

# Macroevolutionary Patterns of Behavior

## Outline

Adaptive versus Non-adaptive hypotheses

Using phylogenetics to test hypotheses in behavioral ecology

Apostematism, Batesian mimicry, and Mullerian mimicry

Question of the day: When are behaviors are adaptive and when are they non-adaptive? How do you test this?



# Behavior of the Day!

Meet Snowball the cockatoo!

<http://www.youtube.com/watch?v=hF7xTTvU2sM>



[http://www.nature.com/scitable/blog/student-voices/we\\_got\\_the\\_beat\\_and](http://www.nature.com/scitable/blog/student-voices/we_got_the_beat_and)

# Adaptive and Non-adaptive behavior

1. Adaptation: A trait, or integrated suite of traits, that increases the fitness (reproductive success) of its possessor.
2. Gould and Lewontin (1979) criticized the “adaptationist program” = hypothesizing that all traits are adaptive.
3. For example, it was hypothesized that the small forelimbs of *Tyrannosaurus rex* were used to stimulate females. Is this testable?
4. Hypotheses suggesting that a trait is an adaptation must be tested!

# Adaptation vs Exaptation

1. Definition 1: Adaptation = A trait, or integrated suite of traits, that increases the fitness (reproductive success) of its possessor.
2. However, traits can have current utility (i.e. increase fitness), but may not have been selected for that function.
3. Definition 2: Adaptation = a trait shaped by natural selection for its current use.
4. Exaptation (pre-adaptation):
  - a. Trait arises nonadaptively, but is co-opted for useful function later.
  - b. Trait arises adaptively, but is co-opted for a new use.

# Examples of Exaptation

1. Spandrels
2. Feathers and flight
3. Snail that lays eggs in the center of its spiral
4. Dancing in cockatoos

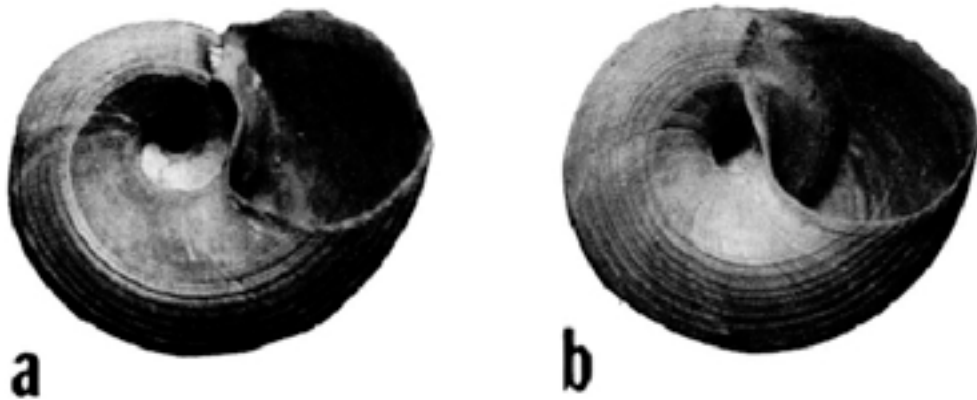


Fig. 4. Ventral view of *M. vorticiferus*. (a) Female, shell diameter = 18.6 mm. (b) Male, shell diameter = 18.2 mm.



Fig. 1. Specimen of *M. vorticiferus* with brood in place in umbilicus.

# Historical Hypotheses

1. Definition 2: Adaptation = a trait shaped by natural selection for its current use.
2. This is a historical hypothesis: Must reconstruct evolutionary history to test it.
3. Also important to observe how evolution proceeds over time.

# Lecture Outline

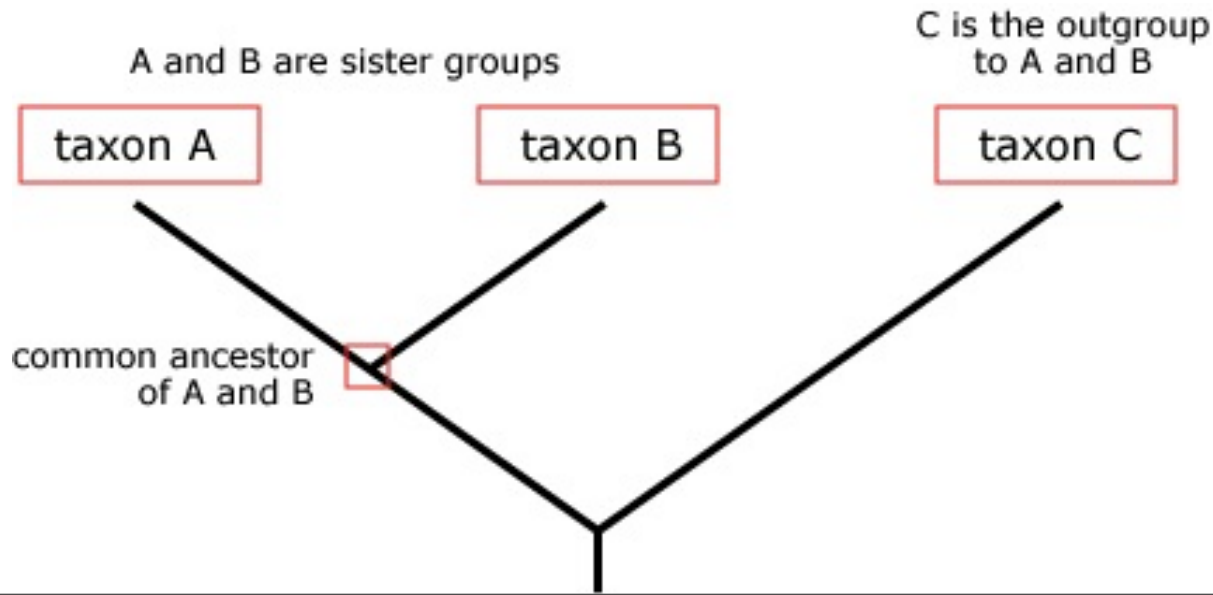
Adaptive versus Non-adaptive hypotheses

**Using phylogenetics to test hypotheses in behavioral ecology**

Batesian and Mullerian mimicry

# Overview of Phylogenetics

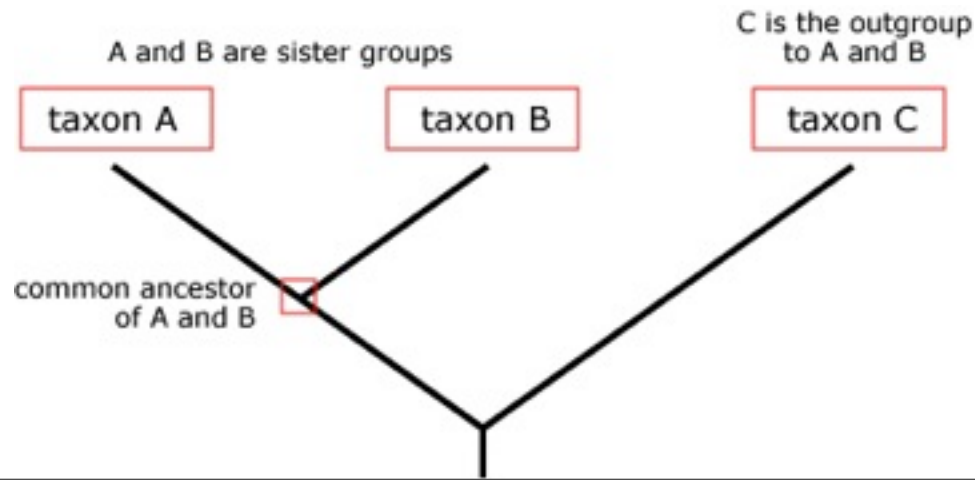
1. A [phylogeny](#), or evolutionary tree, represents the evolutionary relationships among a set of organisms or groups of organisms, called [taxa](#) (singular: taxon).
2. The tips of the tree represent groups of descendent taxa (often [species](#)).
3. The [nodes](#) on the tree represent the [common ancestors](#) of those descendants.





# Overview of Phylogenetics

4. Two descendants that split from the same node are called [sister groups](#). In the tree below, species A & B are sister groups — they are each other's closest relatives.
5. [Outgroup](#) — a taxon outside the group of interest.
6. All the members of the group of interest are more closely related to each other than they are to the outgroup.
7. The outgroup is useful when constructing evolutionary trees and determining how phenotypic traits have evolved over time.



# Using phylogenies to understand evolution

1. Phylogenies can reconstruct the order of evolutionary changes.

a. Example 1: Spider behavior

Orb-weaving spiders, spin intricate and orderly webs.

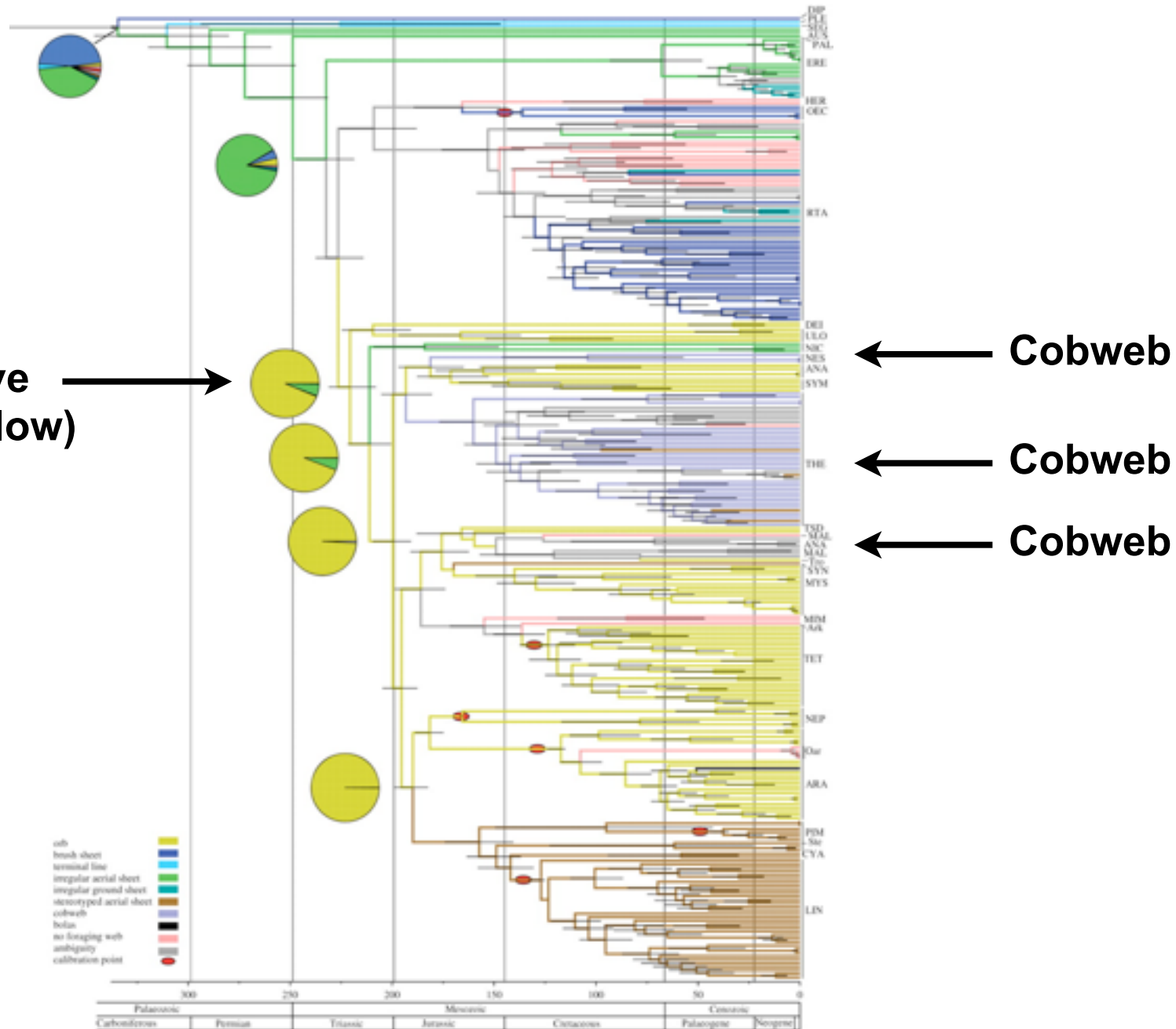
Other spiders spin disorderly cobweb-like webs.

Hypothesis on which came first?



# The Evolutionary History of Spiders and Web Making

Orb webs evolve  
(species in yellow)



Dimitrov et al 2012 Tangled in a sparse spider web: single origin of orb weavers and their spinning work unravelled by denser taxonomic sampling

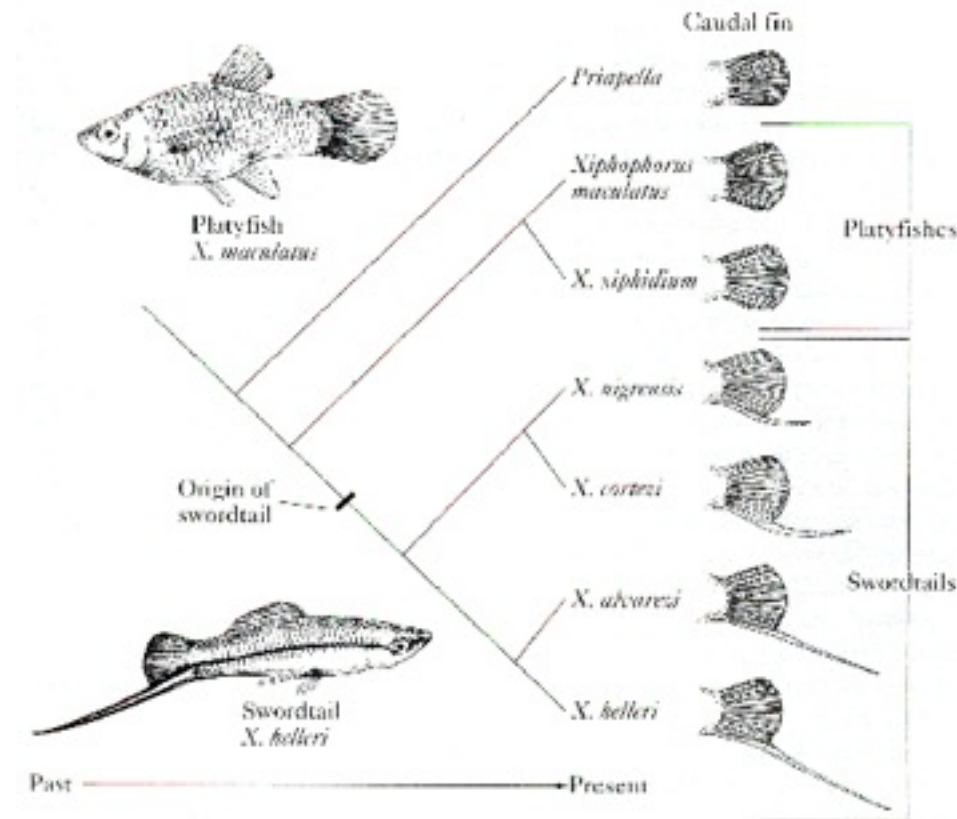
# Using phylogenies to understand evolution

1. Hypothesis: Complex orb webs evolved from less complex cob webs.
2. Results from phylogenetic analysis: Orb-weaving was the ancestral state. Cobweb-weaving evolved from spiders with more orderly webs. Reject hypothesis.
3. Side lesson: Evolution does not always go from less to more complex.



# Using Phylogenies: Sensory bias in Swordtails

1. Test for sensory bias: test whether closely related species that do not have the trait still prefer the trait.
2. Pre-existing preference in females is an exaptation. Occurred before it was used for sexual selection.
3. The male's sword is an adaptation to exploit the sensory bias.

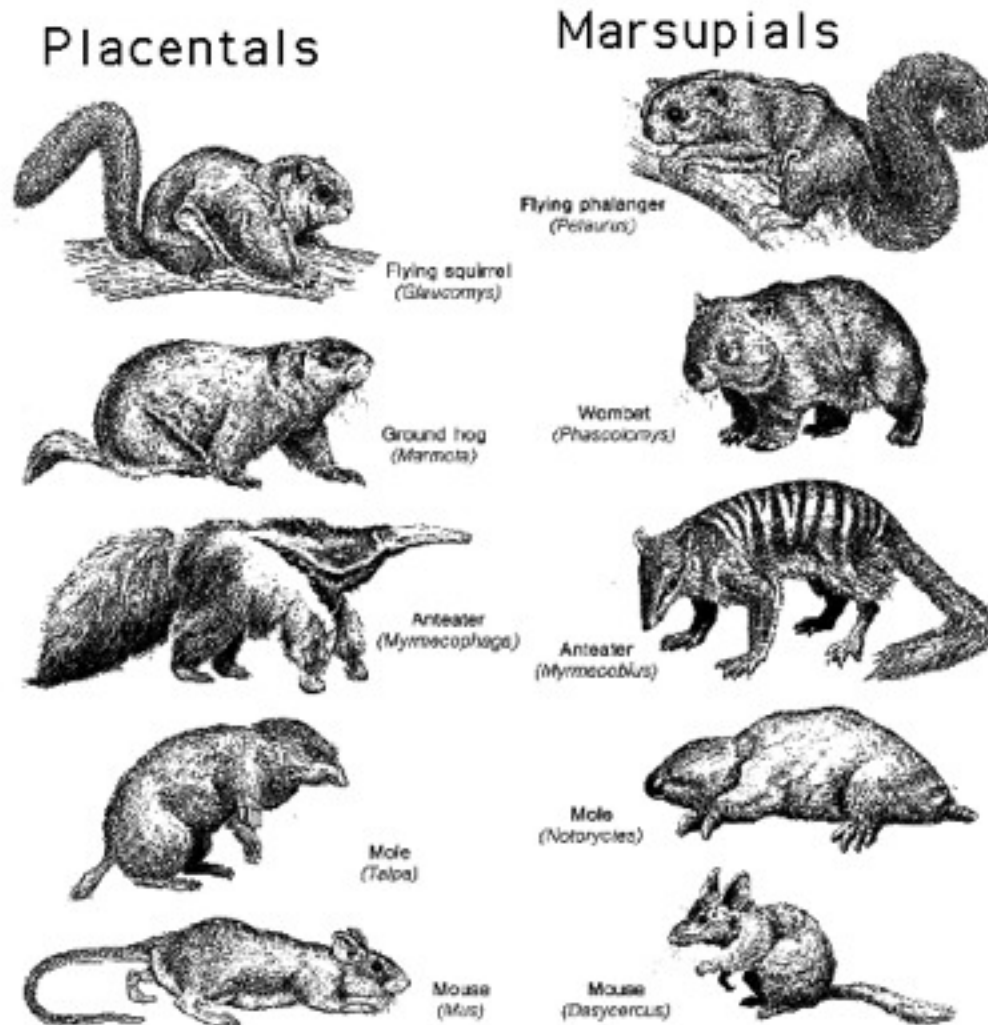


# Convergent Evolution

1. Traits can be shared among species because they have a common ancestor.
  - a. All birds have feathers because they have the same common ancestor that had feathers.
2. Traits can be shared among species that are not closely related due to convergent evolution.
  - a. Bats, birds, and pterodactyls all have wings. But wings independently evolved in all of these groups.
3. Convergent evolution: Similarity between species is caused by a similar, but evolutionarily independent, response to a common environmental problem.
4. Allows tests of the conditions that cause traits to evolve because evolution has been replicated.

# Convergent Evolution

1. Many mammals and marsupials have independently converged on similar morphologies due to similar ecologies.



# Crypsis/Camouflage







# Aposematic Coloration

1. Darwin realized that sexual selection could not explain the bright coloring of some caterpillars since they were not sexually active.
2. Alfred Wallace suggested that as the contrasting colored bands of a hornet warned of its defensive sting, so could the bright colors of the caterpillar warn of its unpalatability.
3. Aposematism: an antipredator adaptation in which a warning signal is associated with the unprofitability of a prey item to potential predators. Warning coloration.
2. Aposematic signals are beneficial for both the predator and prey, who both avoid potential harm.
5. These signals evolve to become more conspicuous. Opposite of crypsis.

# Convergent Evolution of Bright, Aposematic Coloration

1. Monarchs ingest milkweed toxins as larvae. These compounds make birds vomit.
2. Coral Snakes have deadly venom (same family as cobras).
3. Bees and Wasps have bright black and yellow abdomens. Warnings of their sting.
4. Newts possess tetrodotoxin that is deadly poisonous.



# How does Aposematism Evolve?

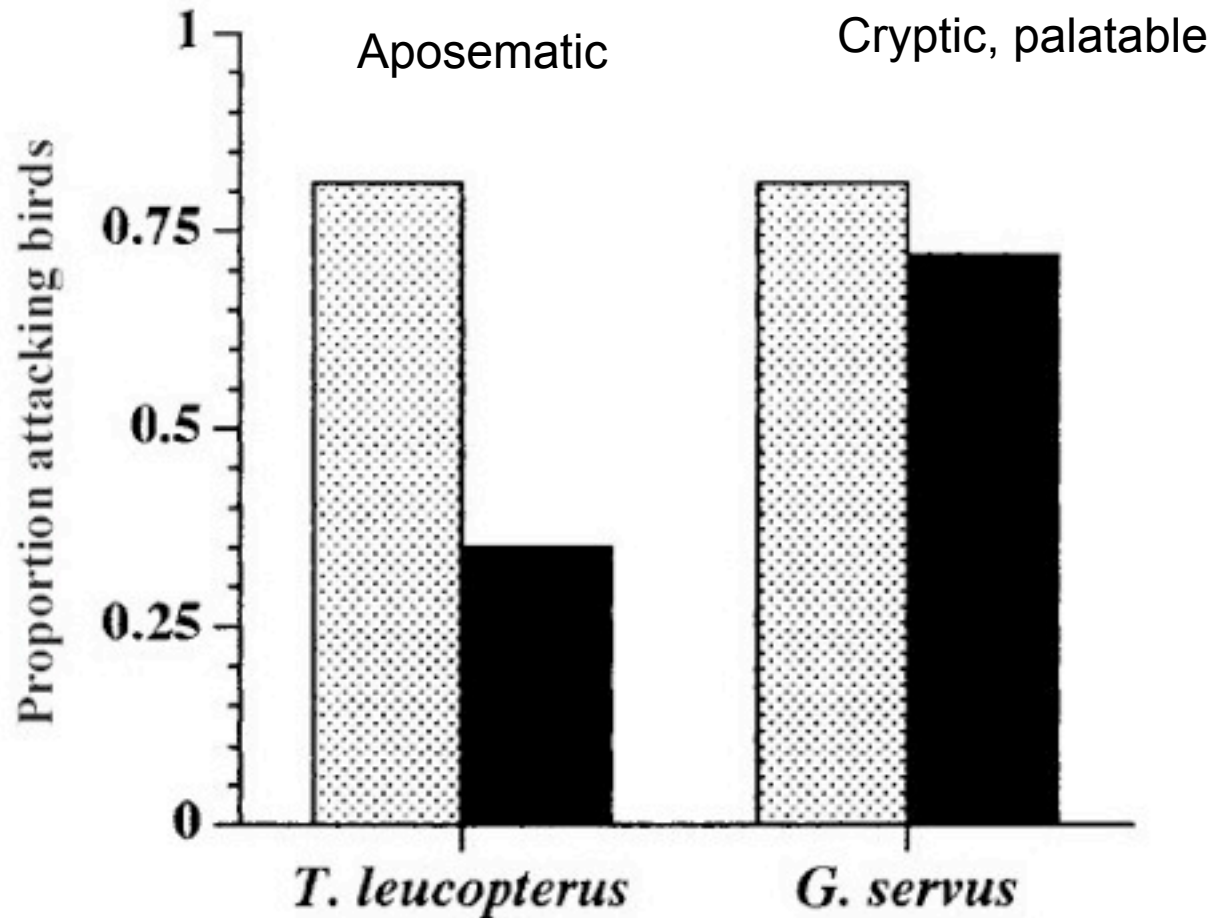
1. Imagine a population of unpalatable, but cryptic larvae.
2. A mutation makes a larva more conspicuous. Makes it more obvious to predators and more likely to perish.
3. Predator may now avoid the conspicuous larvae, but they are rare so the predator will never encounter another such larva. Mutation goes extinct during the sampling by the predator.
4. Fisher's solution: Distasteful, brightly colored insects often occur in family groups. In this situation, if one larva is sampled its nearby kin will be saved.

# Testing Benefits of Being in a group

1. Experiment by Gamberale and Tullberg, 1998.
2. Tested how naive chicks respond to solitary or grouped prey of two types.
  - a. Aposematic, distasteful prey
  - b. Cryptic, palatable prey
2. Prey were the larvae of two different bug species.

# Testing Fisher's Model

Being in a group reduces attack rates of aposematic prey.  
(Gamberale and Tullberg, 1998).



Grey = solitary  
Black = grouped

# Testing Fisher's Model

1. Fisher's model assumes that kin groups evolve first, which then allows the evolution of warning colors.
2. Sillen-Tullberg (1988) analyzed independent origins of warning colors and of larval groupings.
3. Warning coloration evolves before groupings. This is opposite expectation from Fisher's model.
4. Possible solution: Bright colors may give direct advantages. If some insects are released unharmed, then bright colors may result in fewer subsequent attacks from the same predator. (Sillen-Tullberg, 1985).
5. Thus, aposematism may be able to evolve due to direct benefits. Grouping evolves afterwards to reinforce predator learning.





# Mimicry

Coral Snake



California Mountain King Snake



# Batesian Mimicry

1. Henry Walter Bates (1852)
2. Three-player system
  - a. Model: noxious/dangerous prey
  - b. Mimic: palatable prey
  - c. Predator: the signal-receiver
3. Model uses aposematic coloration as a warning of its defenses or unpalatability to predators.
  - a. Honest signal
4. A Batesian mimic gains protection by convergence upon the aposematic signal of the model.
  - a. Dishonest signal

# Batesian Mimicry

5. Selection favors the mimic when it is less common than the model species. Fitness is negatively frequency-dependent.
6. Model species experiences increased mortality as the number of mimics in the system increase.
  - a. Due to predators relaxing the association of the aposematic signal with a secondary defense.
7. If mimics become common, the system is unstable and selection promotes signal divergence between model and mimic.

# Batesian Mimicry

Coloration of the model changes over time, mimics selected to keep up.



Model species on left, mimic species on right, from Greene, 1981

# Batesian Mimicry by *Ensatina*

1. Prediction: A Batesian mimic should gain protection from predators by resembling the model.

Mimic = Yellow-eyed *Ensatina*

Model = Pacific Newt

A *Ensatina eschscholtzii xanthoptica*



B *Taricha torosa*



C *E. e. xanthoptica* & *T. torosa*



D *E. e. oregonensis*



Not Mimic = *E. e oregonensis*

# Batesian Mimicry by *Ensatina*

1. Test: Compare predation rates between Batesian mimics and closely related species that do not mimic.
2. Kuchta (2005) deployed clay salamander replicas in the field and recorded attack rates.
3. Models with yellow and orange aposematic colors were depredated less than models lacking the colors.
4. Suggests that *E. e. xanthoptica* benefits from aposematic coloration.

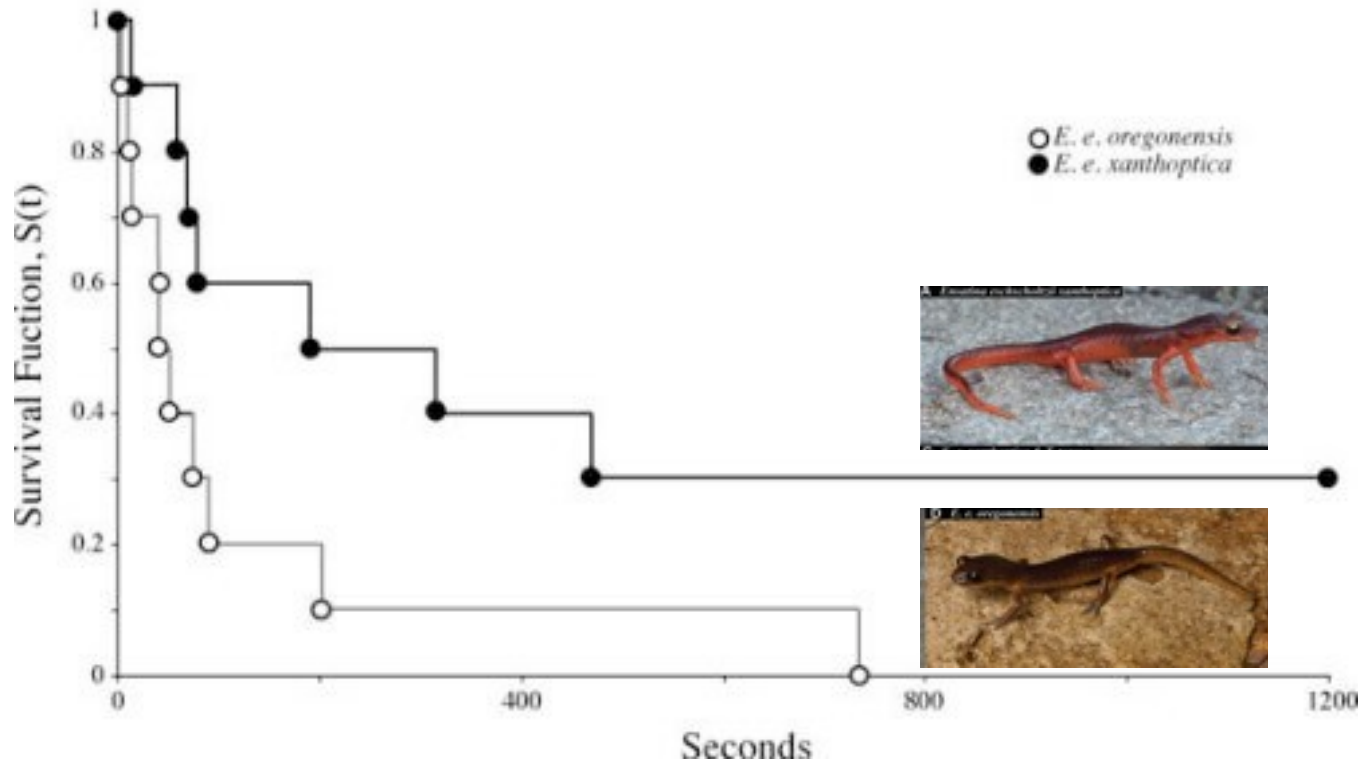


## Batesian Mimicry by *Ensatina*

1. Kuchta *et al*, 2008 conducted feeding trials using Western Scrub-Jays.
2. Jays were first presented with the model (newt). Then presented with either the presumed mimic (*E. e. xanthoptica*) or a control subspecies lacking the postulated aposematic colors (*E. e. oregonensis*).
3. No newts were eaten. Some *Ensatina* salamanders were eaten.
4. The median time to contact was 315 sec for the mimic and 52 sec for the control.
5. Mimicking the newts confers protection from a bird predator.

# Batesian Mimicry by *Ensatina*

Mimic (black line) is more likely to survive than a salamander lacking coloration similar to the toxic newts.





# Mullerian Mimicry



*Heliconius erato* on the left  
*H. melpomene* on the right.

# Mullerian Mimicry

1. Proposed by Fritz Muller (1878) to explain why unrelated distasteful butterfly species share a single warning color.
2. Mullerian mimics share aposematic signals due to the mutual benefit of spreading the selective burden of educating predators that they are distasteful.
3. In this case, signals are standardized and the predator avoids all models.
4. Mullerian mimics give honest signals.

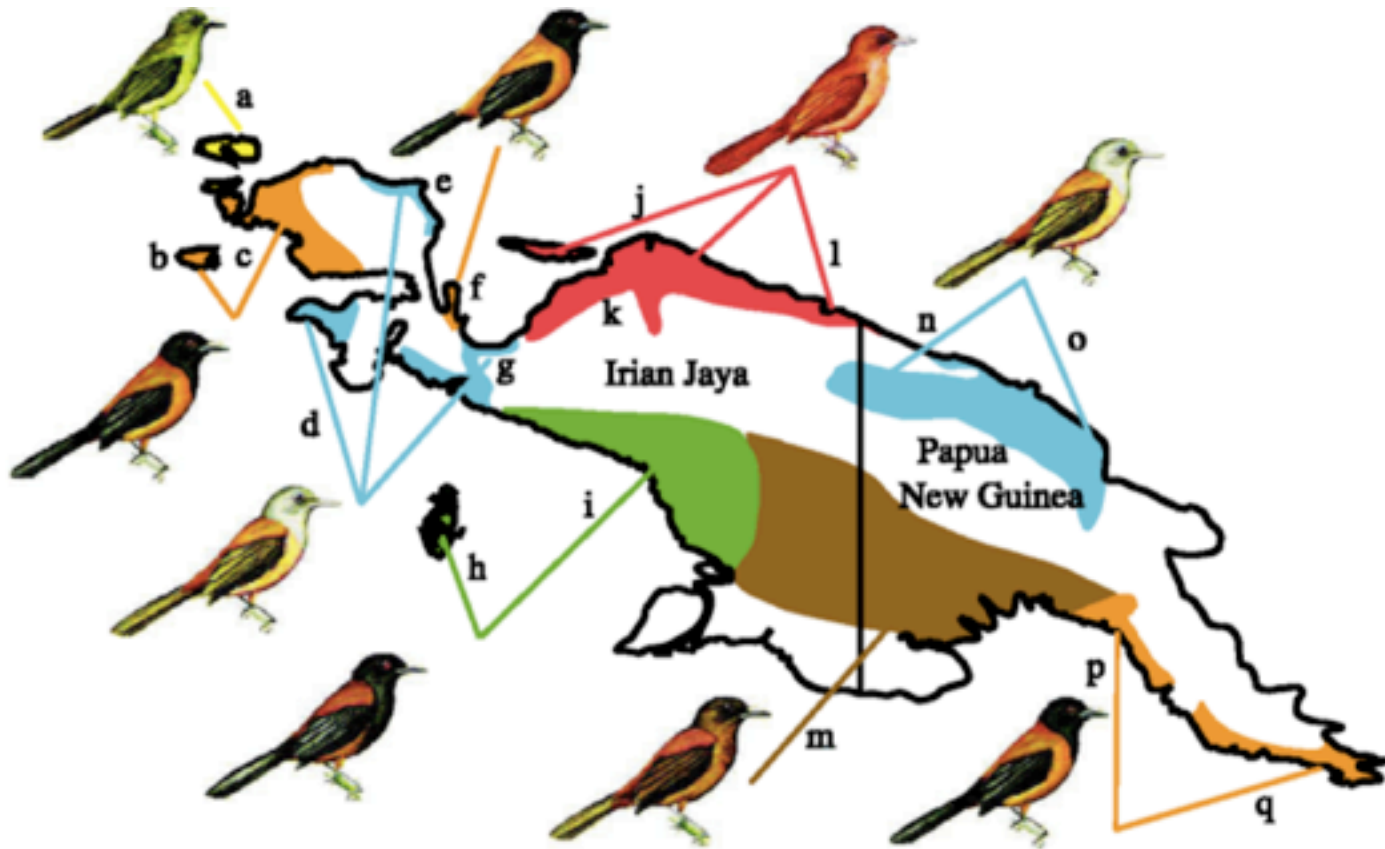
# The Poisonous Pitohuis

Top = Hooded Pitohuis, *Pitohui dichrous*



Bottom = Variable Pitohui, *P. kirhocephalus*

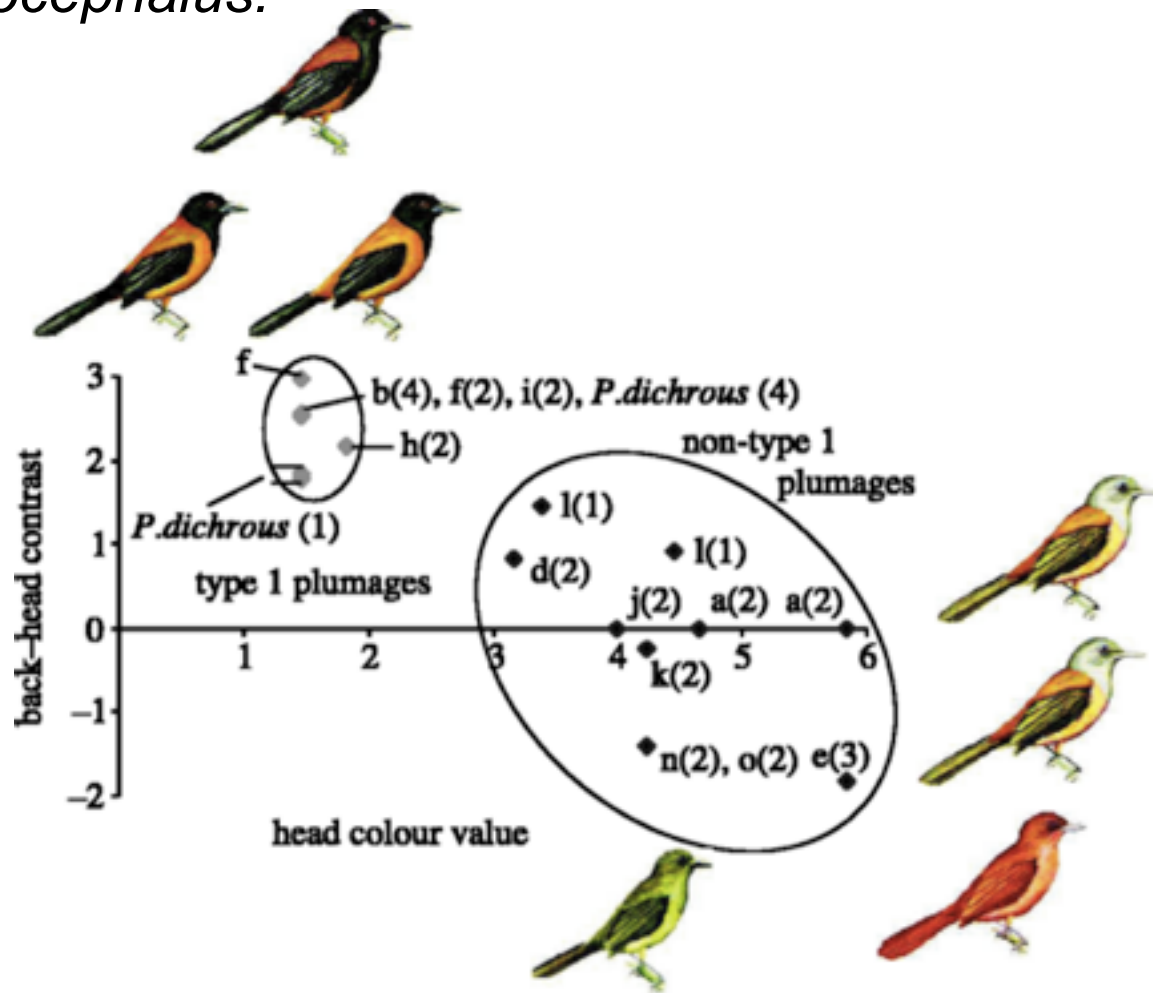
# Mullerian Mimicry in Pitohui Coloration?



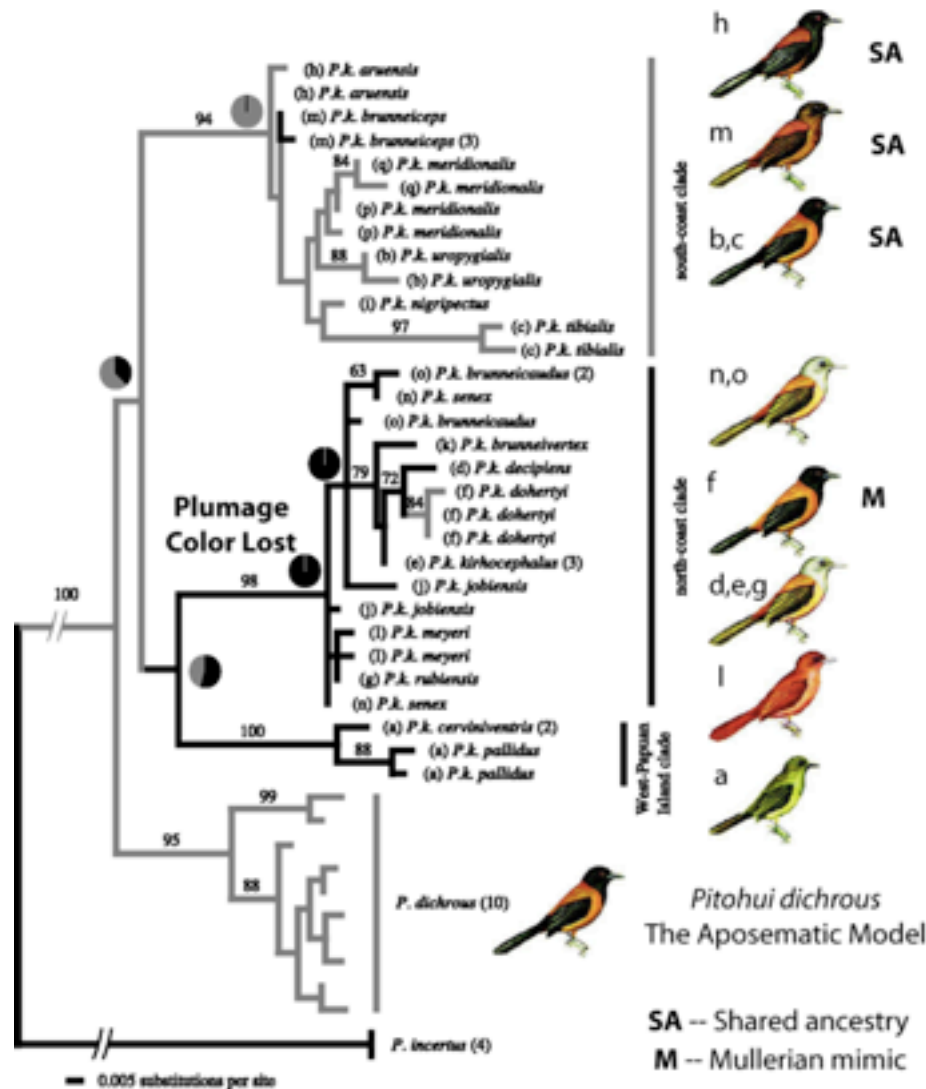
1. Hypothesis 1: Different populations share coloration because of common ancestry.
2. Hypothesis 2: Different populations share coloration because of convergent evolution leading to Mullerian mimicry.

# Testing Mullerian Mimicry

Test 1: Verified that there was resemblance among *P. dichrous* and *P. kirhocephalus*.



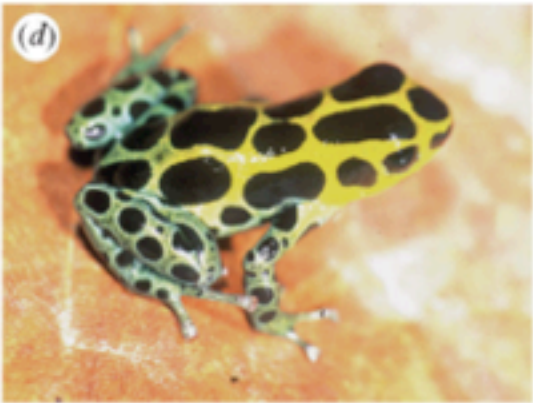
# Evolution of Pitohui Coloration



**Test 2: Phylogenetic reconstruction.** Shows one example of Mullerian mimicry through convergence, but shared ancestry explains most populations.

# Mullerian Mimicry in Poison Frogs?

*Dendrobates imitator*

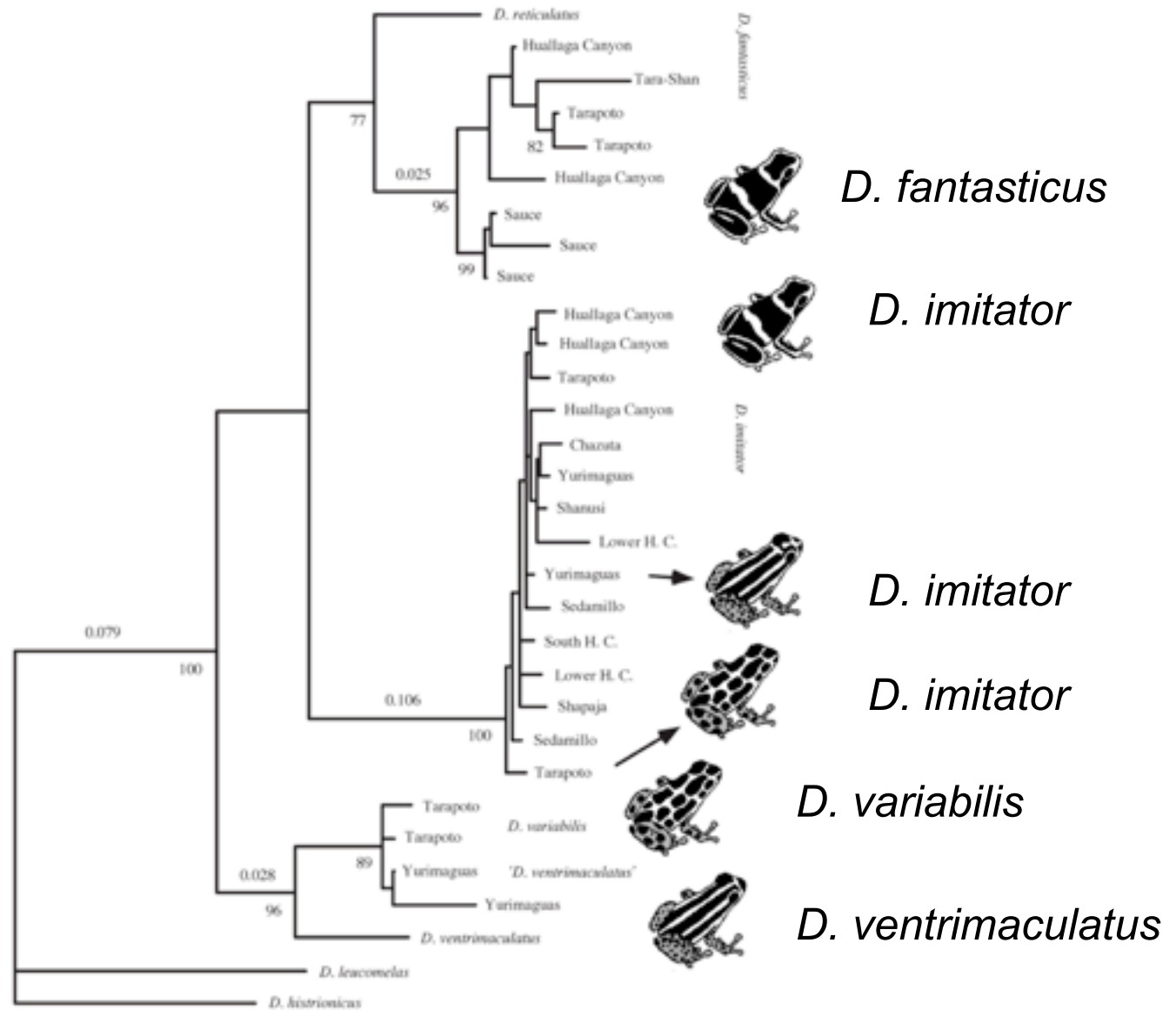


*Dendrobates variabilis*

*Dendrobates fantasticus*

*Dendrobates ventrimaculatus*

# Evolution of Poison Frog Coloration



Phylogenetic reconstruction is consistent with *Dendrobates imitator* being a Mullerian mimic.



# Mini Review

1. Name some examples of non-adaptive traits and behaviors.
2. Name some examples of adaptive traits and behaviors.
3. Possible test question: Give an example of a non-adaptive behavior and explain the evidence that supports that conclusion.



# **More on non-adaptive behavior**

1. We will cover the following material if there is time.

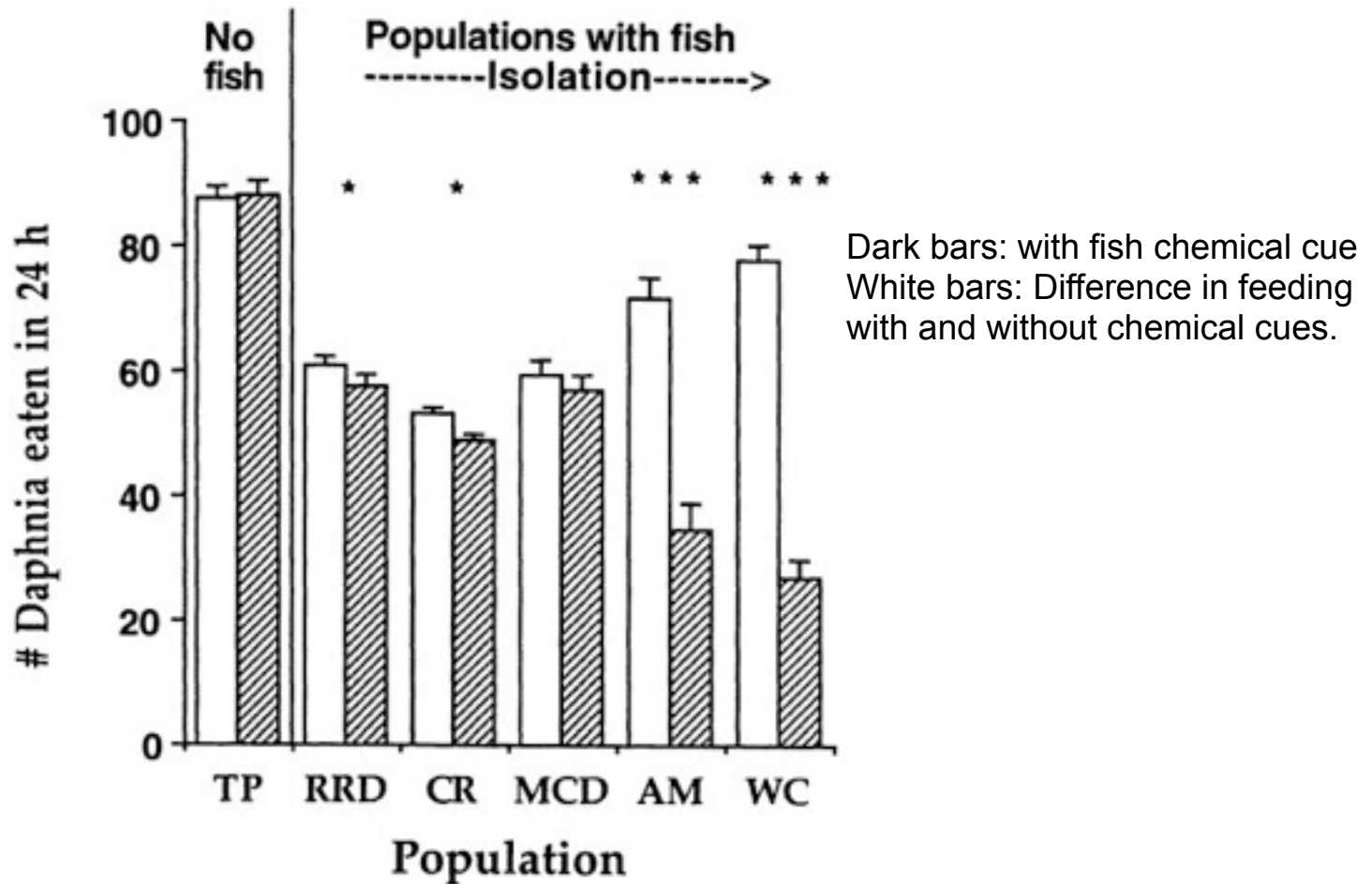
# Migration and adaptation

1. Migration (gene flow) = movement of alleles between populations.
2. Migration and selection can oppose one another.
  - a. Low migration: selection is strong enough to remove non-adaptive alleles from other populations.
  - b. High migration: selection can be overwhelmed by alleles from other populations.
5. Migration can limit local adaptation.

# Gene flow and ineffective anti-predator behavior

1. Work by Storfer and Sih, 1998 on a salamander, *Ambystoma barbouri*.
2. Different habitats have different selection pressures:
  - a. No sunfish predators: selection should favor active larvae. Need to maximize feeding rate to metamorphose before the stream dries out.
  - b. With predators: selection should favor larvae that are inactive to avoid predation.
4. Migration between habitats may limit adaptation.

# Feeding behavior in presence/absence of predators

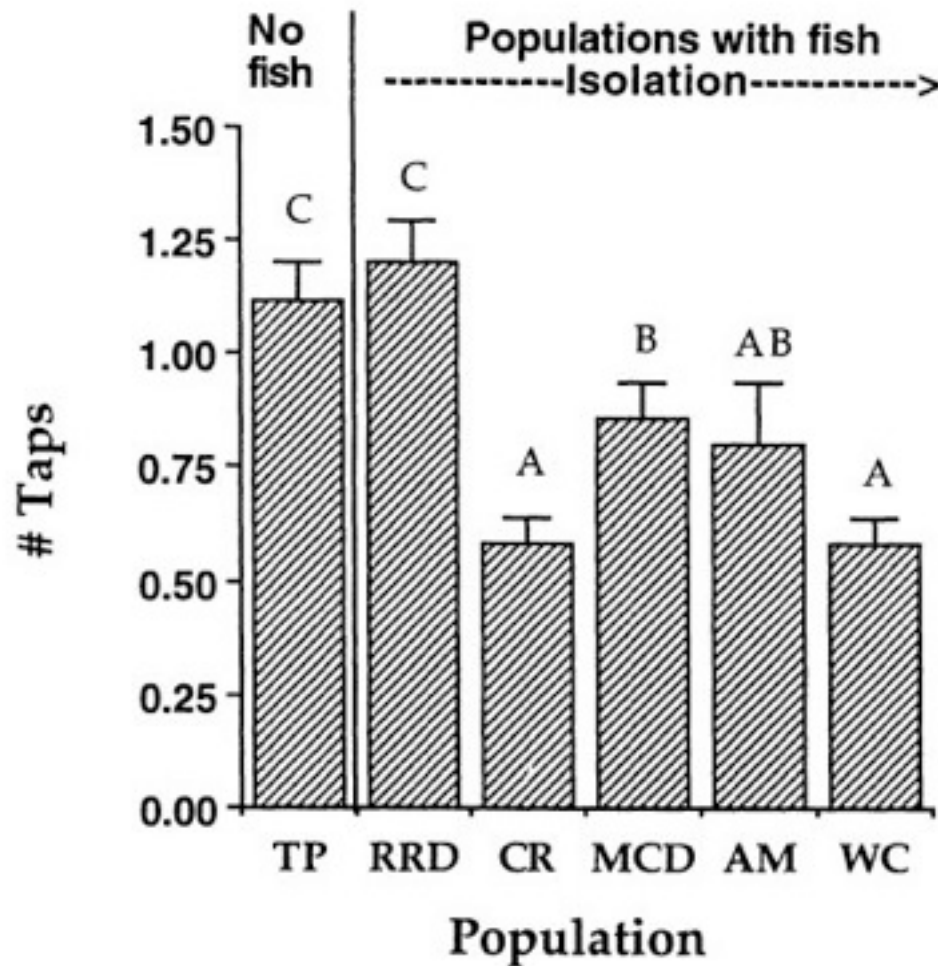


No fish: Salamanders are more active

Isolated, with fish: adjust activity based on predator cues.

Not isolated, with fish: less active, do not plastically adjust activity.

# Escape behavior in salamanders

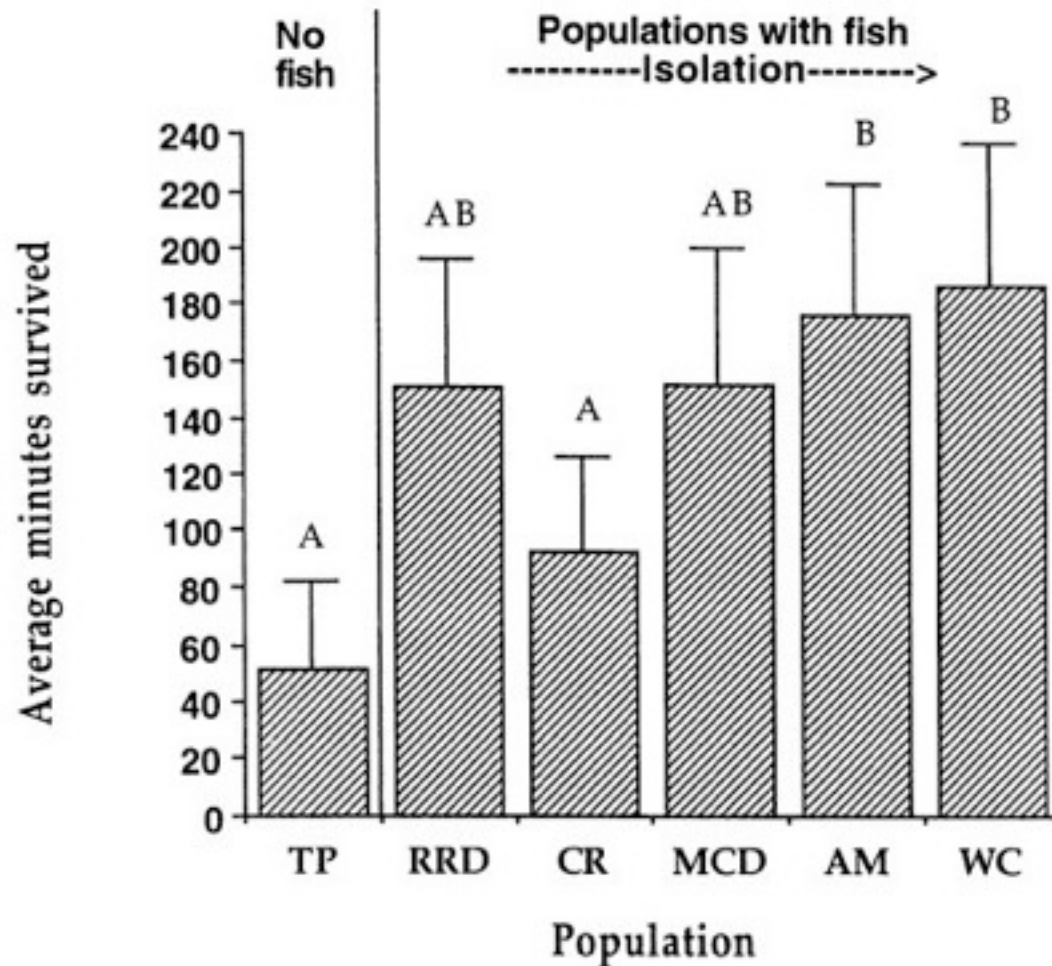


No fish: Slow response

Isolated, with fish: Fast response.

Not isolated, with fish: Slow response = non-adaptive.

# Salamander survival in presence of fish



No fish: Eaten fast! Low survival.

Isolated, with fish: High survival

Not isolated, with fish: Intermediate survival.