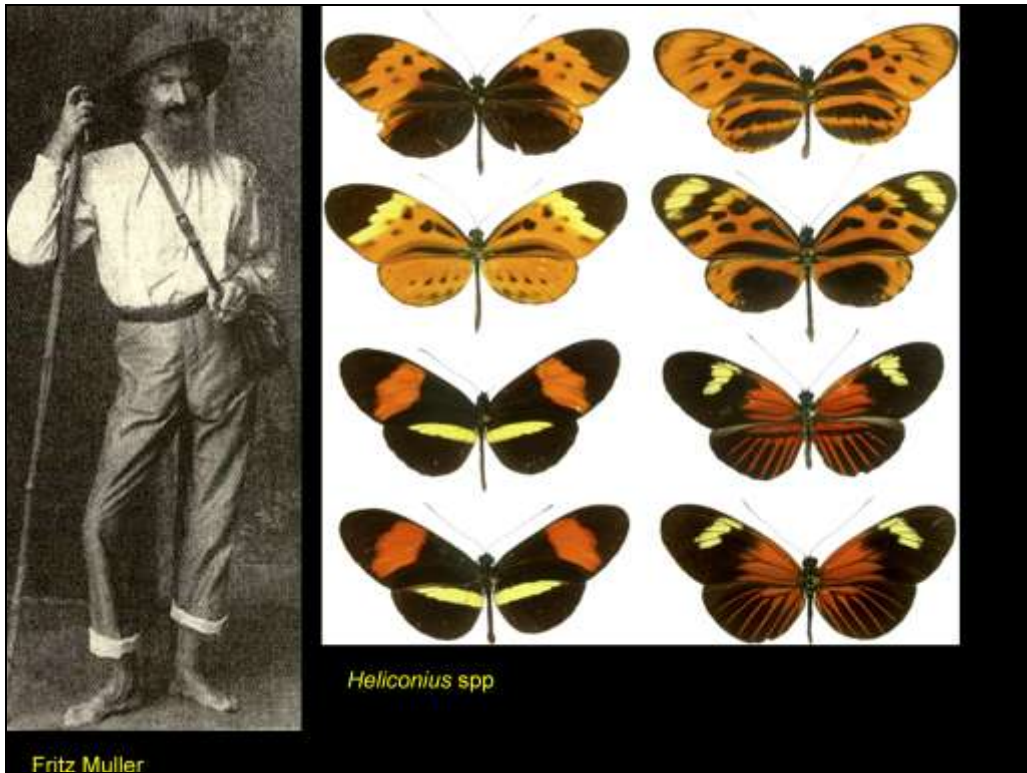




Coevolutionary dynamics in predator-prey can usually be modeled as 'arms races' or as another sort of Red Queen scenario; both parties are under constant directional selection to either avoid being eaten or to overcome prey defenses. 'Break-downs' are quite likely to occur; if it's a failure of defense, it might lead to extinction of prey populations. If a prey species evolves a 'perfect' defense against some predator, that predator may switch to another prey type – but if it's a specialist it may be doomed. Does predator-prey coevolution tend to drive towards highly specialized predators and prey with 'targeted' defenses (e.g., cheetahs and impalas – two of the fastest mammals)?



Chemical defenses are one of the most-studied (at least from evolutionary perspective) types of prey defense. Chemical defenses are often matched with 'warning coloration', or aposematic coloration. Toxic animals are highly visible; how do predators learn to avoid them without killing some? How is the fitness of an aposematic individual affected by 'naïve' predators? Can selection make recognition of warning colors 'innate' in predators? If so, does the system become so vulnerable to exploitation that it breaks down? There are many tricky aspects to evolution of what seems a highly 'logical' system...



Many species seem to have converged, evolutionarily, on similar color schemes to signal distastefulness or toxicity (often orange and black). All of the above species of butterflies in genus *Heliconius* are toxic. Presumably, this reinforces the signaling system, and likely enhances individual fitness of all parties (more opportunities for predators to learn the code without eating a particular 'target'). This sort of 'mimicry' was first described by naturalist Fritz Muller and is referred to as Mullerian mimicry. The species participating in a 'mullerian mimicry complex' might be seen as mutualists; presence of each enhances fitness of individuals of others...

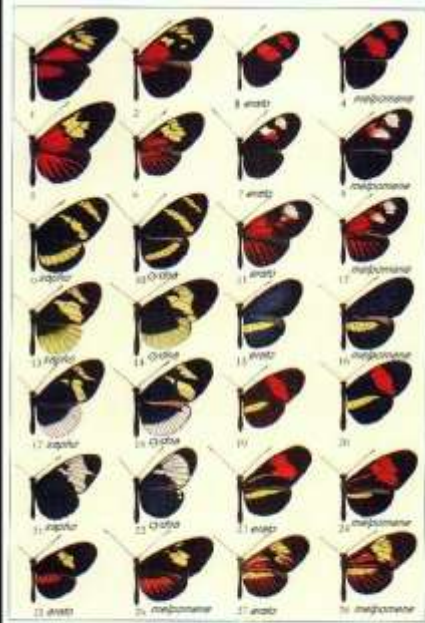


PLATE 1

"Each pair of butterflies in the two leftmost columns... and likewise in the two rightmost columns... belong to sympatric populations of two different, distasteful, warningly colored species... Experiments have shown that butterflies suffer less predation from birds if they conform to the locally common color pattern to which a pair of species has converged."

[plate from Shugham 1916; courtesy of L. E. Gilbert; text from Patrycia 1997]





Henry Walter Bates



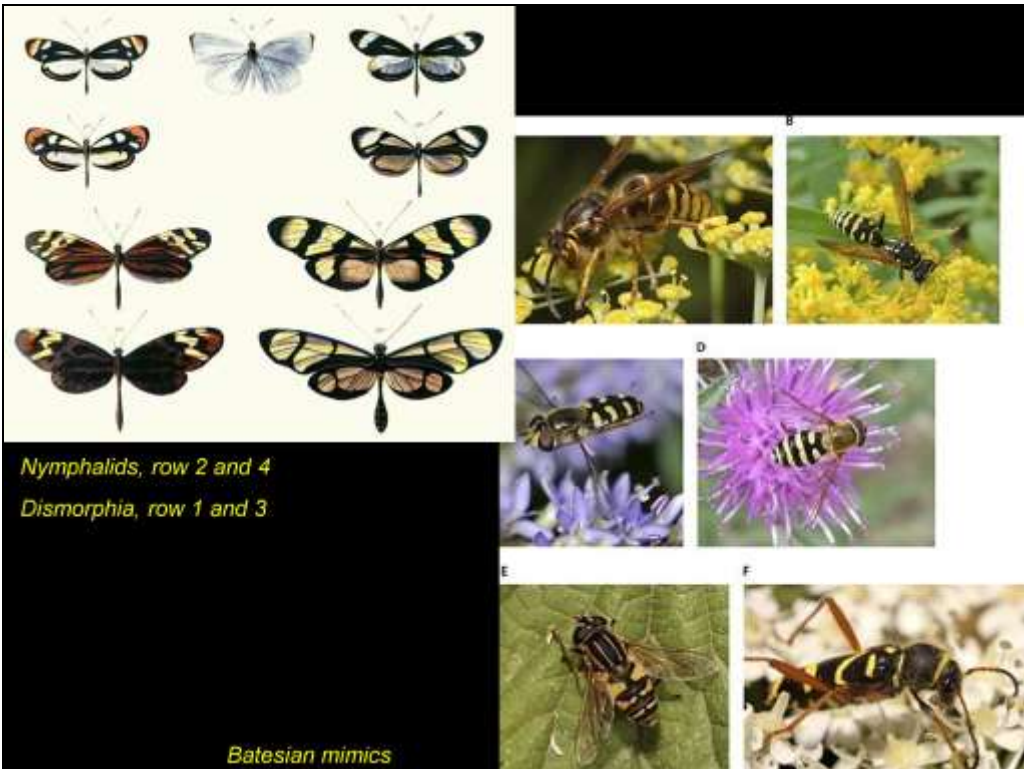
viceroy



monarch

Henry Bates – another 19th-century naturalist-explorer -- recognized another sort of mimicry where non-toxic, palatable species resemble toxic/distasteful ones and presumably benefit from predators taking them for nasty. How does this affect fitness of individuals of the 'model' (actually toxic) species? What sort of selective dynamics might be involved?







Madagascar hissing cockroach

It's hissing sounds snake-like; a Batesian sound-mimic?

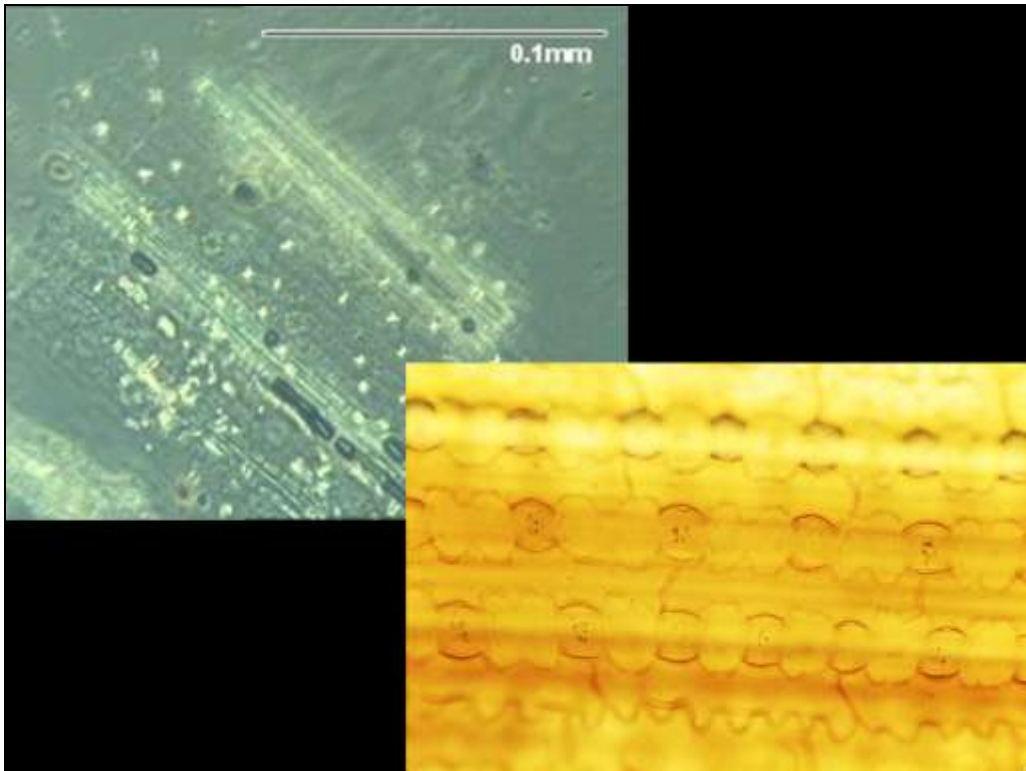


Evolution of warning coloration in extremely toxic mimics has been difficult to explain; if every bite kills, how does selection on predators/enemies ever produce capacity to learn to avoid or tendency to avoid? Steve Emsley has suggested that these snakes are actually mimicing *less* toxic species on which predators have been 'trained'.

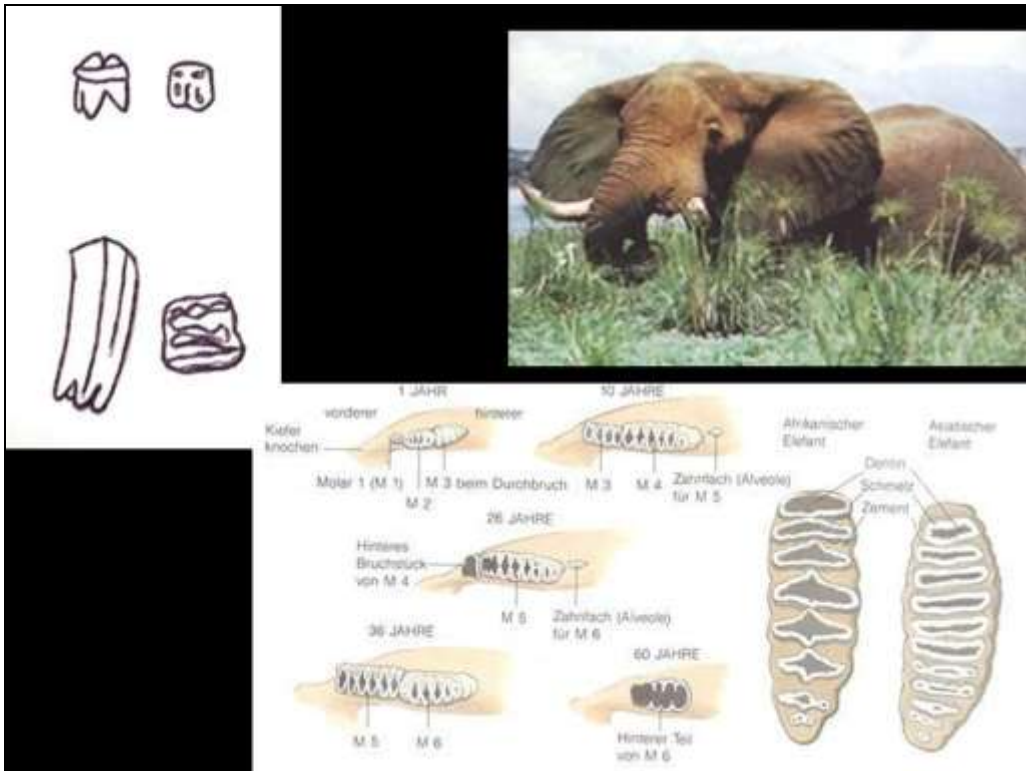




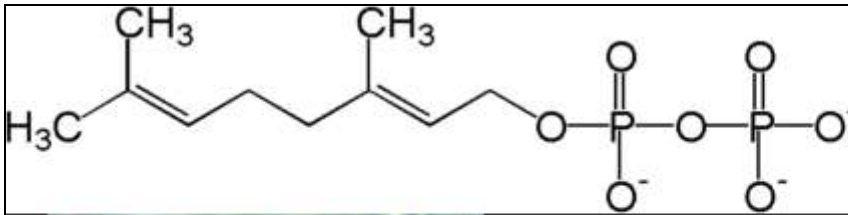
Mimicry can involve other patterns than aposematic coloration; this moth can 'flash' its rear wings which may repel potential predators by looking like an owl – a higher trophic-level predator.



Plants are constrained in terms of modes of predator (herbivore) avoidance because they are sessile (can't hide) and must necessarily place their vulnerable, delicious parts (leaves) where they can be seen since their function is to gather light. Grasses are an unusually successful (and relatively young) plant family. Their success may be associated with an unusual herbivore defense; they produce silica granules ("phytoliths") in their leaves. Herbivores chewing these leaves ultimately grind their teeth away, presumably reducing fitness of individuals who don't avoid grasses.



But, with the ecological success of grasses, selection powerfully favors adaptations to this defense; the coevolutionary dynamic has led, for example, to the ability of most grazers to produce more sets of teeth in sequence than other, related animals. Elephants can produce 6 sets of molars, new ones growing in as old ones wear away. (Predators, by contrast, have just one or two sets over their lifetime.)



But most plant defenses are chemical. Chemical defenses fall in two broad (and overlapping) categories. Many trees produce 'quantitative' defenses that make their tissues of little food value and/or indigestible (resins in conifers, tannins and celluloses in most species). These defenses have to be present in high concentrations to be effective – thus, they're often called 'quantitative chemical defenses'.



Other species produce simpler but more acutely toxic molecules. Because they're small and effective in low concentrations, they are contrasted with 'quantitative defenses' and are called 'qualitative chemical defenses'. This one is capsaicin – what makes chiles hot – and may be both a defense against mammalian predators (birds are intended dispersers) and fungi that attack the seeds.

(A second way of categorizing plant chemical defenses; some are always present – constitutive – and others are produced only when plant sustains herbivore damage – inducible.)



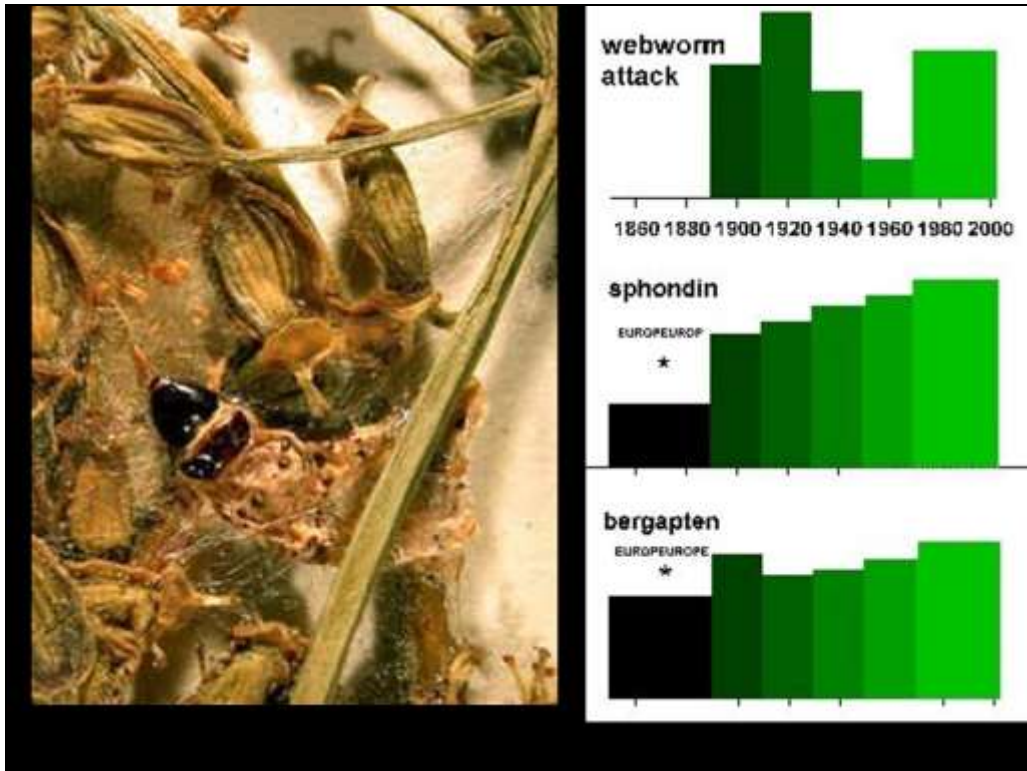


But chemical defenses – particular toxins – can be 'beat' by animals; selection will favor any biochemical variation in the herbivore that confers resistance to the toxin. Caterpillars (genus *Heliconia*) feeding on *Passiflora* vines sequester toxins in fat tissues where they do no damage to caterpillar (but make it toxic to birds, thus defending it; note the aposematic coloration).

Various species of *Passiflora* plants have evolved leaf parts that mimic *Heliconias* eggs. The caterpillars are aggressive towards one another, and butterflies will tend to lay eggs only on leaves where eggs have not already been laid. Thus, the plant is practicing protective mimicry of its herbivores eggs to repel egg-laying butterflies!



Most of our understanding of predator-prey (plant-herbivore) coevolution is based on inference from current patterns. An unusual study that follows actual coevolutionary dynamics involves wild parsnip – a European native naturalized in the New World for several centuries – and its coevolved herbivore, the parsnip webworm. The plant is chemically defended, but the caterpillar is resistant. It feeds on the inflorescence of the plant so has large effects on fitness. When parsnip was first introduced to the New World, the webworm was not present and the New World remained webworm-free for upwards of a century. The webworm was finally introduced (accidentally) and has been spreading for several decades.



Researchers in the May Berenbaum lab at Univ. of Illinois have studied this system, using preserved herbarium specimens of parsnip to a) determine when webworms arrived in different areas (they're often pressed with the plants) and b) to measure changing levels of defensive compounds. They have shown conclusively that toxin levels decreased following parsnips naturalization in the new world – presumably, plants producing less toxins had more resources to allocate to reproduction. When webworms arrived, concentrations of toxins gradually began to increase again; where webworms have been present for several decades, toxin concentrations approach those in European populations of parsnip.



Rufous-colored sparrow and shiny cowbird



Reed warbler and cuckoo

Brood parasites provide a distinctive example of predator-prey coevolution and have been intensively studied. Researchers have documented evolution of 'discrimination' against parasite eggs or chicks by host species, followed by evolution of mimicry of host eggs and chicks by the parasite eggs and chicks. There are many intricacies here, and brood parasitism has become a significant evolutionary 'laboratory'.





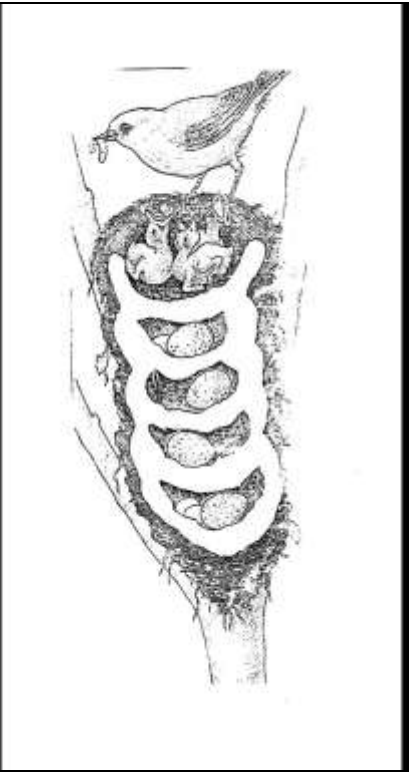
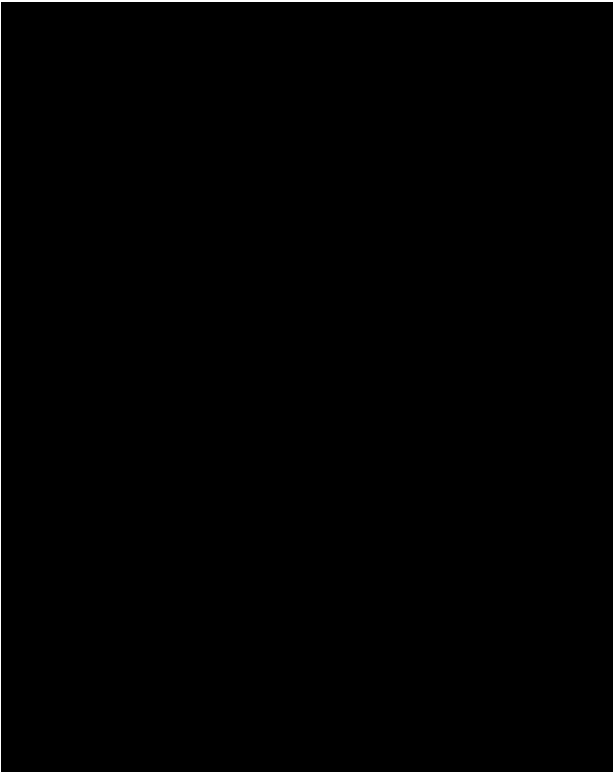
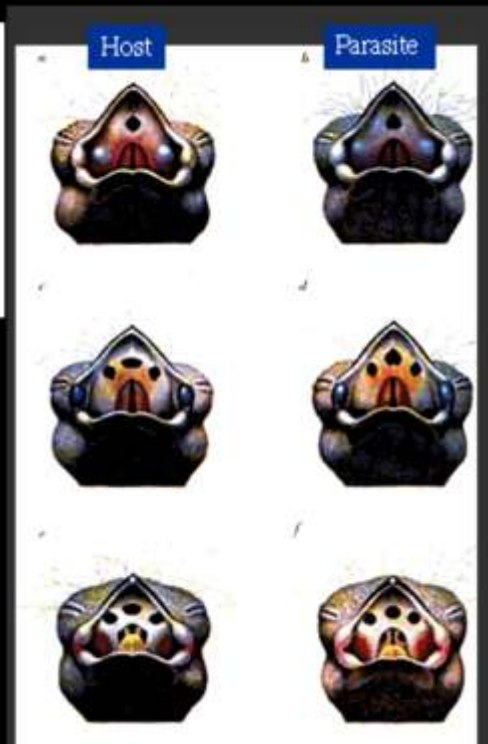
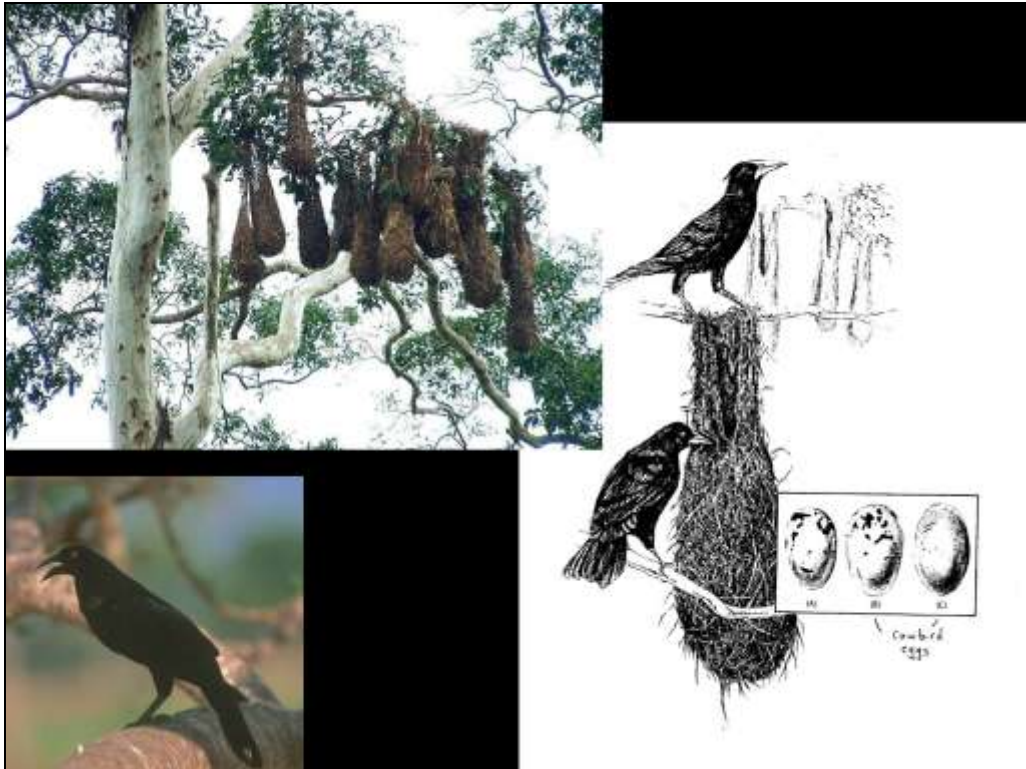






Figure 19-7 The mouth patterns of nesting parasitic whydahs match those of their hosts. (A) Northern Paradise-Whydah and Green-winged Pytilia; (B) Scraw-tailed Whydah and Purple Grenadier; (C) Village Indigobird and Jameson's Fin-  
 finch. (After Nicolai 1974; Lack 1968)





A complex coevolutionary story: Oropendolas – colonially nesting tropical New World birds – are parasitized by cowbirds. Some cowbirds have 'mimic' eggs; others don't. Correspondingly, some oropendola colonies are 'discriminators' (ejecting parasite eggs), and some are not. It appears that cowbird chicks – more precocial than host chicks – help clear the nest of parasitic botflies and can enhance host fitness. Where oropendola colonies are near hornet nests, the hornets chase away the bots, so cowbirds now cause a fitness cost for hosts – and these hosts discriminate.



Ants also exhibit brood parasitism; some species move into other species' colonies, manage to evade their chemosensory detection of intruders, and lay eggs for workers of the other species to raise. This is a step beyond that; some ants actually enslave workers of other species, taking larvae to their own nest where they raise young of host species.