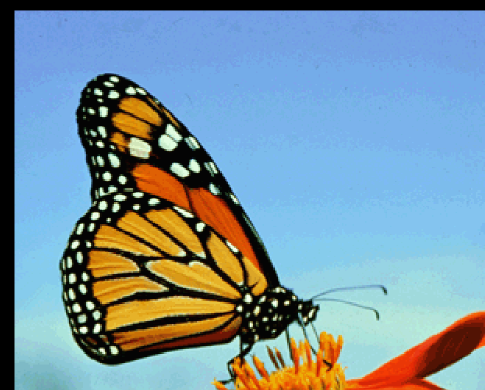
Example 1: butterflies

remember:

- all members of a Muellerian mimicry complex are distasteful
- distinction between mimic and model is ambiguous (co-mimics)

Limentis archippus
Viceroy

Danaus plexippus
Monarch



Examples of the mechanisms and consequences of co-evolution

Crypsis
Mimicry
Phytophagy
Pollination

PHYTOPHAGY

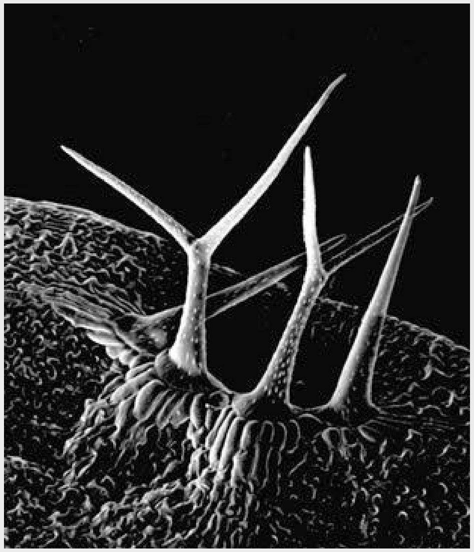
- = plant feeding
- comes in many different ways, e.g. leaf chewing, sap sucking, seed predation, gall formation, leaf mining
- 9 orders use herbivory as primary means of food acquisition

PLANT DEFENSE MECHANISMS AGAINST INSECT HERBIVORES

1. Physical defense mechanisms

2. Chemical defense mechanisms

1. Physical defense mechanisms



- thickened cuticula on leaves
- thickened leaf edges to prevent edge feeding by caterpillars
- glandular hairs with sticky compounds to entangle insects
- trichomes
- latex and resin

2. Chemical defense mechanisms

Three basic strategies:

a) Protection through secondary compounds

b) Protection through deficiency

c) Protection through replacement

2. Chemical defense mechanisms

a) Protection through secondary compounds

Strategy: plants evolved chemical pathways to synthesize substances toxic to insects and incorporate them into their tissues (in particular leaves and seeds)

Examples:

Alkaloids
• nicotine, caffeine, cocaine, mescaline, colchicine, vincristine
• disrupt DNA and RNA synthesis, inhibit cell division, destroy membranes, disrupt microtubule formation

Cyanide
• various cyanogenic compounds; release HCN upon ingestion
• disrupt electron transport chain in mitochondria (??)

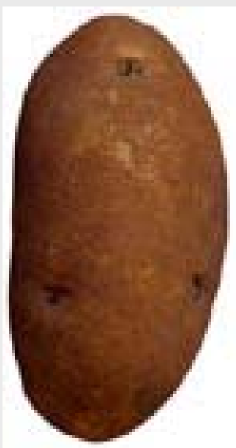
Terpenoids
• citronella, camphor, pyrethrum
• disrupt electron transport chain in mitochondria
• pyrethrum delays closing of sodium ion channel along nerve membranes (??)

2. Chemical defense mechanisms

b) Protection through deficiency

Strategy: plants removed substances from their tissues that are particularly important to insects

Example:



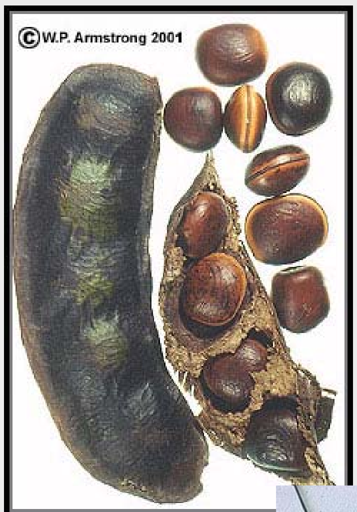
Fat and proteins

- leaves and flowers are very poor in fat and proteins
- storage instead in specialized tissues that are heavily chemically defended or hidden underground

2. Chemical defense mechanisms

c) Protection through replacement

Strategy: plants removed substances from their tissues and replaced them with something that is hard to handle for insects



<u>*Example:*</u>

Use of *non-protein* aminoacids

- use of L-Canavanine by legumes (Fabaceae)
- very common in some seeds (~12% dry weight)
- plant does not use it during protein synthesis
- ....

2. Chemical defense mechanisms

c) Protection through replacement

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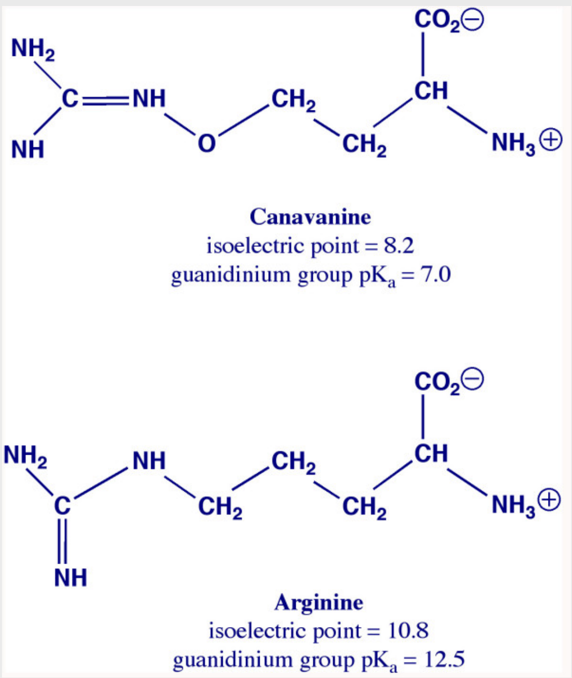

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Use of *non-protein* aminoacids

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- plant does not use it during protein synthesis
- when insect herbivores ingest Canavanine it mimics arginine and becomes incorporated into many proteins
- induces severe denaturations and renders proteins non-functional

PLANT DEFENSE MECHANISMS AGAINST INSECT HERBIVORES

1. Physical defense mechanisms
2. Chemical defense mechanisms

↓

INSECT RESPONSE TO PLANT DEFENSES

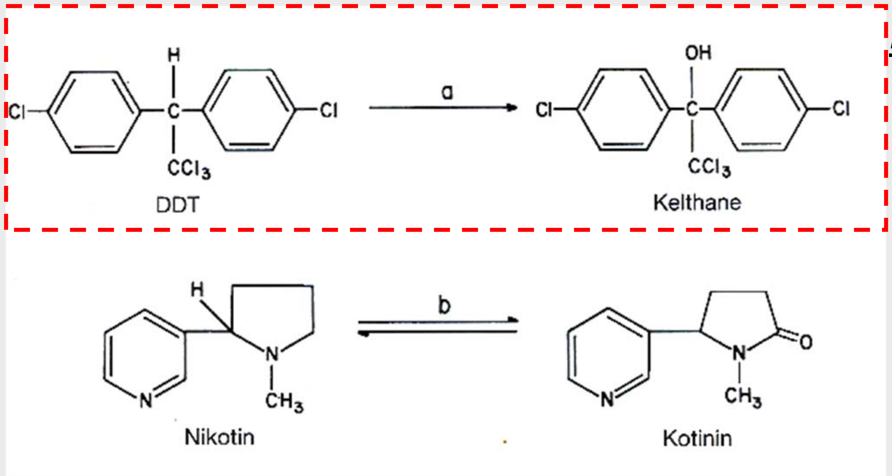
INSECT RESPONSE TO PLANT DEFENSES

a) Tolerance

insects evolved novel enzyme tertiary structures such that denaturing plant chemicals can no longer affect them, or affect them less

b) Detoxification

insects have evolved biochemical pathways that allow them to detoxify defensive plant chemicals



Example: mixed-function oxidases (MFO's)

- found in all animals
- group of various enzymes that modify toxic substances; attach large # of functional groups to

a) increase water solubility (why?)
b) induce shape changes (why?)

INSECT RESPONSE TO PLANT DEFENSES

a) Tolerance ✓

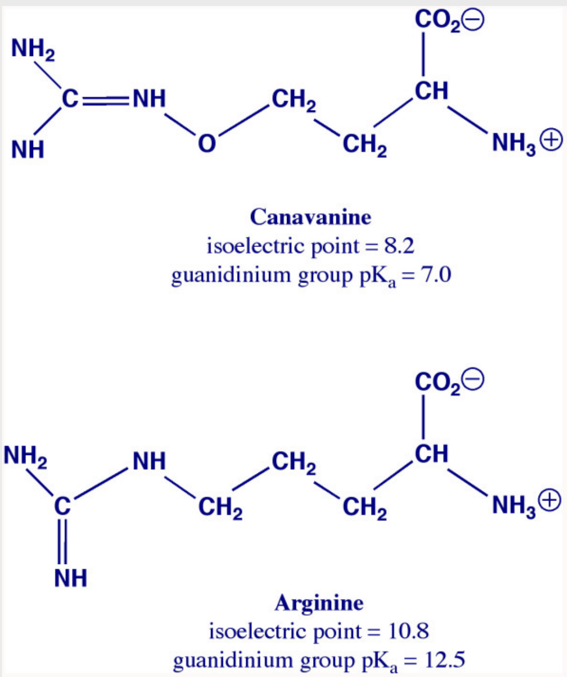
b) Detoxification ✓

c) Detoxification and re-utilization

2. Chemical defense mechanisms

c) Protection through replacement

Strategy: plants removed substances from their tissues and replaced them with something that is hard to handle for insects



Canavanine
isoelectric point = 8.2
guanidinium group pK_a = 7.0

Arginine
isoelectric point = 10.8
guanidinium group pK_a = 12.5

<u>*Example:*</u>

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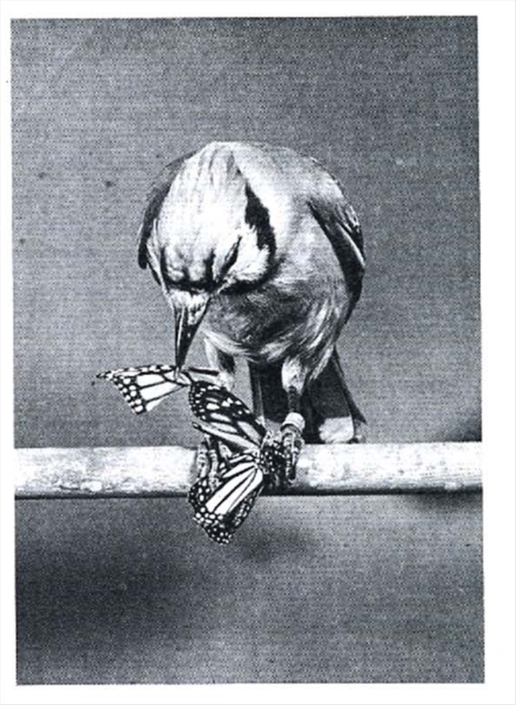
<u>Example 1:</u> insect adaptation to overcoming and utilizing non-protein aminoacids

- *Caryedes brasiliensis* (Curculionidae)
- specialized on *Dioclea* seeds (~12% Canavanine)
- has discriminating tRNAs *(what the h..??)* that will not bind Canavanine
- instead can fully digest Canavanine to CO_2 and NH_3
- incorporates NH_3 into 11 of 17 AA

This beetle is far away from avoiding Canavanin - it actually depends on it!!!

Example 2: insect adaptation to overcoming and utilizing cardiac glycosides (digitoxin)

- *Danaus plexippus,* Monarch butterfly
- caterpillars ingest cardiac glycosides from host plant (Asclepiadaceae, milkweeds)
- able to store compound and incoporate into adult cuticle during metamorphosis
- makes them <u>highy</u> distasteful!



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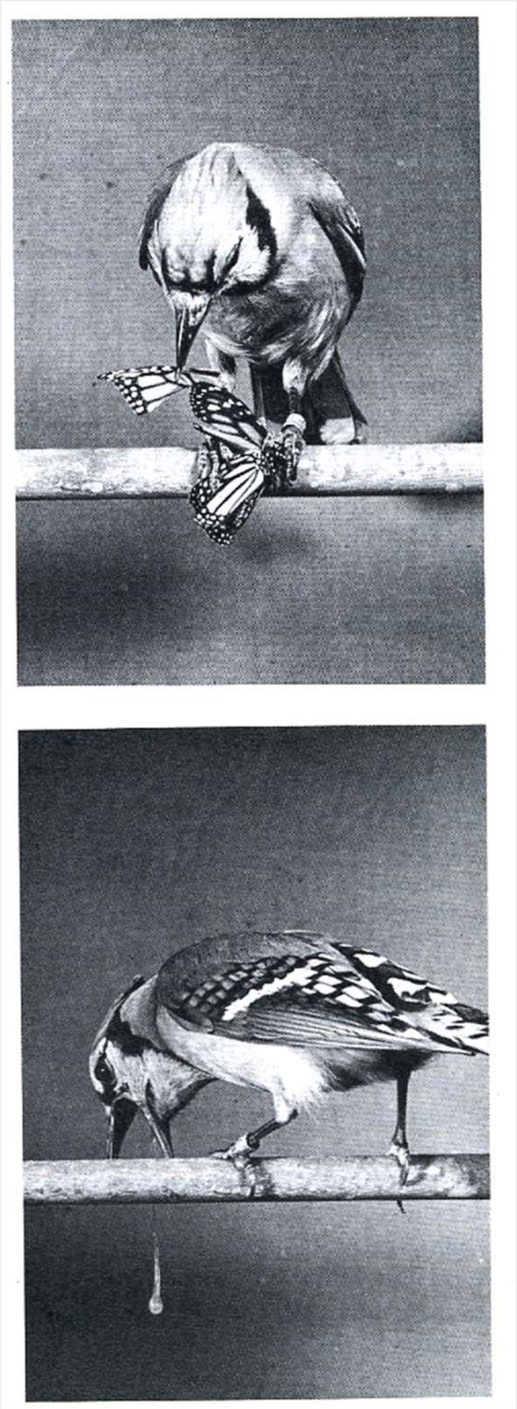

Example 2: *insect adaptation to overcoming and utilizing cardiac glycosides (digitoxin)*

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As with the weevil example before, the monarch is now far away from avoiding its larval host plant, instead it now depends on it for efficient defense!

Examples of the mechanisms and consequences of co-evolution

Crypsis
Mimicry
Phytophagy
Pollination

POLLINATION

- = transfer of pollen from male (stamen) to female flower parts (stigma)

- all sexually producing plants depend on pollination

- insect pollination is advantageous over wind pollination because...
  a) you don't need wind!
  b) reduces pollen wasteage through increased specificity
  c) allows large numbers of plant species to co-exist (why we will see in a few slides)

POLLINATION as a MUTUALISM

- Mutualism = both partners (plant and pollinator) benefit
- pollinators benefits because of rewards provided by plant

  a) nectar
  = sugar solution (sucrose, fructose, glucose)
  b) pollen
  = high in protein, starch, fat, some vitamins and salts

- plant benefits because....?

THEREFORE: From the perspective of the plant a plant-pollinator relationship only works if pollination is species-specific.

Mechanisms that enhance pollination specificity

1) exploitation of pollinator memory

• pollinators (in particular bumble bees), form short term memory of most lucrative nectar and pollen sources and visit those preferentially

• plant species in turn restrict their flowering to particular times of the year, during which they present bees with an overabundance of flowers and rewards

2) restricted access to certain times of day/night

• many flowering plants open and close their flowers actively to match periods of activity and inactivity of their pollinators (moths = night, butterflies = day)

3) flower morphology

• many flowering plants have adapted their flower appearance to cater preferentially towards certain, and discriminate against other, potential pollinators.

Mechanisms that enhance pollination specificity

continued

4) rewards match demands

- plant rewards match particular physiological demands of their pollinators, in particular:

a) total sugar content in nectar (15 to 88 % percent by weight)

b) ratio of disaccharides to monosaccharides
(Saccharose/ Fructose + Glucose)
→ hummingbirds like lots of disaccharides
→ butterflies prefer higher monosaccharide content

c) presence of AS in nectar
caters towards pollinators (esp. flies) that do not feed on pollen and depend on alternative AS sources

Mechanisms that enhance pollination specificity

continued

5) Chemical cues

- plants use chemical cues to attract specific pollinators

e.g: highly fragrant flowers: bees, moths
carrion-like smell: carrion-flies, dung-flies

This is also were the mutualism often ends and deception, tricks, and traps enter the stage

Pollination without mutualism

Common mechanisms:

1) Use of chemical attractants but no nectar/pollen reward – many orchids

2) Use of physical traps that confine pollinator for a certain amount of time (arums, *Rafflesia*)
   Isn't that a problem for the plant?? *only works with forgetful pollinators and long-lived flowers*

3) Pseudocopulation – many orchids (using mainly wasps and bees)

- chemical attractant of flower mimics female sex pheromone
- flower resembles aspects of female anatomy
- attract male wasps that "copulate" with flower

Pollination without mutualism

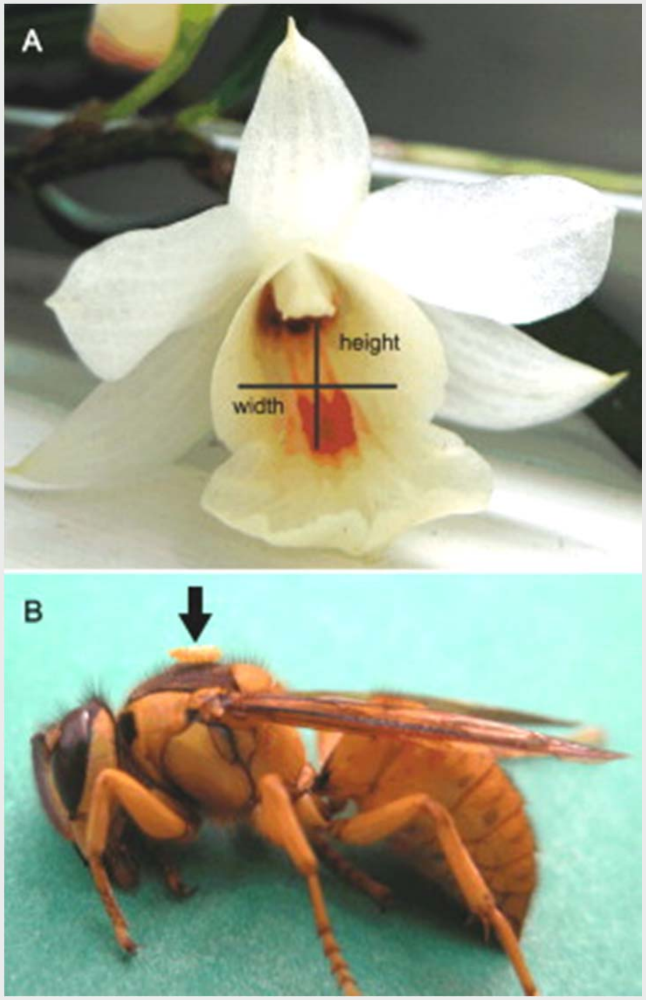
Recent study:

Initial observation:

(a) Dendrobium sinense is a species of orchid endemic to the Chinese island Hainan

(b) Orchid is pollinated by the hornet *Vespa bicolor (what do they normally eat?)*

(c) Orchid provides no reward.



Current Biology
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Article | Figures/Tables | References | PDF (271 K)

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Report

Orchid Mimics Honey Bee Alarm Pheromone in Order to Attract Hornets for Pollination

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Summary

Approximately one-third of the world's estimated 30,000 orchid species are deceptive and do not reward their pollinators with nectar or pollen [1]. Most of these deceptive orchids imitate the scent of rewarding flowers or potential mates [2] and [3]. In this study, we investigated the floral scent involved in pollinator attraction to the rewardless orchid *Dendrobium sinense*, a species endemic to the Chinese island Hainan that is pollinated by the hornet *Vespa bicolor*. Via chemical analyses and electrophysiological methods, we demonstrate that the flowers of *D. sinense* produce (Z)-11-eicosen-1-ol and that the pollinator can smell this compound. This is a major compound in the alarm pheromones of both Asian (*Apis cerana*) and European (*Apis mellifera*) honey bees [4] and [5] and is also exploited by the European beewolf (*Philanthus triangulum*) to locate its prey [6]. This is the first time that (Z)-11-eicosen-1-ol has been identified as a floral volatile. In behavioral experiments, we demonstrate that the floral scent of *D. sinense* and synthetic (Z)-11-eicosen-1-ol are both attractive to hornets. Because hornets frequently capture honey bees to feed to their larvae, we suggest that the flowers of *D. sinense* mimic the alarm pheromone of honey bees in order to attract prey-hunting hornets for pollination.

Summary: Interactions between organisms provide fantastic opportunities for co-evolution

Today: Crypsis, Mimicry, Phytophagy, Pollination

But this is also true for many other contexts, e.g. diseases and their hosts, insects and the insectizides we throw at them (bedbugs!), antibiotic resistance in hospitals, invasive species and the habitat they are invading and many more.

For the rest of today - one particularly extreme example of co-evolution: *carnivorous plants and their insect prey*






Carnivorous plants – some background

1) Carnivorous plants always grow in poor nitrogen conditions

2) They photosynthesize like regular plants

3) But they also catch insects

4) If insects are withheld carnivorous plants can still grow but do less well

YOUR TASK:

The plants before you are all carnivorous

Given what you know about insects and plants, please investigate the following questions

1) Why do they catch insects?
2) How do they catch insects?
3) Once caught, what do they do with them?

We may not have time for all questions, but pick at least 2. Then form hypotheses that address these questions, and brainstorm about potential tests .

We will ask you to share your progress and insight periodically, and also provide you with some additional information along the way (which may or may not further complicate your analysis ☺

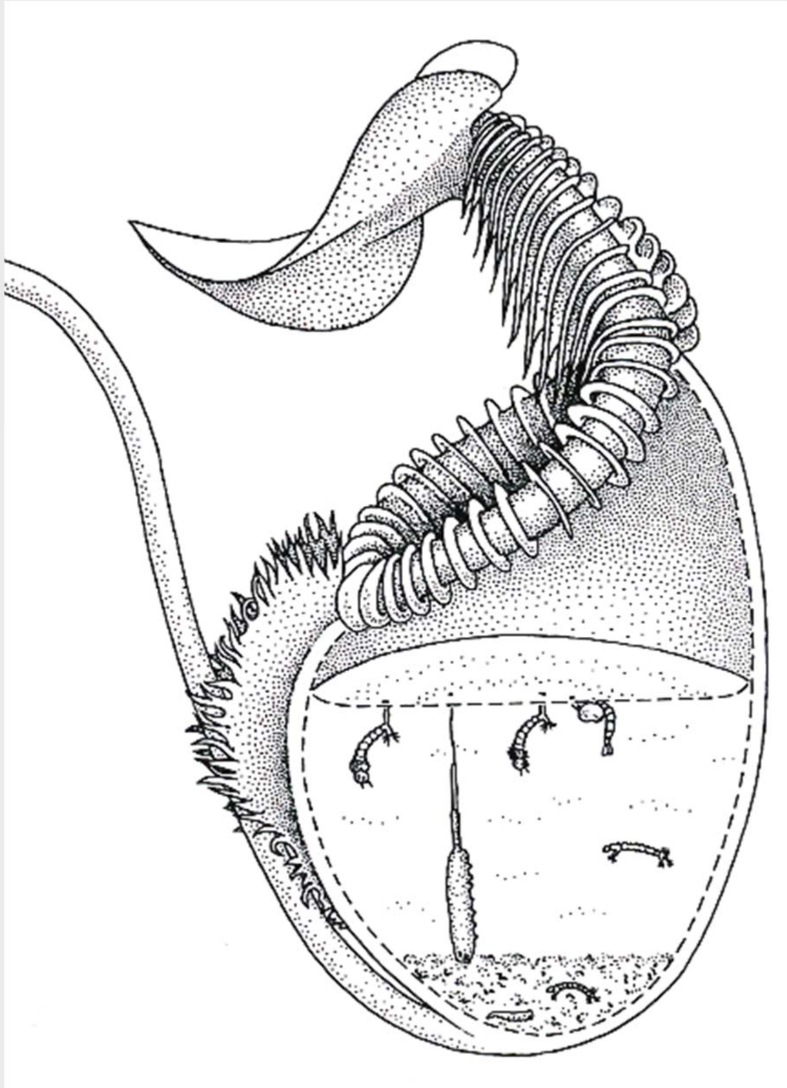
Additional information I

Many carnivorous plants lack the ability to digest insects!

(i.e. they can't make the right enzymes)

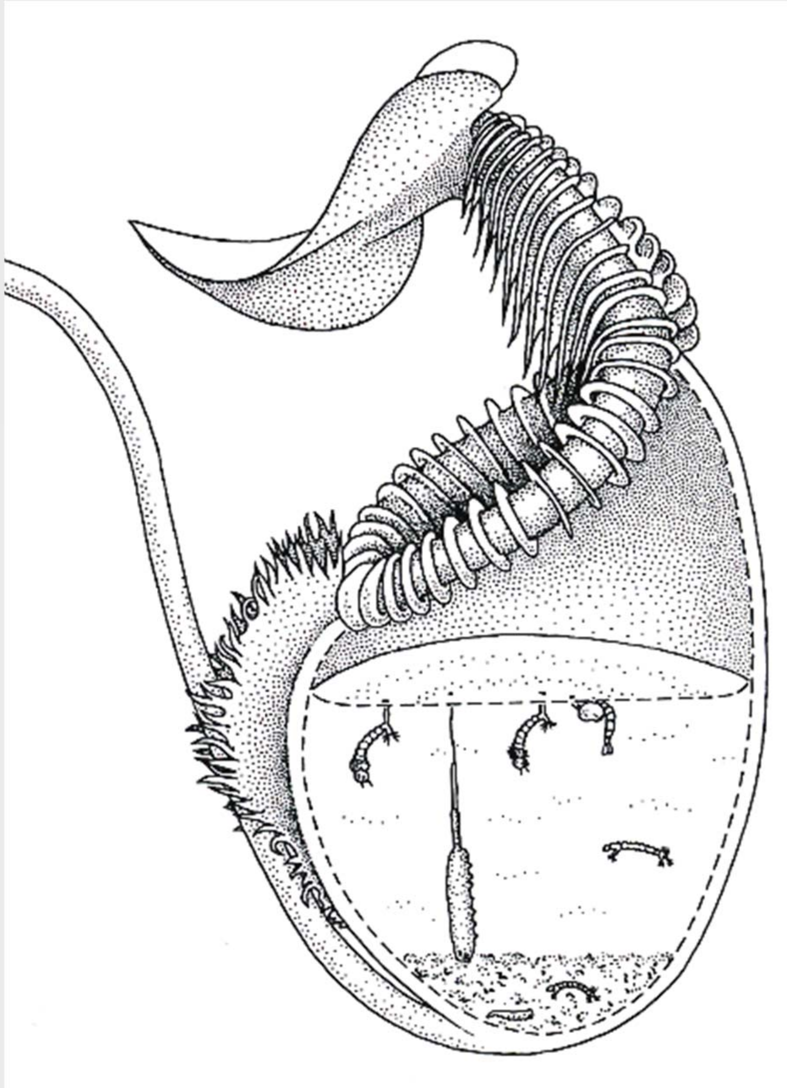
Additional information II

The pitchers of many carnivorous plants are home to specialized insects that do not get eaten by the plant

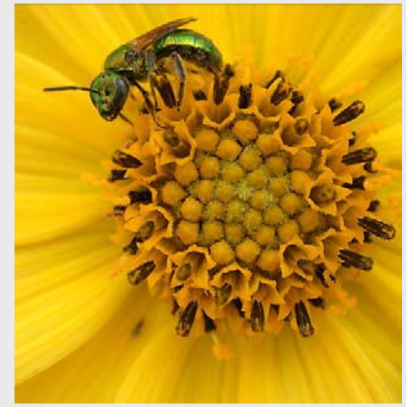


Additional information III

If these insects are removed the plant does poorly, just like when you remove the plant's insect prey





Thank you!