

# Coevolution of predators and prey

- 1) Evolution of predator-prey interactions
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- 3) Examples of predator-prey coevolution?
- 4) Steady-state theory
- 5) Geographic variation in predator-prey coevolution
- 6) Evolution of aposematic coloration
- 7) Example exam questions

# 1) Evolution of predator-prey interactions

## Definitions

**Predation:** One species kills and consumes members of another species

(Host-parasite coevolution will be dealt with separately)

**Coevolution (strictly):** Reciprocal evolutionary change of interacting species

# 1) Evolution of predator-prey interactions

Camouflage of prey; visual acuity of predators

Prey escape speed; predator pursuit speed

Flocking and herding in prey; predator strategies to isolate individuals

Prey toxicity, aposematic coloration; predator resistance

Hard seed coats; large beaks

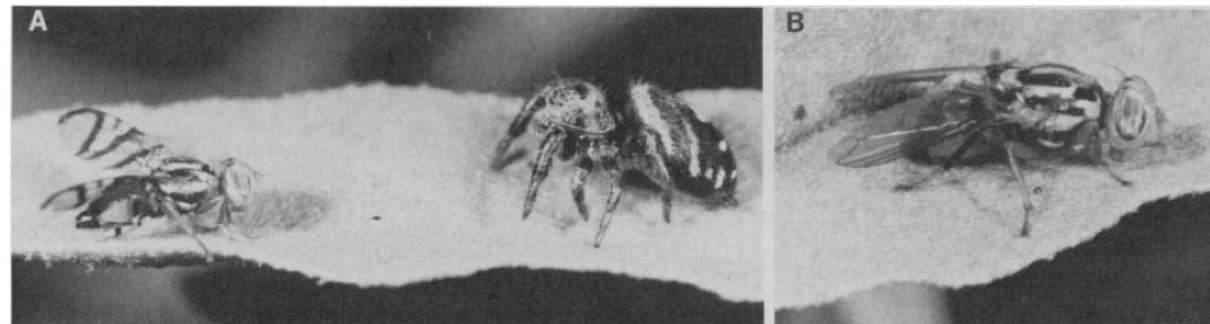
Prey mimicry; ?

# 1) Evolution of predator-prey interactions

## A Tephritid Fly Mimics the Territorial Displays of Its Jumping Spider Predators

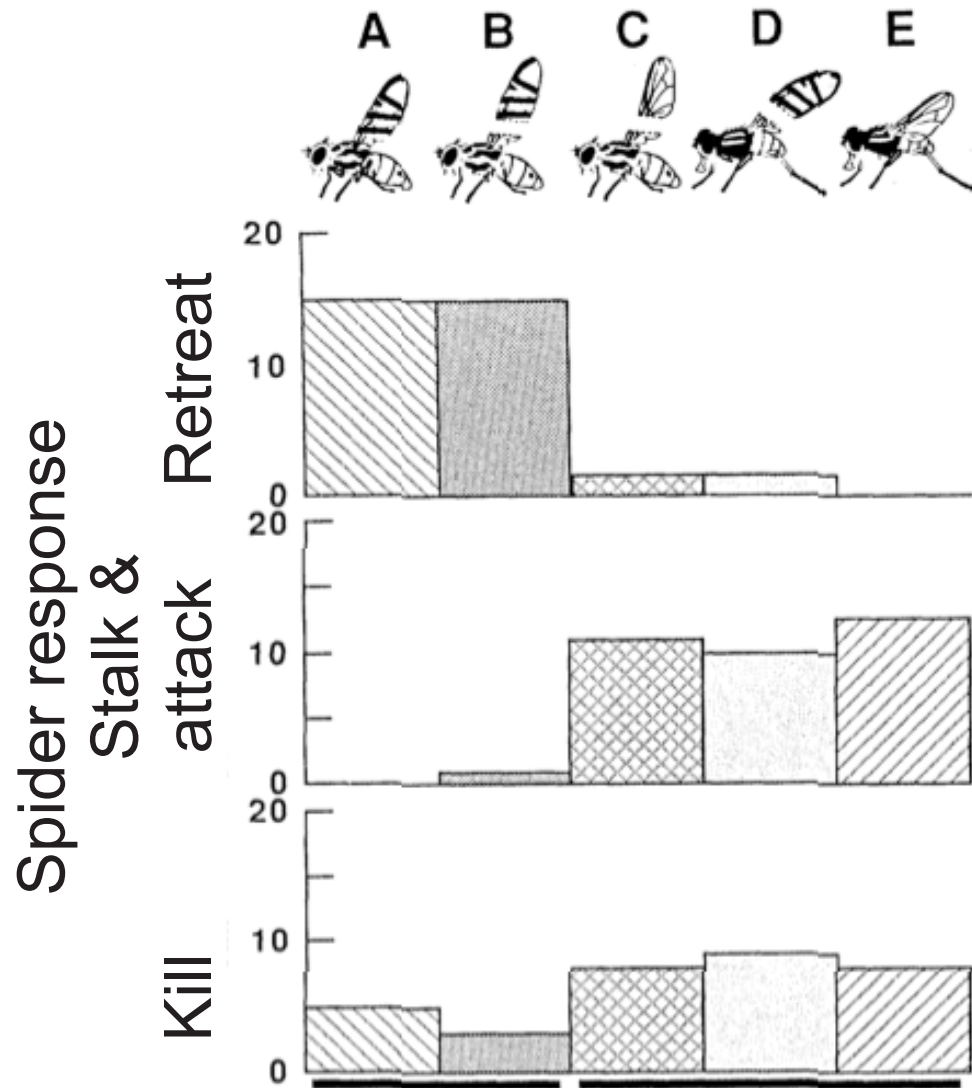
ERICK GREENE, LARRY J. ORSAK, DOUGLAS W. WHITMAN

The tephritid fly *Zonosemata vittigera* (Coquillett) has a leg-like pattern on its wings and a wing-waving display that together mimic the agonistic territorial displays of jumping spiders (Salticidae). *Zonosemata* flies initiate this display when stalked by jumping spiders, causing the spiders to display back and retreat. Wing transplant experiments showed that both the wing pattern and wing-waving displays are necessary for effective mimicry: *Zonosemata* flies with transplanted house fly wings and house flies with transplanted *Zonosemata* wings were attacked by jumping spiders. Similar experiments showed that this mimicry does not protect *Zonosemata* against nonsalticid predators. This is a novel form of sign stimulus mimicry that may occur more generally.



**Fig. 1.** (A) A female *Zonosemata vittigera* beginning its wing-waving display toward a stalking jumping spider (*Phidippus apacheanus*). The jumping spider stopped stalking, waved its legs at the fly, and then retreated. (B) A *Zonosemata vittigera* fly with transplanted house fly wings. Such flies can display normally and fly.

# 1) Evolution of predator-prey interactions



**Fig. 2.** Behavioral responses of jumping spiders to fly presentations. The response is the highest level of aggression attained during 5 minutes of behavioral interaction in a test arena. The fly treatments are: A, normal *Zonosemata*; B, *Zonosemata* with *Zonosemata* wings glued on (control for the operation); C, *Zonosemata* with house fly wings; D, house fly with *Zonosemata* wings; and E, normal house fly. Sample sizes are 20 for each fly treatment. The bars connect homogeneous groups (G tests,  $P$ 's > 0.1). All other combinations are heterogeneous (all  $P$ 's < 0.01).



## 2) Arms race analogy

“The five fastest runners among mammal species are the cheetah, the pronghorn ..., the gnu ..., the lion, and the Thompsons’s gazelle. Note that these top-ranked runners are a mixture of hunted and hunters, and my point is that this is no accident”

- Dawkins (2009; *The greatest show on earth*)

## 2) Arms race analogy

Is the analogy apt?

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### Arms races between and within species

BY R. DAWKINS AND J. R. KREBS

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An adaptation in one lineage (e.g. predators) may change the selection pressure on another lineage (e.g. prey), giving rise to a counter-adaptation. If this occurs reciprocally, an unstable runaway escalation or ‘arms race’ may result.

### 3) Examples of predator-prey coevolution?

Running speed of carnivores and herbivores through the fossil record

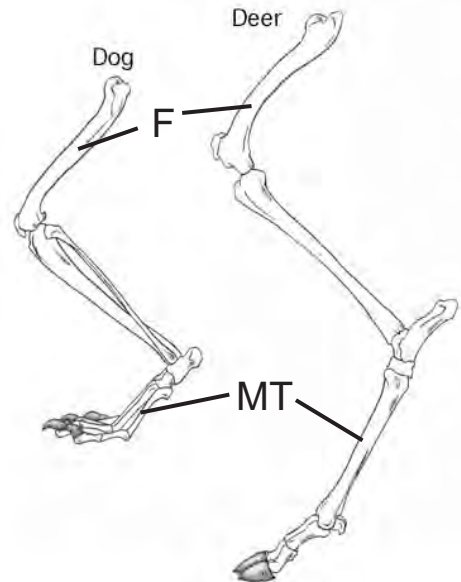
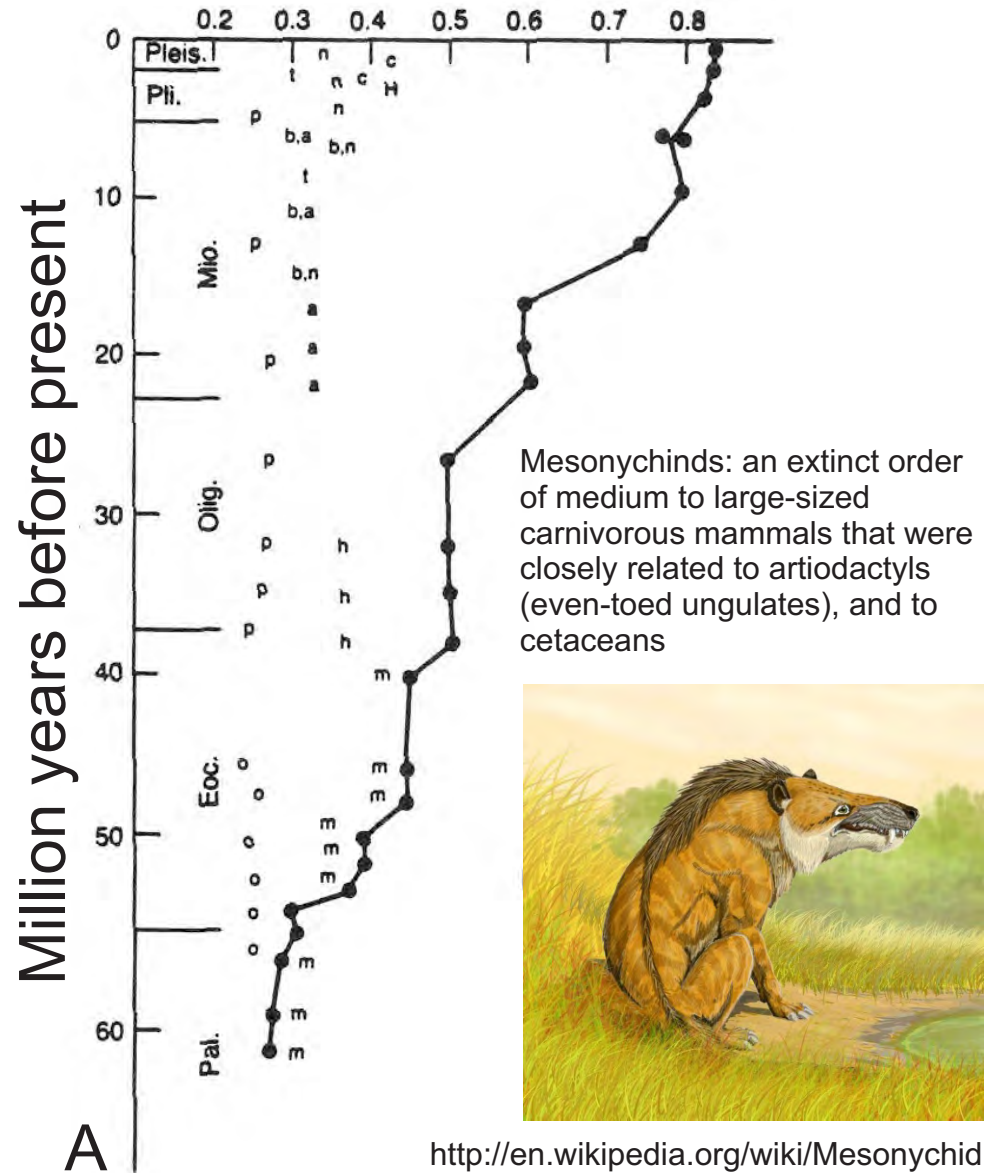


FIGURE 7

Indices of running speeds of North American carnivores and ungulates throughout the Cenozoic. The horizontal axis in A is the ratio of the length of the metatarsus (MT) to the femur (F); in B it is the ratio of the depth (D) to the width (W) of the groove on the astragalus. Both indices are greater in rapidly running than in slow mammals. In each graph, the solid line connects the mean values for all species of ungulates in paleontological faunas: both indices increased, indicating that later ungulates were swifter than earlier forms. Each letter represents the mean value for a particular group of carnivorous mammals at that time. Within most carnivorous taxa (e.g., paleofelids, *p*), there was little if any evolution of greater speed. The data suggest that coevolution between predators and their prey did not occur, at least with respect to speed. (Abbreviations for the predators are: *m*, mesonychid; *o*, oxyaenid; *p*, paleofelid; *h*, hyaenodontid; *a*, amphicyonid; *n*, neofelid; *b*, borophagine; *c*, canine; *H*, hyaenid; and *t*, *Thylacinus*, the Tasmanian wolf, a marsupial given for comparison with North American fauna.) (From Bakker 1983)





### 3) Examples of predator-prey coevolution?

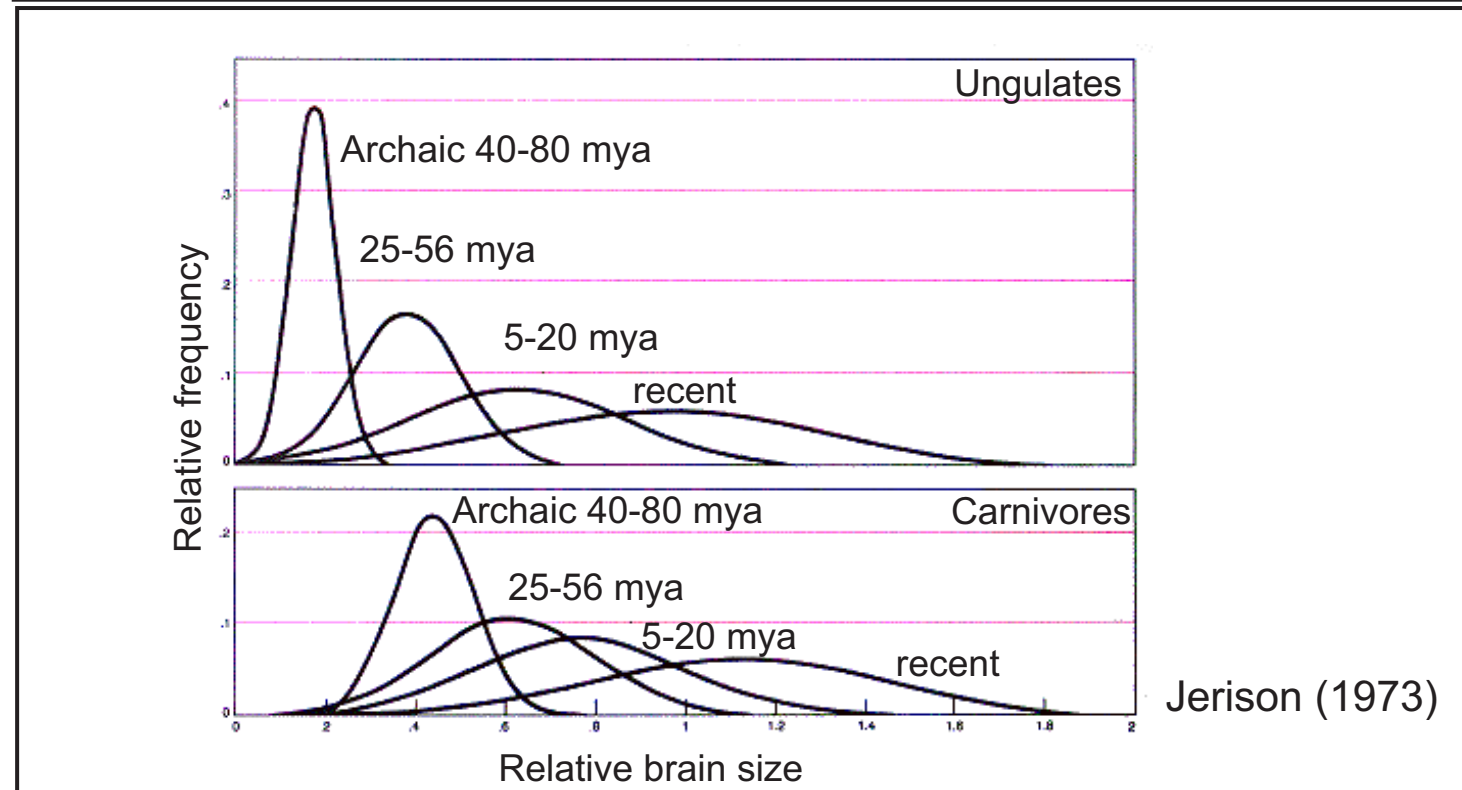
Relative brain sizes of carnivores and herbivores through the fossil record

$EQ = (\text{brain mass})/k(\text{body mass})^{0.66}$

TABLE 7. Evolution of relative brain size (after Jerison 1973). Means with sample size in brackets.

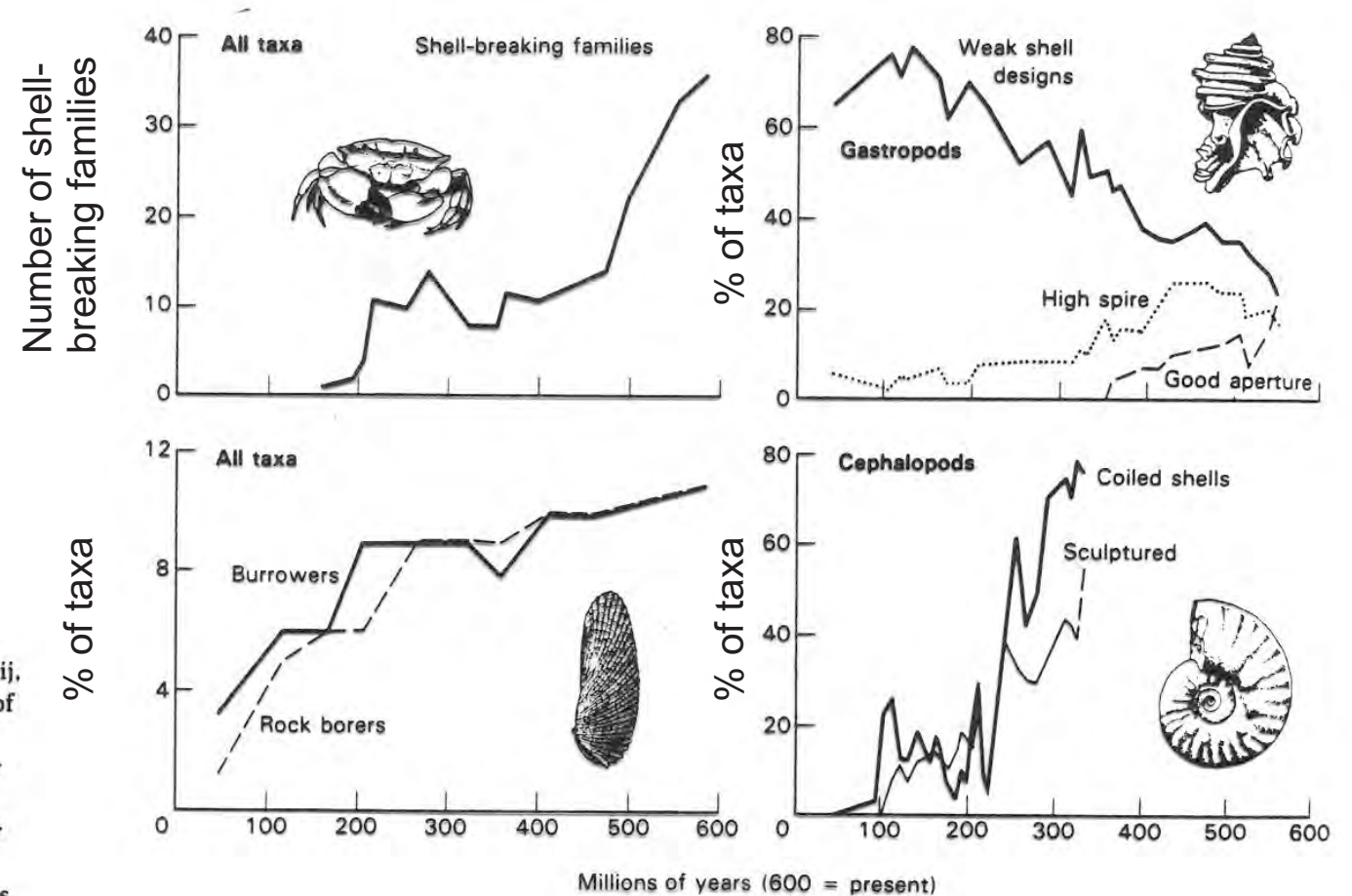
	Ungulates	Carnivores	
Archaic	0.18 (13)	0.48 (5)	Creodonta (lived 35-55 mya) Carnivora
28-70 mya Palaeogene	0.38 (26)	0.61 (11)	
4-28 mya Neogene	0.63 (13)	0.76 (6)	..
< 3 mya Recent	0.95 (25)	1.10 (15)	..

Savage (1977)



### 3) Examples of predator-prey coevolution?

#### Escalation of predators and prey through the fossil record



*Fig. 6.10* Diffuse coevolution of predators and prey in the fossil record (data from Vermeij, 1987). Except for number of shell-breaking families, the vertical axes are the percentage of taxa with the noted traits. High-spired gastropod shells are more difficult to break. Gastropods with good apertures are those where the aperture is internally thickened or narrowed, both excellent defences against predators. Tightly coiled and sculptured cephalopod shells are also excellent defences against predation. Note how as the number of shell-breaking families increased, the fraction of taxa that burrow in soft or hard substrates increases, the fraction of taxa with predation-resistant shell designs increases, and the fraction of taxa (gastropods) with weak shell designs (umbilicate or loosely coiled) declines. The frequency of damaged and drilled shells has also increased in time (not shown).

## 4) Steady-state theory of predator-prey coevolution

Alternative to the arms race model (Abrams 1986)

Based on the assumption that adaptation by predators and by prey entails significant costs (not an explicit component of the arms race model).

Also incorporates effects that predators might have on the numerical abundance of prey (and hence their encounter rate by predators).

Main prediction: a steady state (evolutionary equilibrium) is reached in which costs and benefits are balanced in both the predator and the prey.

This is distinct from the continuous escalation that is presumed to occur under the arms race scenario.

Which idea is more realistic?

## 4) Steady-state theory of predator-prey coevolution

Abrams took the theoretical inquiry one step further, to investigate whether his cost/benefit type of model might predict outcomes consistent with an arms race:

Q1. Once a steady state (evolutionary equilibrium) is reached, what is the predicted outcome in the prey population if we allow the predator to evolve an even greater investment in catching prey (in theory)?

## 4) Steady-state theory of predator-prey coevolution

Abrams took the theoretical inquiry one step further, to investigate whether his cost/benefit type of model might predict outcomes consistent with an arms race:

Q1. Once a steady state (evolutionary equilibrium) is reached, what is the predicted outcome in the prey population if we allow the predator to evolve an even greater investment in catching prey?

A1: Under most of the theoretical conditions explored, the model predicted that prey should respond by evolving a greater investment in evading predators.

This is what we would expect under an arms race.

## 4) Steady-state theory of predator-prey coevolution

Q2. Once a steady state (evolutionary equilibrium) is reached, what is the predicted outcome in the predator population if we allow the prey to evolve an even greater investment in evading capture?

## 4) Steady-state theory of predator-prey coevolution

Q2. Once a steady state (evolutionary equilibrium) is reached, what is the predicted outcome in the predator population if we allow the prey to evolve an even greater investment in evading capture?

A2: The model did not always predict that predators should respond by evolving a greater investment in capturing prey.

This is not what an arms race would predict.

## 4) Steady-state theory of predator-prey coevolution

Why not?

One reason is that evolution of greater investment by prey might lead to an increase in prey abundance, diminishing selection for greater investment by predators.

Abrams argues that the arms race analogy fails to take such features as population size into account, and therefore is not a satisfactory model for predator-prey coevolution.



## 4) Steady-state theory of predator-prey coevolution

It is challenging to think of observations or experiments that could distinguish explanations based on an arms race vs steady-state coevolution.

A prediction of the Abrams model is that the outcome of predator-prey coevolution should vary with the costs and benefits of adaptations and counter-adaptations.

I'm not aware of a convincing test of this prediction in the literature.

## 5) Geographic variation in predator-prey coevolution

### Rough-skinned newt & garter snake

Rough-skinned newts, like pufferfish, contain tetrodotoxin (TTX).

TTX is synthesized by at least 4 different genera of bacteria of the newt's skin microbiome.  
(wash your hands after you play with them!)

TTX binds to sodium channels and prevents transmission between neurons, causing paralysis.

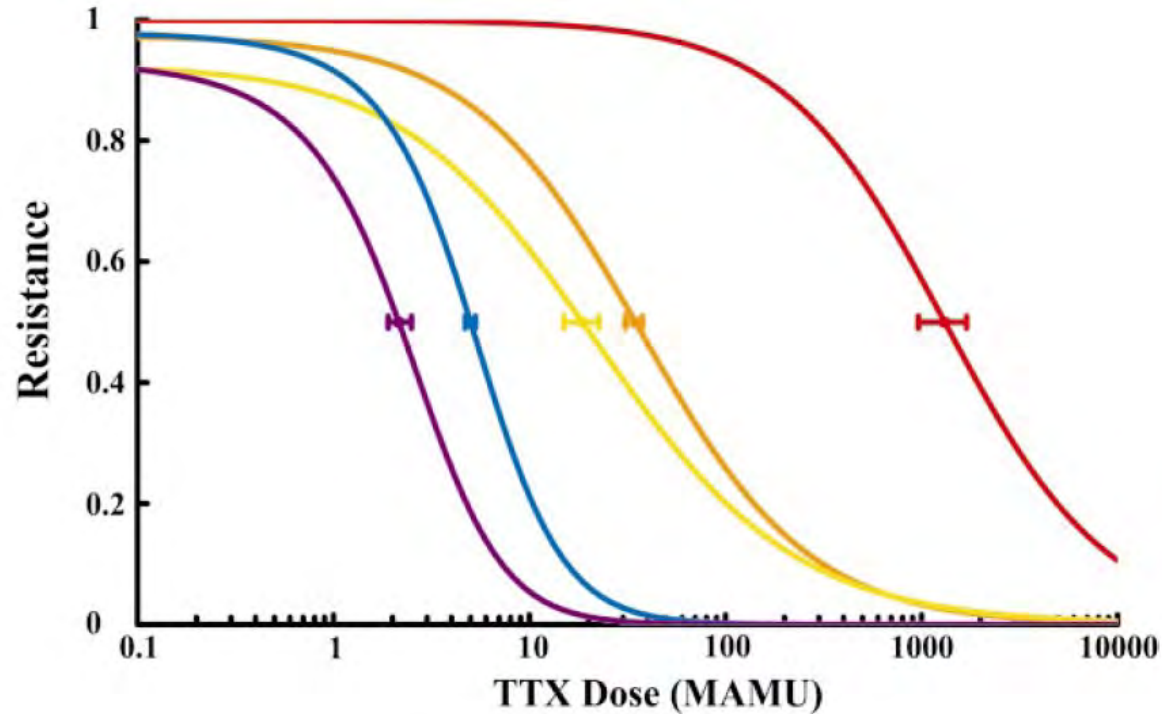
Newts have multiple mutations in binding sites of sodium channel genes that protect them against TTX.

Garter snakes eat newts.



## 5) Geographic variation in predator-prey coevolution

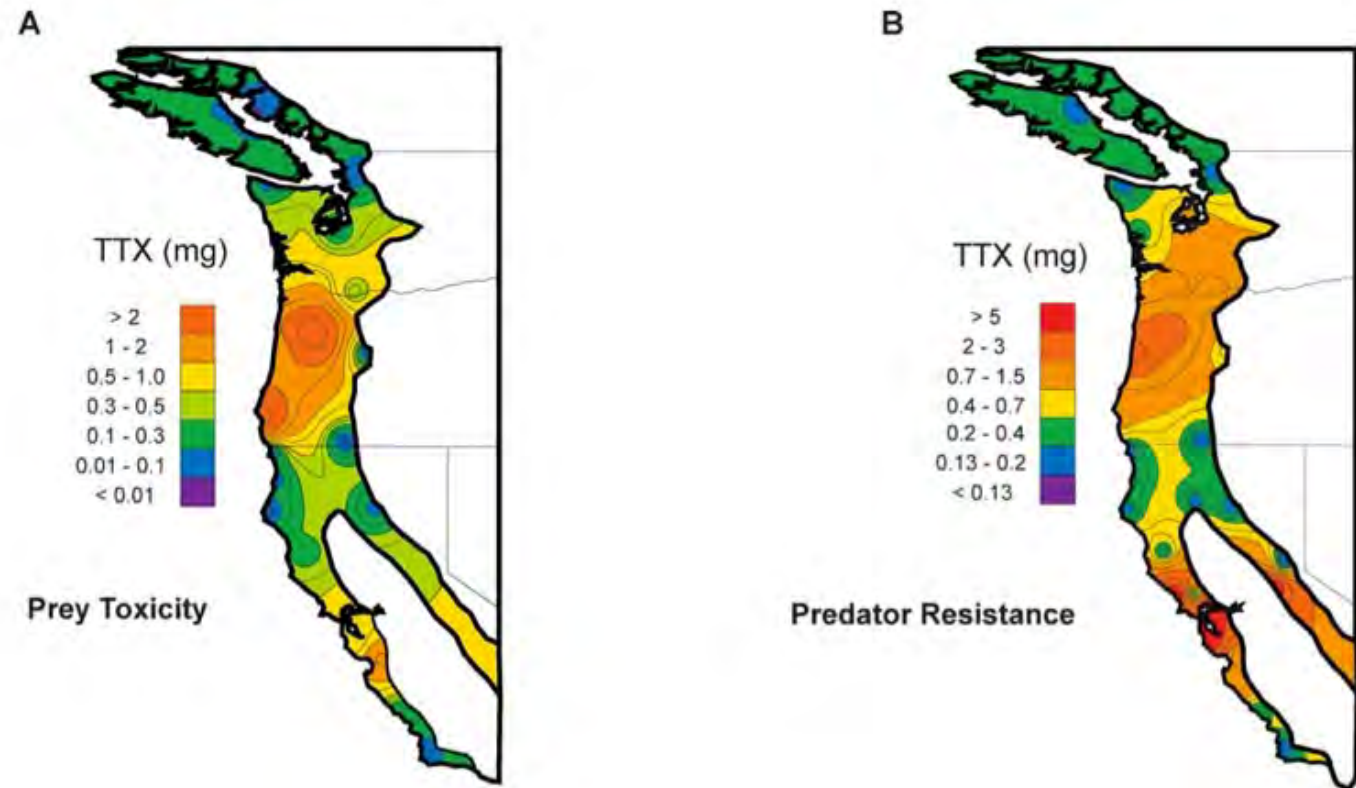
### Population variation in garter snake resistance to tetrodotoxin



The dose of CI required to reduce crawl speed to 50% is shown with 95% confidence interval. Representative dose-response curves and estimated 50% doses (with 95% TTX) are shown for five representative garter snake populations (from left to right: Lofton Lake, Inland Lake, Gilroy, Benton, San Mateo).

## 5) Geographic variation in predator-prey coevolution

Correlated geographic variation in newt toxicity and garter snake resistance



**Figure 2.** The Interpolated Geographic Distribution of Phenotypes and Phenotypic matching for Newts and Snakes in Western North America

The interpolated geographic distribution of (A) prey toxicity, (B) predator resistance, and (C) the degree of phenotypic matching of these traits shown as isocline maps across the geographic range of sympatry in western North America.

(A) Toxicity of prey shown as the total amount of tetrodotoxin (TTX) (mg) expected in the skin of an average adult animal based on the toxicity of 28 populations of *Taricha* newts in Figure 1.

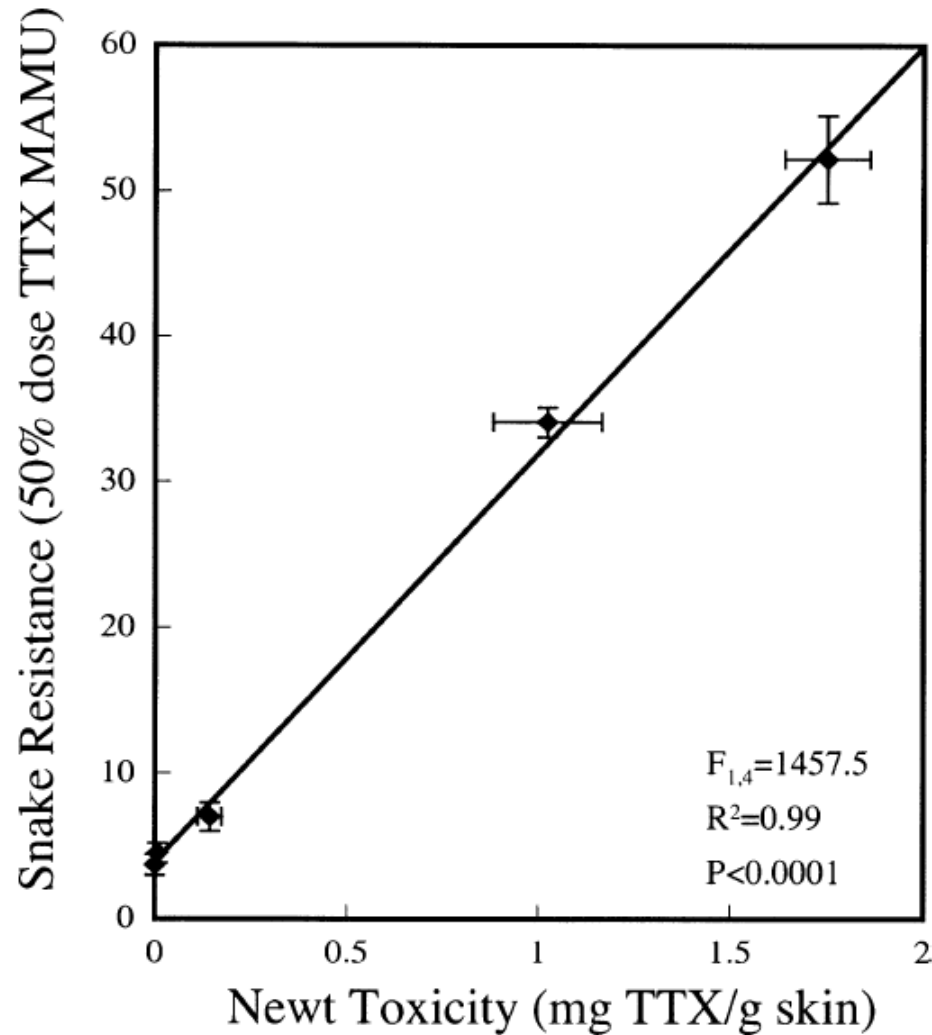
(B) Predator resistance shown as the amount of TTX (mg) required to reduce an average adult female *T. sirtalis* to 50% of its baseline performance based on the 28 populations in Figure 1.

(C) The degree of phenotypic matching plotted as  $d$ , which measures the deviation from estimated match, at each locality, of the phenotypic interface of coevolution (i.e., TTX toxicity in newts and TTX resistance of co-occurring snakes). Note that general overall patterns of relative phenotype exaggeration (yellow, orange, and red in (A) and (B)) are generally similar for newts and snakes throughout their range of sympatry. The matching analysis (Figure 3, Figure 4) and (C) shows that similarly elevated phenotypes do not necessarily match functionally.

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## 5) Geographic variation in predator-prey coevolution

Correlation between garter snake resistance and newt toxicity

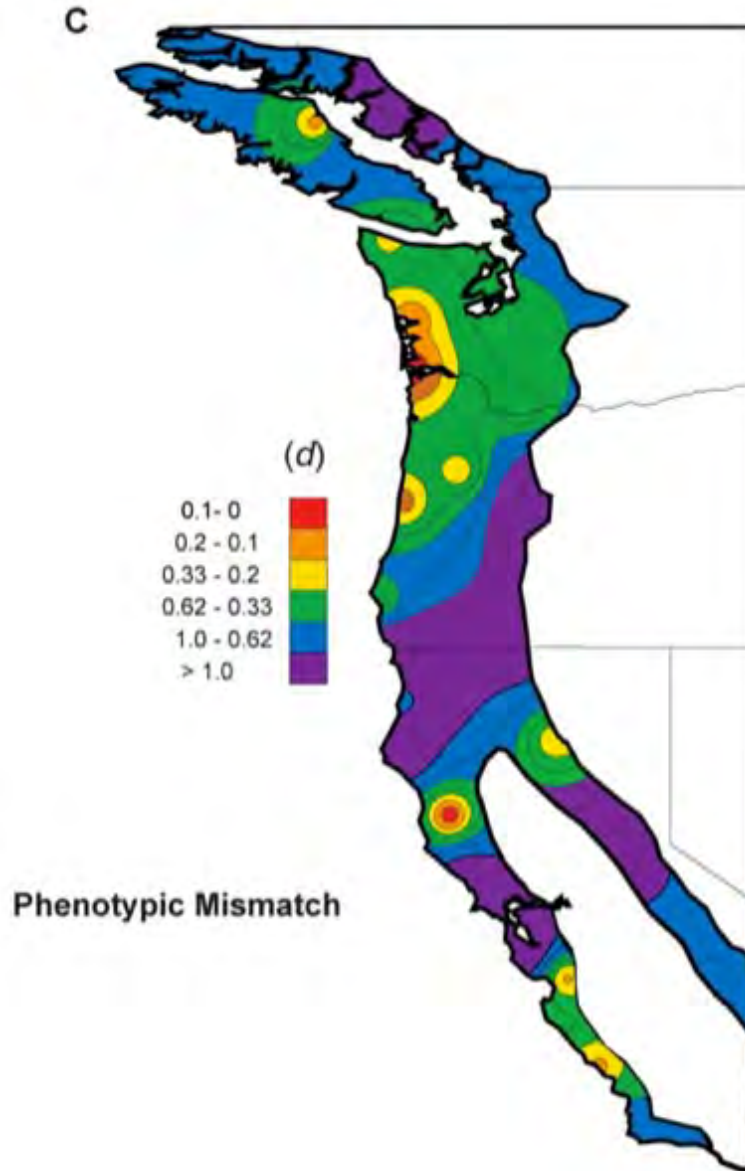


TTX resistance relative to sympatric newt toxicity.

TTX resistance (50% dose) for five populations of snakes is plotted against newt toxicity (mg TTX/g skin; Hanifin et al. 1999) from the same localities. Resistance is tightly predicted by toxicity of newts as shown by regression line (model: 50% dose  $3.8 + 28.03[\text{mg TTX/g skin of newts}]$ ).

## 5) Geographic variation in predator-prey coevolution

### Geographic variation in newt toxicity and garter snake resistance



The mismatches represent geographical locations in which the difference in toxicity and resistance are greater than the average.

These locations might provide an opportunity to investigate the dynamics of predator-prey coevolution, and perhaps answer basic questions about the costs and benefits of toxicity and resistance.

## 6) Evolution of aposematic coloration

The evolution of conspicuous coloration by prey as advertisement of noxious properties to predators.

Rough skinned newt  
*Taricha granulosa*



[http://simple.wikipedia.org/wiki/File:Rough-skinned\\_newt.jpg](http://simple.wikipedia.org/wiki/File:Rough-skinned_newt.jpg)

Defensive posture showing  
colorful belly



<http://blogs.scientificamerican.com/guest-blog/2012/08/21/poisonous-snakes-cant-resist-toxic-toad-tucker-or-can-they/>

## 6) Evolution of aposematic coloration

Experiments show:

Predators are capable of learning rapidly to associate noxious prey with bright colors

This leads to frequency-dependent selection in favor of common warning color phenotypes in prey populations

Birds have some degree of unlearned aversion to prey with certain color patterns, but this is thought not to be sufficient to explain the evolution of warning coloration.





## 6) Evolution of aposematic coloration

How did aposematic coloration evolve?

H1: Conspicuousness evolved first (e.g., by sexual selection), favoring the evolution of unpalatability. This is not considered likely.

H2: Palatability evolved first. Warning color evolved in cryptic, unpalatable prey populations. Under this scenario, how would a new mutation fare that produced the first brightly colored individual? Probably not well.

H3: The first mutation causing conspicuousness caused a whole brood to be brightly colored. Such a mutation might be ill-fated unless the offspring were in close proximity: local predators would learn the warning coloration by testing a few individuals, protecting the rest of the family.

This thinking led the expectation that warning coloration should be more likely to evolve in species whose offspring live in family groups ("gregarious"). There is an association, although warning coloration is exhibited by many solitary species too.

# 6) Evolution of aposematic coloration

## Phylogeny of gregariousness and warning coloration in swallowtail butterfly larvae

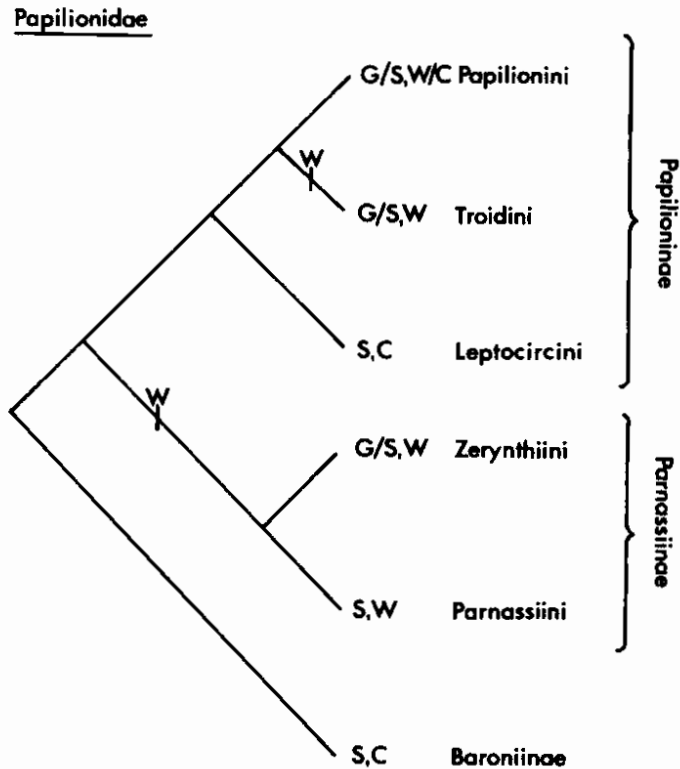


FIG. 3. Phylogeny showing the subfamilies and tribes of Papilionidae (after Hancock [1983] and Scott [1984]). Warning coloration (W) is inferred to have evolved twice from cryptic coloration (C) at this level. Gregariousness has been found in three tribes: Zerynthiini, Troidini, and Papilionini.

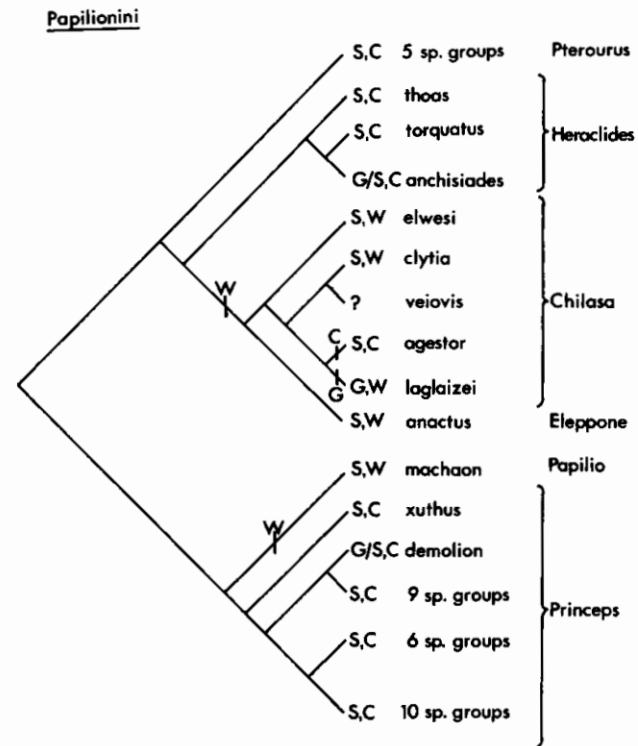


FIG. 4. Phylogeny at the level of genus and species-group of the tribe Papilionini (after Hancock [1983]). Warning coloration (W) has probably evolved twice within this group and gregariousness (G) has probably evolved three times. Two of these evolutionary events took place after further lineage-splitting, namely in the species groups *anchisiades* and *demolition* (see text), and are therefore not included in the figure.

Problem: the ancestral states cannot be estimated reliably when evolution is repeatable.



[http://upload.wikimedia.org/wikipedia/commons/7/77/Papilio\\_machaon\\_caterpillar.jpg](http://upload.wikimedia.org/wikipedia/commons/7/77/Papilio_machaon_caterpillar.jpg)

# 6) Evolution of aposematic coloration

## Warning signal experiment













		Type of dispersion	
		Solitary prey	Aggregated prey
Background	+	palatable 16x1  unpalatable 8x1  aposematic 8x1 	palatable 4x4  unpalatable 2x4  aposematic 2x4 
	■	palatable 16x1  unpalatable 8x1  aposematic 8x1 	palatable 4x4  unpalatable 2x4  aposematic 2x4 

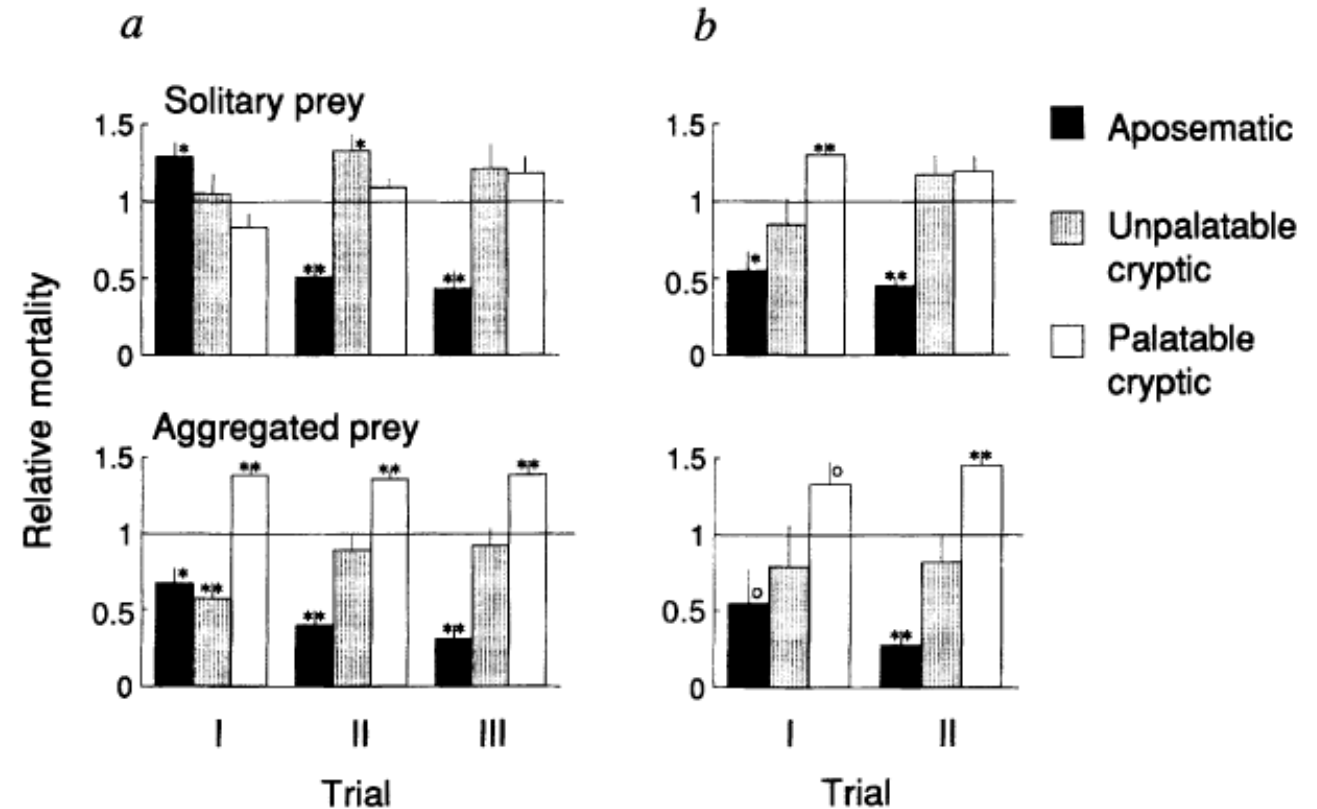
FIG. 1 The experimental set-up to test the origin of warning signals among straw prey. Each individual great tit was randomly assigned to one of the four treatments shown. The background was either a cross or a square and the prey were presented either solitary or in aggregation. In each case, there were 16 palatable cryptic prey, 8 unpalatable cryptic prey and 8 unpalatable signalling prey (aposematic). Palatable items consisted of animal fat in a 6-mm rye straw with paper wings. Unpalatable items had a 12% concentration of chloroquine. Prey items were randomly placed on a  $2 \times 2$  m floor of an aviary, where there were  $6 \times 6 = 36$  pieces of white A4 paper ( $21 \times 30$  cm) with symbols as the background. To train the tits to use their cryptic items, they were offered two palatable pieces of straw filled with fat on two consecutive days. Before the trials, the tits were not allowed to feed for two hours, and each trial lasted one hour. We used only the 12 first items in the analyses, but in the first trials only the 6 first items were included to obtain the initial predation risks before birds could learn the signals. In the second experiment, almond slices were reduced to  $\sim 6 \times 6$  mm, with symbols glued to each slice with non-toxic glue. Unpalatable slices were dipped in a 40% solution of chloroquine.



# 6) Evolution of aposematic coloration

## Warning signal experiment

FIG. 2 Relative mortality for aposematic, unpalatable cryptic and palatable cryptic prey items when presented solitarily dispersed or in clumped aggregations. The proportions of killed items in each group were divided by the randomly expected proportions, which were 0.25 for aposematic and unpalatable cryptic items, and 0.50 for palatable cryptic items. In this way, the average mortality over the three types of items is standardized to unity. In the first stage (a) with artificial straw prey, the experiment was repeated three times with the same birds, and in the second stage (b), the same predator individuals each encountered a similar set-up of slices of almond with similar signals in two consecutive trials. Standard errors are shown; asterisks indicate two-tailed significance (circle symbol,  $P < 0.10$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ) of a difference from the average mortality of all items, scaled to unity as indicated by the horizontal lines. We used repeated measures ANOVA for arcsin-square-root transformed proportions of each type of item to be 'killed'. The type of background (square or cross) had no effect in either setup for any of the three prey types ( $P > 0.50$ ), so for simplicity we have combined the presentation of data. In the 'initial origin' experiment (a), for aposematic items both the type of prey dispersion ( $F_{(1,23)} = 8.47, P < 0.01$ ) and the trial number ( $F_{(2,46)} = 12.10, P < 0.01$ ) indicated significant effects. Likewise, type of prey dispersion ( $F_{(1,23)} = 15.86, P < 0.010$ ) and trial number ( $F_{(2,46)} = 5.32, P < 0.01$ ) had a significant effect on the proportion of unpalatable cryptic items being killed. For the cryptic palatable items, the type of dispersion was significant ( $F_{(1,23)} = 24.38, P < 0.001$ ) but trial



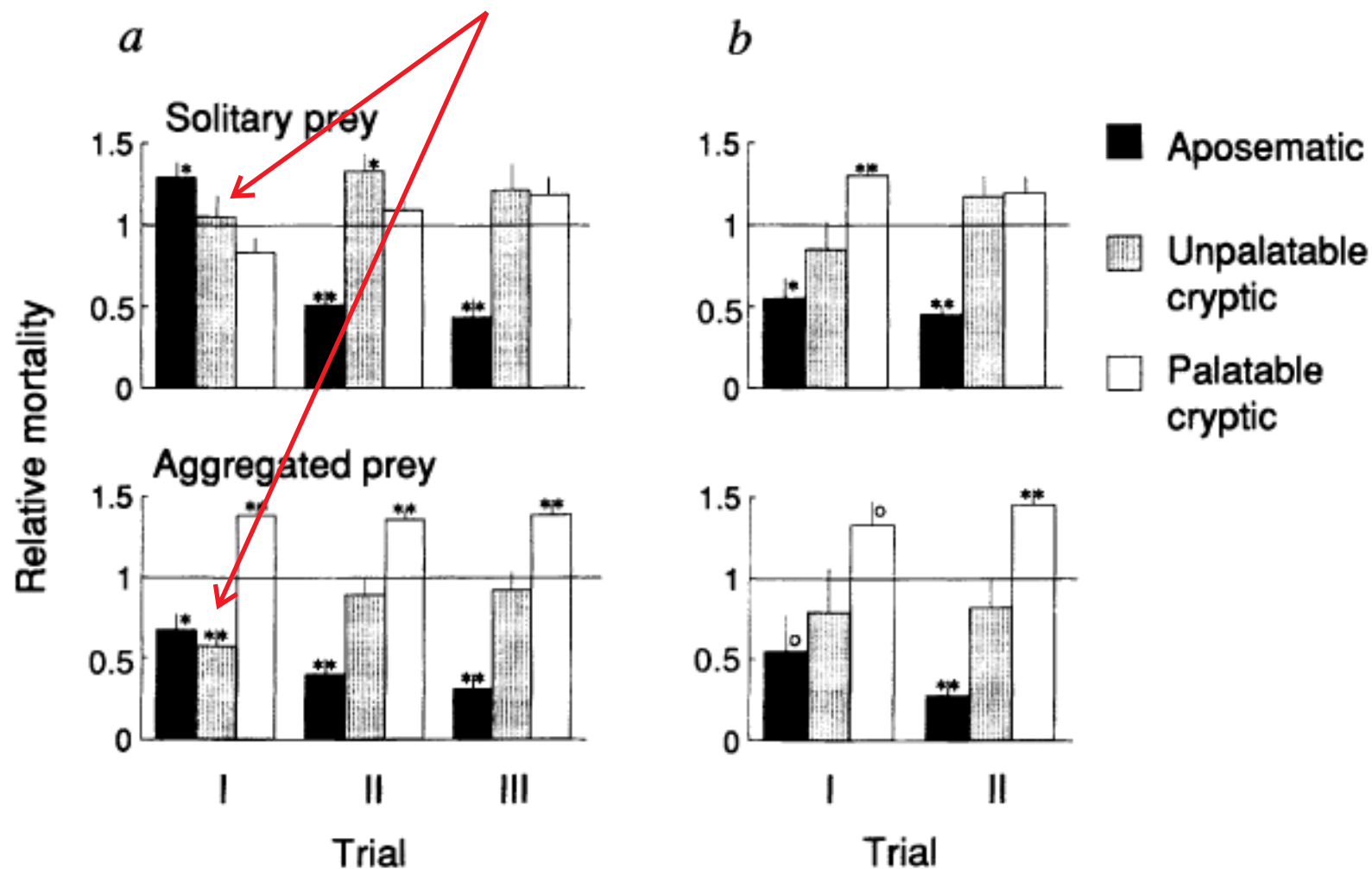
number was not ( $F_{(2,46)} = 2.39, P < 0.10$ ). In the 'secondary origin' experiment (b) the proportion of aposematic items handled was not significantly dependent on the type of prey dispersion ( $F_{(1,17)} = 1.85, P = 0.19$ , repeated measures ANOVA) or the trial number ( $F_{(1,17)} = 0.37, P = 0.58$ ).

# 6) Evolution of aposematic coloration

## Warning signal experiment

Initially, unpalatable prey survived better when aggregated than when solitary, unlike palatable prey (this weakened but persisted as birds learned).

Thus: unpalatability favors aggregation / gregariousness

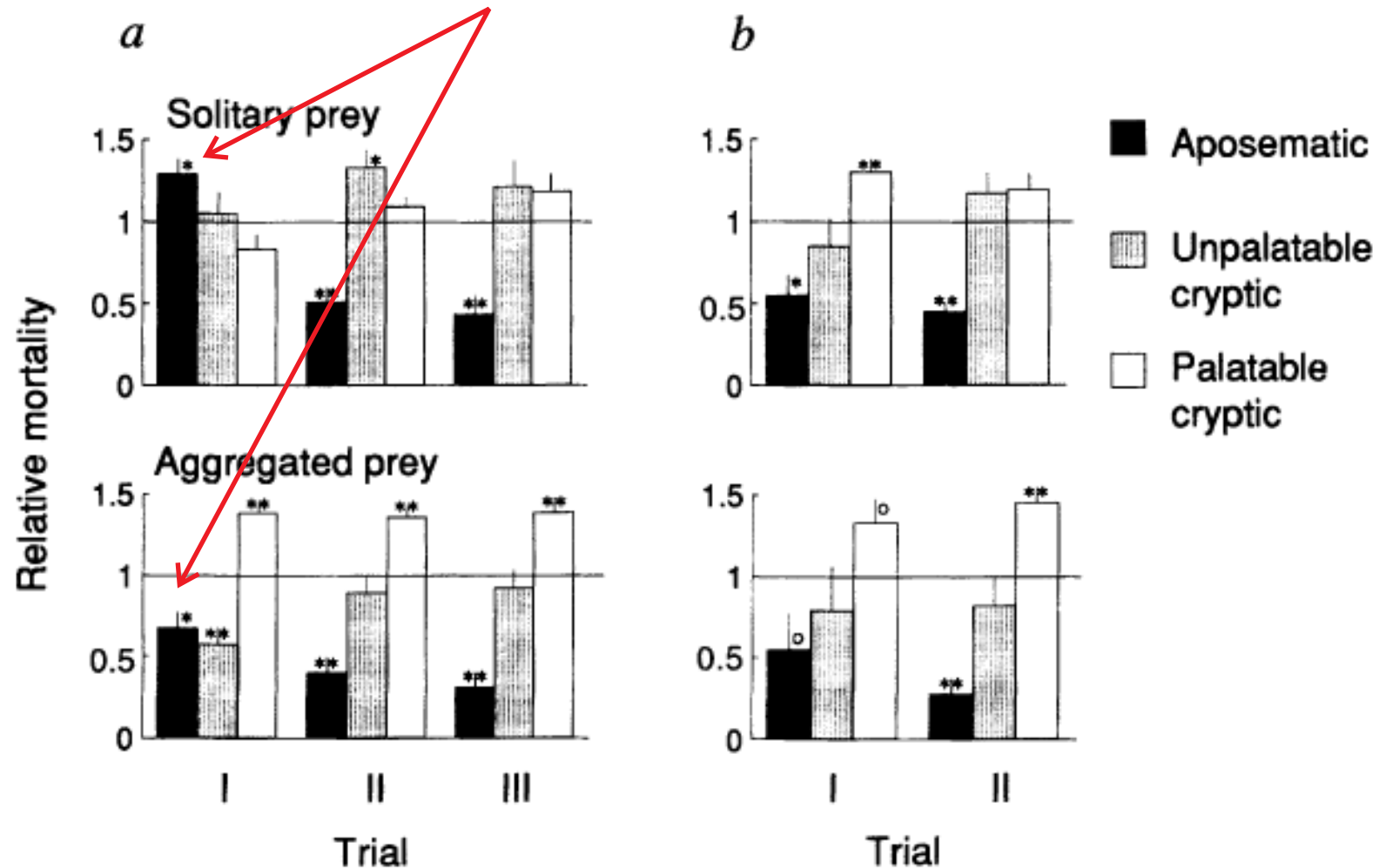


# 6) Evolution of aposematic coloration

## Warning signal experiment

Initially, aposematic prey survived better when aggregated than when solitary (though in time aposematic was advantageous even when prey solitary).

Thus: aggregation / gregariousness favors aposematic coloration right from the start.

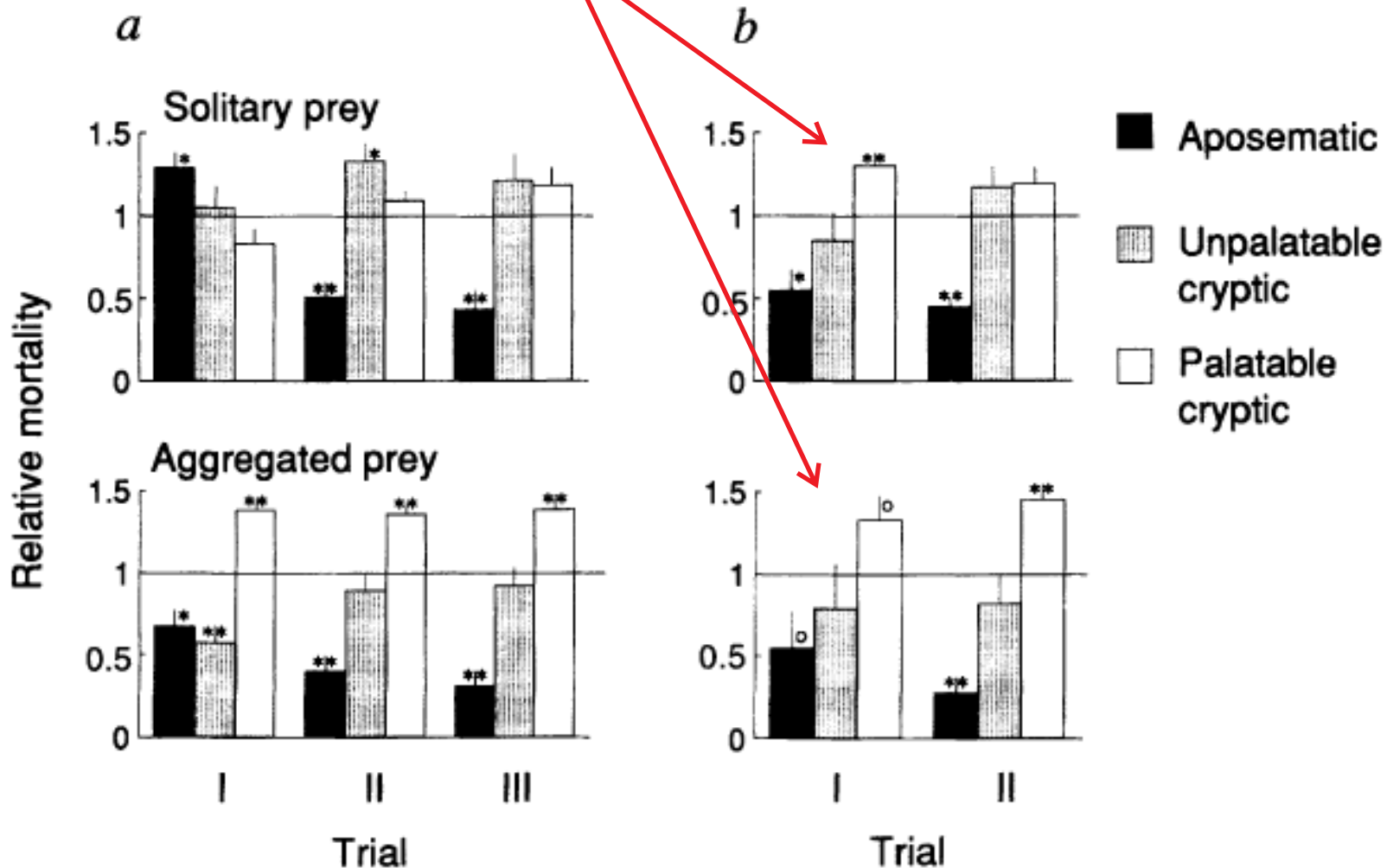


# 6) Evolution of aposematic coloration

## Warning signal experiment

But when presented with new prey types partly resembling those in the first trial, there was no longer an effect of aggregation vs solitary on mortality.

Thus: once aposematic coloration is “established”, it can evolve in other prey types independent of a gregarious lifestyle.



## 7) Example exam questions

What criteria do you think would need to be fulfilled before you were convinced that a case of adaptation of prey to predator, and predator to prey, represented coevolution in the strict sense?

Abrams recognized two general models or hypotheses to explain coevolution between predators and prey (or parasites and hosts). The first is the arms race model, and the second is the steady model. Explain the differences between these two hypotheses and their expected outcomes.

Which model do you regard as the better explanation for coevolution of running speed between carnivorous mammals and their ungulate prey? Explain your reasoning.

How might kin selection be involved in the evolution of aposematic coloration?