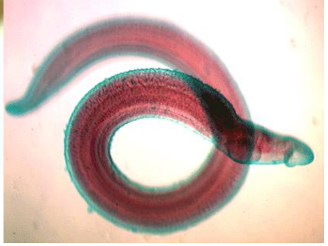
Change to structure of Exam 3

- Equations you do not need to memorize will now be included as an Appendix
- Equations will no longer be included within the question in which they are used

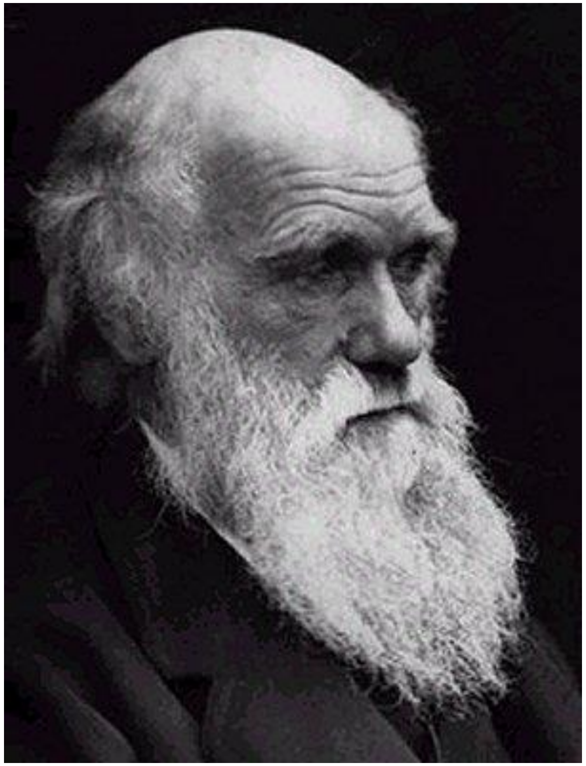
What does this mean for you?

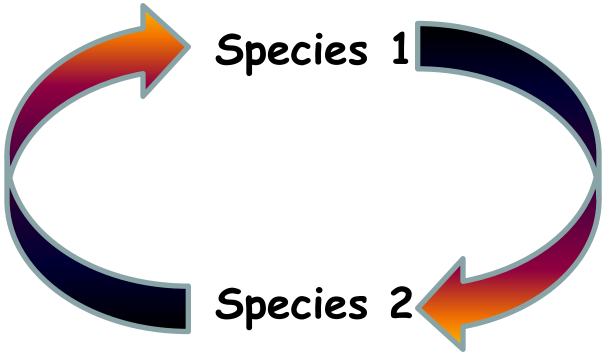
➔ You need to be able to recognize which equation you should use for each type of question

Coevolution



What is Coevolution?





Coevolution: Reciprocal evolutionary change in interacting species (Janzen, 1980)

"Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted to each other in the most perfect manner, by the continued preservation of all the individuals which presented slight deviations of structure mutually favourable to each other."
— Charles Darwin, The Origin of Species

Prerequisites for Coevolution

For coevolution to occur:

- **There must be genetic variation for traits mediating the interaction**

- **There must be reciprocal natural selection**

$$R_1 = \underline{h_1^2} \, \underline{S_1(\phi_2)}$$

$$R_2 = \underline{h_2^2} \, \underline{S_2(\phi_1)}$$

ϕ_i is the genotypic or phenotypic distribution of species i

An example from wild parsnip and webworms

Pastinaca sativa
(Wild parsnip)

- **Introduced to the United States**
- **Contains phototoxic furanocoumarins (secondary plant defensive compounds)**

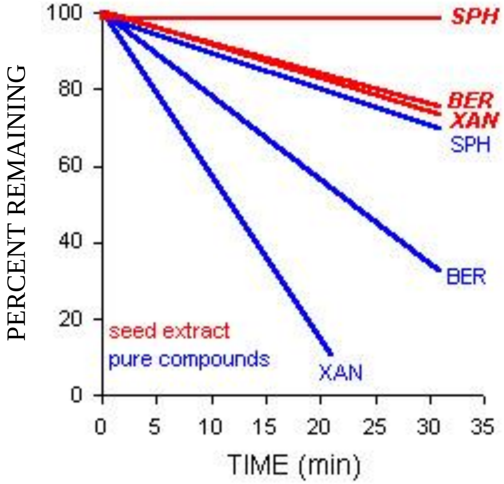
An example from wild parsnip and webworms

Depressaria pastinacella
(Parsnip webworm)

- Feed on wild parsnip
- Eat seeds (how?)

An example from wild parsnip and webworms

How is it that these insects are able to eat such toxic plants?



The larvae can metabolize the toxic furanocoumarins using cytochrome P450

Are the pre-requisites for coevolution met in this system?

<u>Remember, for coevolution to occur:</u>

- **There must be genetic variation for traits mediating the interaction**

- **There must be reciprocal natural selection**

Is there genetic variation for plant toxicity?

$h^2 > 0$?

Berenbaum et. al. (1986):

• Measured concentrations of toxic furanocoumarins in seeds of half-sib families

• Used this data to estimate ***heritabilities*** for furanocoumarin production

• Found substantial genetic variation for furanocoumarin production

Heritabilities for seed furanocoumarin production

Trait	h^2
Bergaptin	.190
Xanthotoxin	.650
Sphondin	1.43

Is there genetic variation for insect resistance?

$h^2 > 0$?

Berenbaum and Zangerl (1992):

•Dissected guts out of larvae from 6 different families

• Measured the rate at which these guts metabolized furanocoumarins

• Used this data to estimate ***heritabilities*** for metabolism of furanocoumarins

• Found substantial genetic variation for furanocoumarin metabolism

Heritabilities for P450 metabolism furanocoumarins

Trait	h^2
Bergaptin	.326
Xanthotoxin	.450
Sphondin	.008

Is there selection for increased plant toxicity?

$S_1(\phi_2)$?

Berenbaum et. al. (1986):

• Measured concentrations of toxic furanocoumarins in plants grown in the field

• Measured the seed set of each plant at the end of the study

• Used this data to estimate *Selection differentials* for furanocoumarin concentration

• Found statistically significant selection acting on the concentration of Bergaptin

Selection differentials for seed furanocoumarin concentration

Trait	S
Bergaptin	.0107
Xanthotoxin	--
Sphondin	.0106

Is there selection for increased insect resistance?

$S_2(\phi_1)$?

Zangerl and Berenbaum (1993):

• Measured concentrations of toxic furanocoumarins in plants

• Measured the growth rate of larvae on each plant

• Measured the rate of larval metabolism for furanocoumarins

• Found that larvae with a high metabolic rate grew faster on highly toxic plants

→ This interaction meets all the criteria for coevolution

- **Genetic variation exists for plant production of furanocoumarins**
- **Genetic variation exists for furanocoumarin metabolism in the moth**
- **Natural selection favors plants with greater concentrations of furanocoumarins**
- **Natural selection favors moths with an increased rate of furanocoumarin metabolism**

Have the webworm and parsnip coevolved?

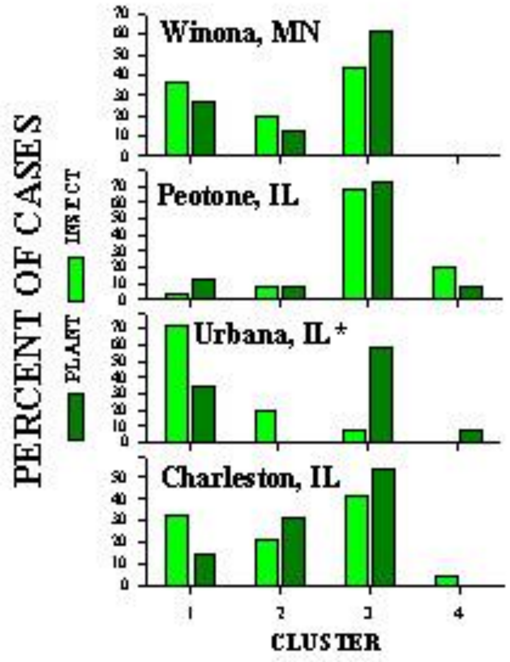
<u>Spatial data (Berenbaum and Zangerl, 1998):</u>

• Concentrations of plant furanocoumarins were measured in four different populations

• Moth furanocoumarin metabolic rates were measured within these same populations

• There is a striking amount of phenotypic matching between species

• Is this evidence for coevolution?



Have the webworm and parsnip coevolved?

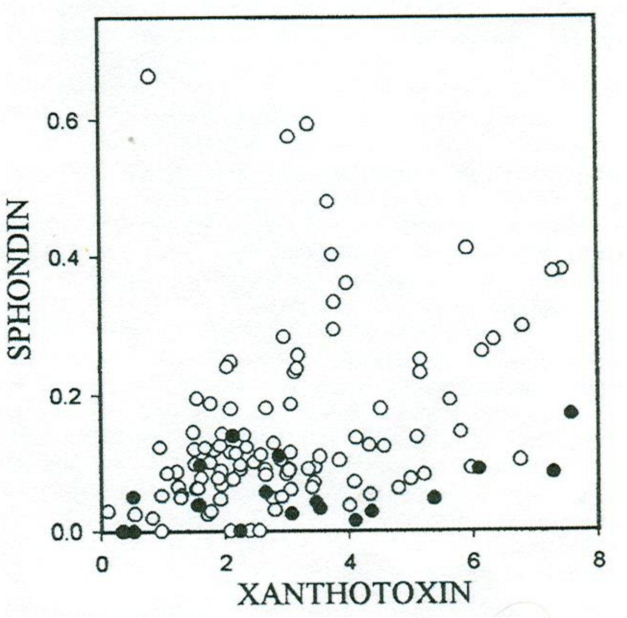
<u>Temporal data (Berenbaum and Zangerl, 1998):</u>

• Concentrations of plant furanocoumarins were measured in herbarium samples

• Concentrations in herbarium samples and present day populations were compared

• It appears that the concentration of the furanocoumarin Sphondin has increased over time

• Is this evidence for coevolution?



Present day samples ○

Herbarium samples ●

Summary for wild parsnip and parsnip webworm

- Genetic variation exists for plant production of furanocoumarins
- Genetic variation exists for furanocoumarin metabolism in the moth
- Natural selection favors plants with greater concentrations of furanocoumarins
- Natural selection favors moths with an increased rate of furanocoumarin metabolism
- Phenotypic matching occurs between moth and plant in most populations
- Plant furanocoumarin concentrations may be increasing over time

What about other types of interactions?

Practice Problem

You have observed that a butterfly species, *Papilio falsificada*, is regularly associated with the plant, *Prunus fauxviflorum*. Based on your observations, it is clear that the butterfly can, in principle, pollinate the plant and that the plant generally offers a nectar reward to the butterfly. Consequently, you have hypothesized that this interaction is a mutualism. To test this hypothesis, you collected information on plant fitness (seed set) for 22 individual plants visited by the butterfly vs. 22 individual plants that were not. In addition, you measured the fitness (# of surviving offspring) of 48 butterfly individuals that visited the plant vs. 48 butterfly individuals that did not. Your data are shown below as summary statistics:

Visited by butterfly?	**Sample mean of plant seed set**	**Sample variance of plant seed set**		**Visited plant?**	**Sample mean of butterfly fitness**	**Sample variance of butterfly fitness**
Yes	56.2	6.6		Yes	16.6	4.6
No	22.7	3.5		No	6.5	3.2

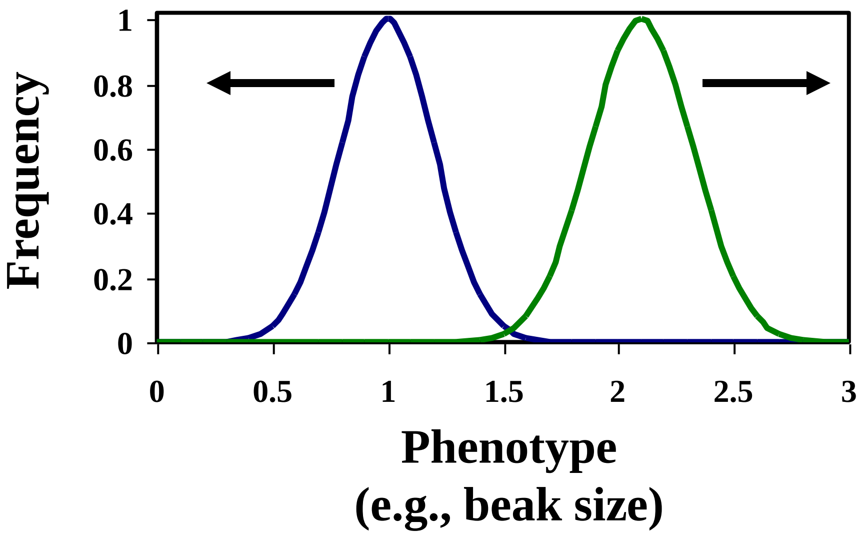
Does your data support your hypothesis that this interaction is a mutualism? Justify your response statistically.

Types of coevolutionary interaction

Interaction	Effect on Species 1	Effect on Species 2
Competition	-	-
Antagonism	-	+
Mutualism	+	+

The interactions differ in the form of ***Reciprocal Selection***

Coevolution in competitive interactions



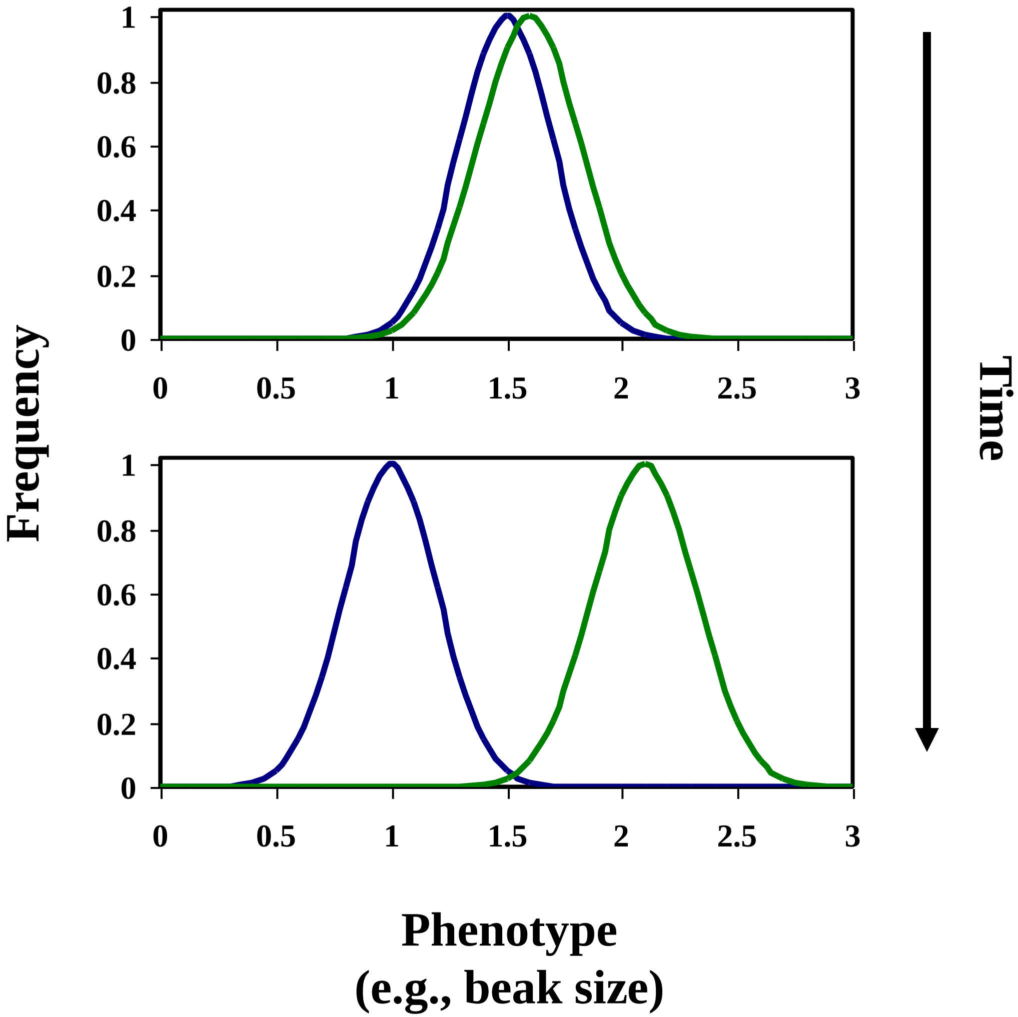
<u>Reciprocal Selection:</u>

• The fitness of Species 1 individuals is decreased by interacting with Species 2

• The fitness of Species 2 individuals is decreased by interacting with Species 1

• Reciprocal selection favors traits in each species that reduce the efficacy or frequency of the interaction

If there is genetic variation in both species…

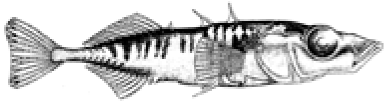


<u>Coevolutionary dynamics:</u>

• Divergence in traits mediating the interaction (i.e., character displacement)

An example from fish

Gasterosteus aculeatus
(Three spined stickleback)

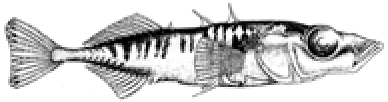


Limnetic (shallow water)

Benthic (deep water)

Studied interactions in lakes in BC

An example from fish



Limnetic (shallow water)

Benthic (deep water)

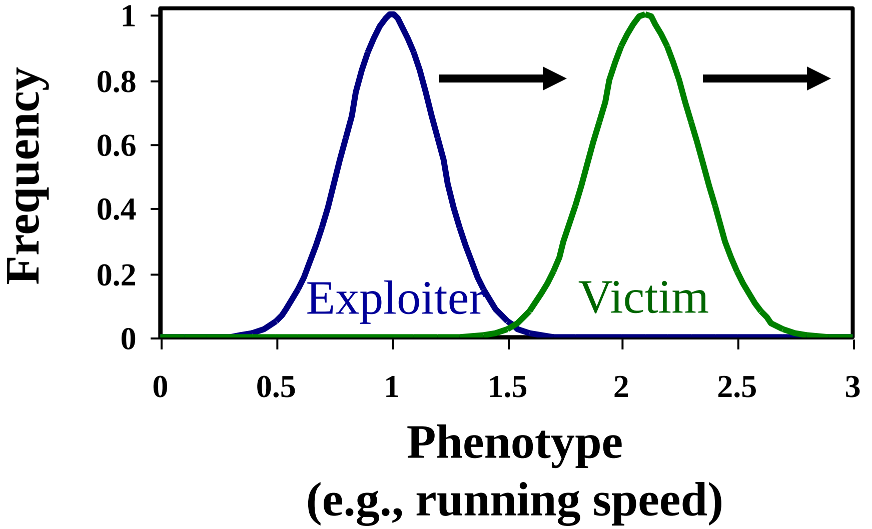
• Individuals with body sizes more similar to the alternate species/morph have lower fitness

• Generates reciprocal selection for divergence in body size

• Measure body size of the two forms where they occur allopatrically vs sympatrically

• The ratio of the trait means (body size and shape) for the two species are exaggerated in sympatry (i.e., character displacement)

Coevolution in antagonistic interactions



Reciprocal Selection:

• The fitness of victim individuals is increased by not interacting

• The fitness of exploiter individuals is increased by interacting

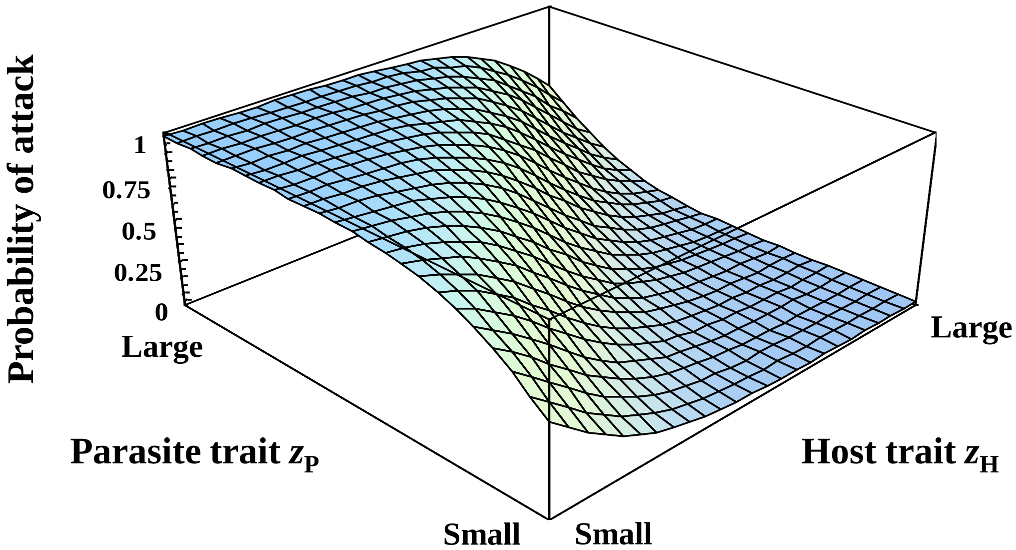
• Reciprocal selection favors victim traits that decrease the efficacy or frequency of interaction, but exploiter traits that increase the efficacy or frequency of the interaction

Antagonistic interactions can be further divided

- **Coevolutionary escalation –** Reciprocal selection favors increased (or decreased) phenotypes in both victim and exploiter (this is the case for the parsnip and parsnip webworm)

- **Coevolutionary matching –** Reciprocal selection favors exploiters that match the phenotype of the victim, but victims that mismatch the phenotype of the exploiter

Coevolutionary escalation

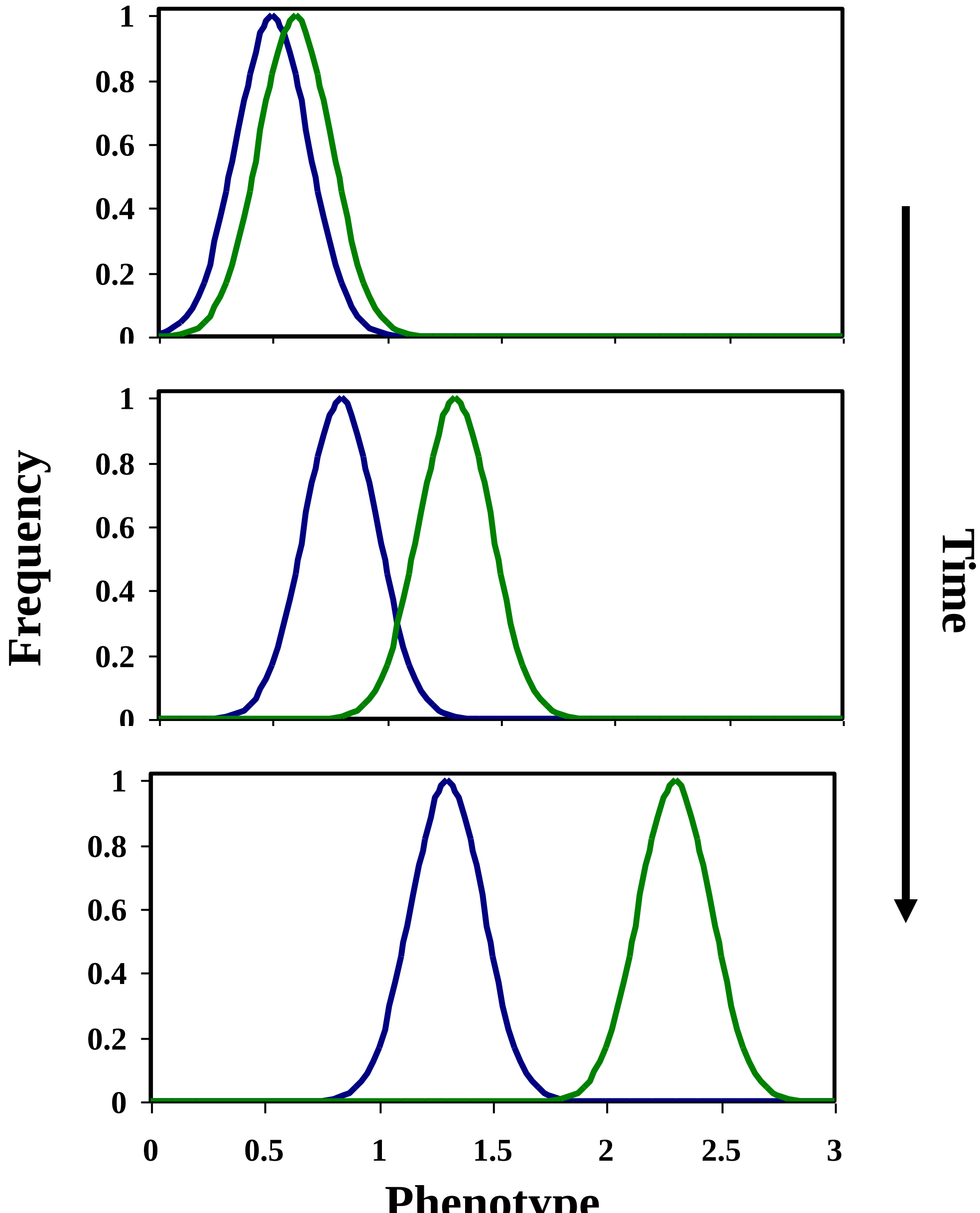


For example:

• Concentration of plant defensive compounds

• Concentration of insect detoxification enzymes

If there is genetic variation in both species…



Coevolutionary dynamics:

• Endless escalation of phenotypes

• The 'winner' is the species with greatest response to selection, *R*

An example from toxic newts and garter snakes

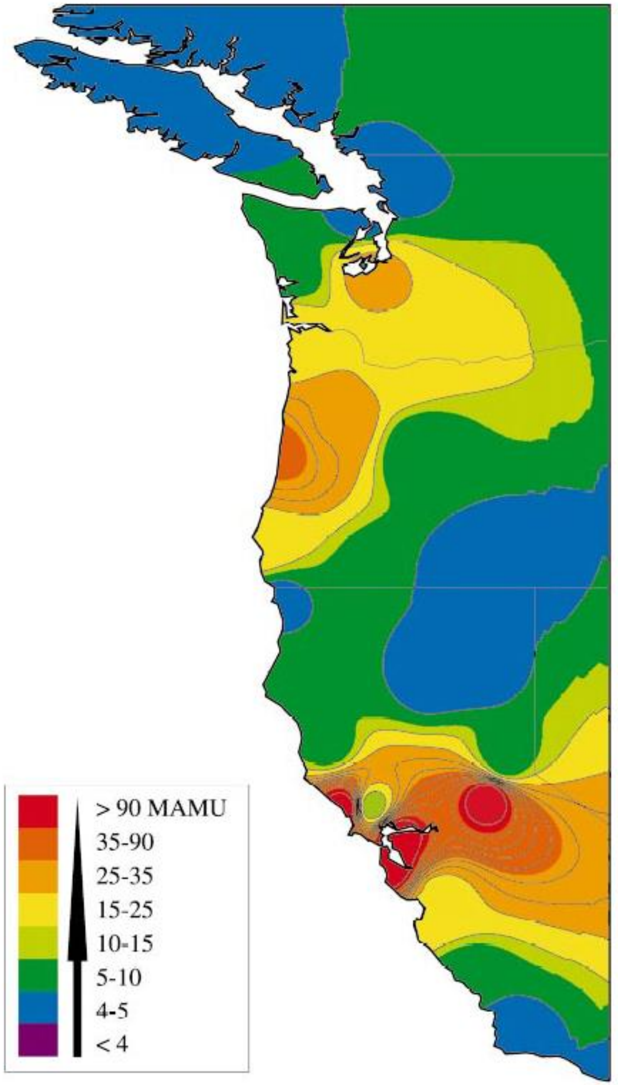
Taricha granulosa

- Newts produce tetrodotoxin (TTX)
- Newts that produce more TTX are less likely to be eaten by snakes
- Snakes that are more resistant to TTX are better able to eat newts

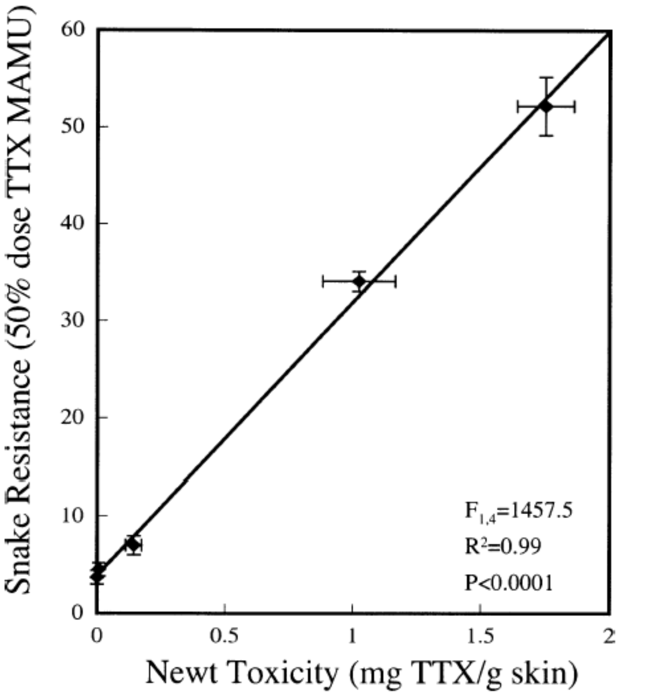
Thamnophus sirtalis
(Garter snake)

Is there evidence for coevolutionary escalation?

Geographic distribution of TTX resistance



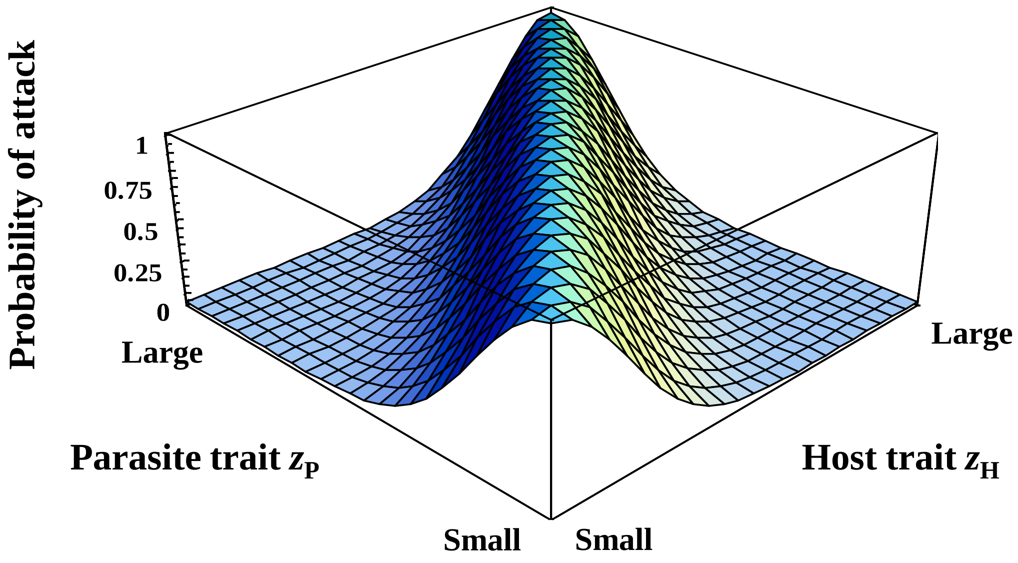
Brodie et. al. 2002



- **Some Garter snake populations have dramatically increased TTX resistance**

- **Suggests the existence of coevolutionary hot spots where escalation has occured**

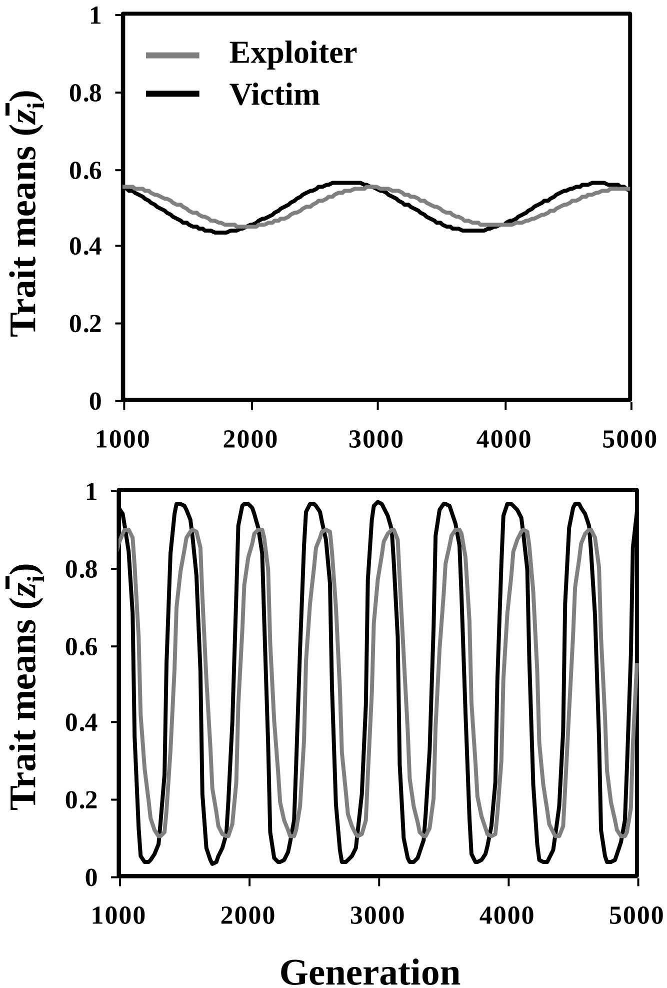
Coevolutionary matching



For example:

- Cuckoo egg coloration

If there is genetic variation in both species…

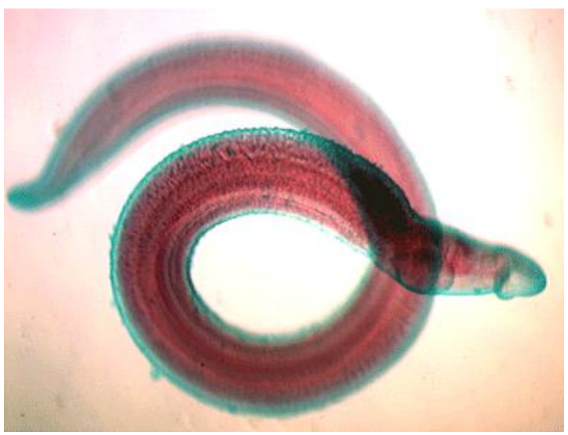


<u>Coevolutionary dynamics:</u>

- Phenotypes cycle endlessly
- Exploiter adapts to common victim phenotypes
- Should produce an advantage for rare victim phenotypes

An example from snails and castrating trematodes

Potamopyrgus antipodarum

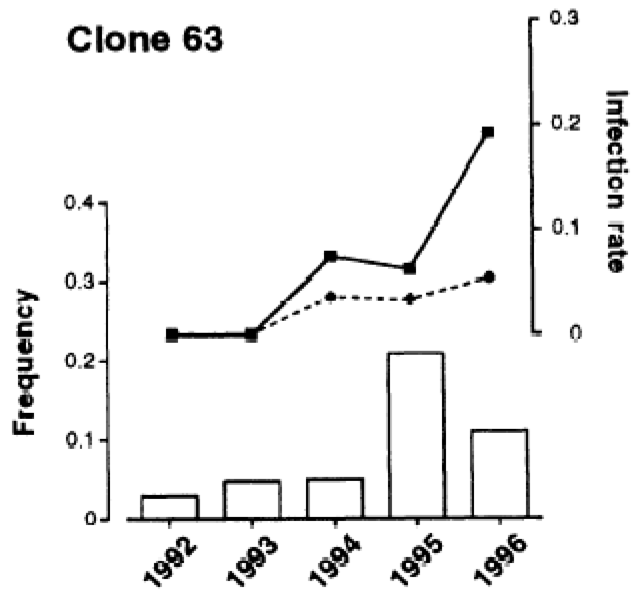


A castrating trematode

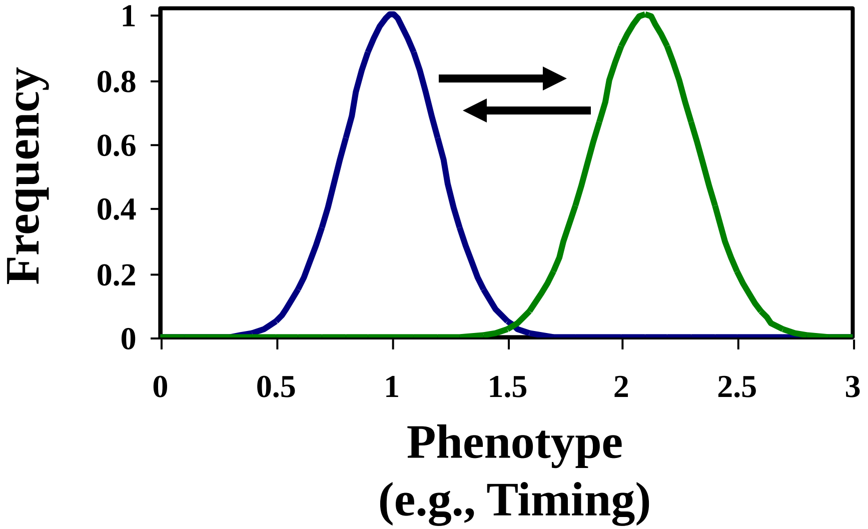
<u>Hypothesized that (Dybdahl and Lively 1998):</u>

• Trematode phenotypes can only infect snails with specific “matching” genotype/phenotypes

• If true, rare snail genotypes/phenotypes should be less frequently infected than common snail phenotypes/genotypes



Coevolution in mutualistic interactions



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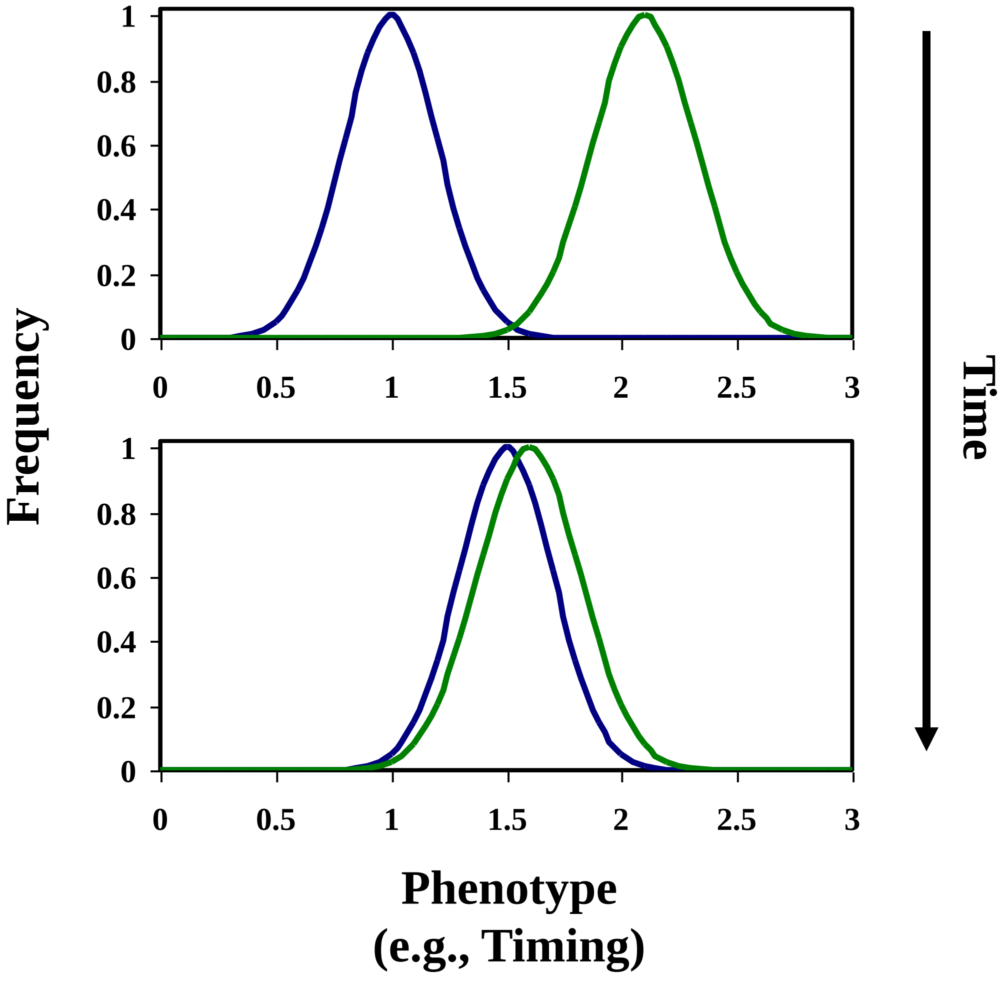

Coevolutionary dynamics:

• Convergence of traits mediating the interaction

An example from plant-insect interactions

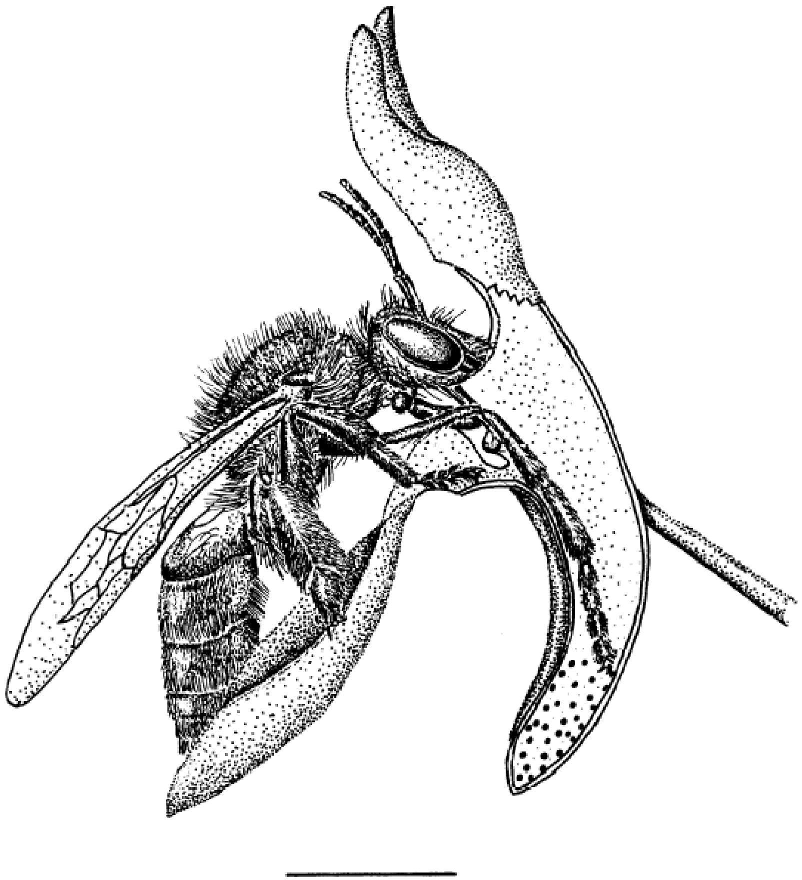

FIG. 1. *Rediviva neliana* visiting flower of *Diascia capsularis*. Scale line = 0.5 cm.

(Steiner and Whitehead 1990)

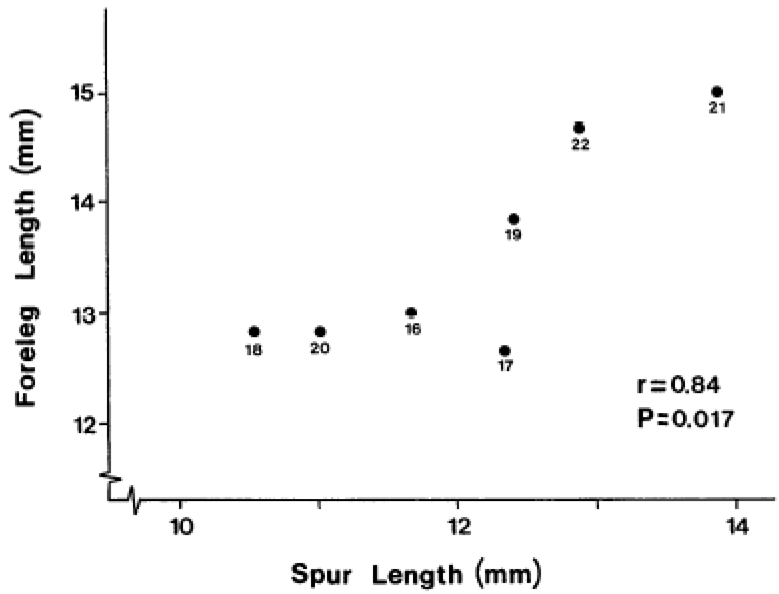

FIG. 6. Relationship between foreleg length and spur length for *R. neliana* and *Diascia capsularis* from 7 sites in southern Africa. Numbers refer to the study sites (Table 1).

- **Data are consistent with coevolutionary convergence**

Conclusions for coevolution

- **Coevolution is likely any time interacting species:**

  - Exert reciprocal selection on one another

  - Possess genetic variation for traits mediating the interaction

- **The dynamics of coevolution differ across types of interactions:**

  - Competitive interactions cause coevolutionary divergence

  - Mutualistic interactions cause coevolutionary convergence

  - Antagonistic interactions cause either coevolutionary escalation or coevolutionary cycles