Phenotypic plasticity in amphibians

Lecture goal

To familiarize students with the basics of phenotypic plasticity, demonstrate the diversity of research that has documented phenotypic plasticity in amphibians, and encourage discussion about phenotypic plasticity

Required readings:

Wells pp. 601-603, 609-610, 618-628, 632-642
Gotthard and Nylin 1995. *Oikos* 74:3-17
Relyea 2007. *Oikos* 152:389-400

Supplemental readings:

Wells pp. 563-564, 573, 575, 596-597, 693-728

Lecture roadmap

Basics of phenotypic plasticity

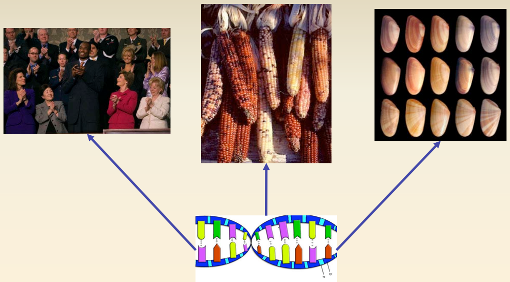
Metamorphosis and paedomorphosis

Cannibalism

Predation

Competition

Phenotypic variation is the basis of biology



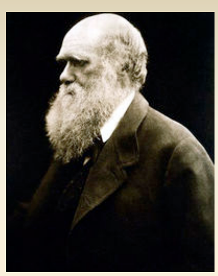
Genetic variation leads to phenotypic variation

Environmental variation leads to phenotypic variation

The phenotype of a single individual can vary depending on environmental conditions

Is this important?

What did Darwin think?

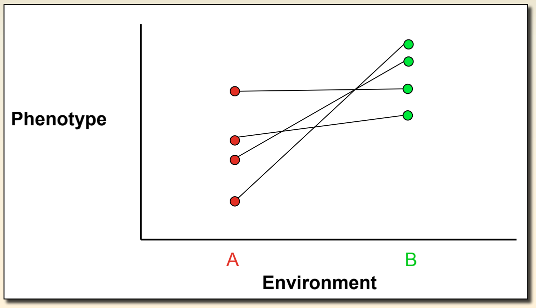


"I speculated whether a species very liable to repeated and great changes of conditions might not assume a fluctuating condition ready to be adapted to either condition."

-letter to Karl Semper 1881

What is this phenomenon that he is hinting at?

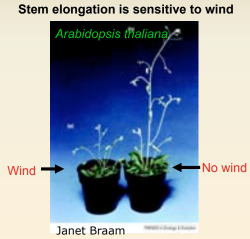
Phenotypic plasticity



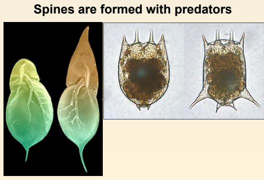
Examples of adaptive phenotypic plasticity

Gene expression depends on the type of food

Stem elongation is sensitive to wind



Spines are formed with predators



Non-adaptive plasticity also occurs

What would favor the evolution of plastic vs. non-plastic phenotypes?

Environmental heterogeneity

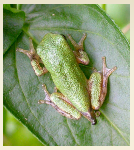
Phenotypic trade-offs

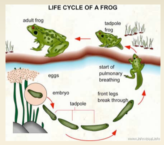
Reliable cues

Heritable variation

Decisions about metamorphosis

Environmental variation





Do these factors affect the decision to metamorphose?

What cues are used to initiate metamorphosis?

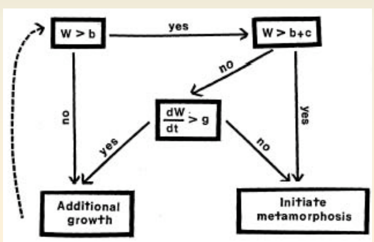
What are the costs and benefits of this flexibility?

Is it adaptive phenotypic plasticity?

The Wilbur & Collins model

W = larval body size
b = min. size to undergo meta

b+c = max. size to remain as larvae
dW/dt = size-specific growth rate
g = current body mass



Wilbur and Collins 1973. Ecological aspects of amphibian metamorphosis

The Wilbur & Collins model

Basic predictions

If food resources decline:

If food resources increase:

The effects of resources & temperature

Experimental design:

Tadpoles were reared individually in small containers
Resource levels were manipulated over time
Two temperatures were used
Time to & size @ metamorphosis recorded

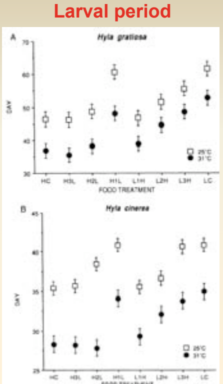
Leips and Travis 1994

TABLE 1. Experimental design. LC = low-food control group. HC = high-food control group. Day of switch shown indicates the number of days after fertilization when the switch to the alternative food level was made.

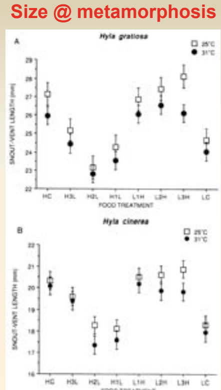
Species	Treatment code*	Food level	Day of switch 25°C	Day of switch 31°C
Hyla gratiosa	LC	L	Never	Never
	L1H	L → H	9	9
	L2H	L → H	21	20
	L3H	L → H	29	28
	HC	H	Never	Never
	H1L	H → L	9	9
	H2L	H → L	21	20
	H3L	H → L	29	28
Hyla cinerea	LC	L	Never	Never
	L1H	L → H	8	7
	L2H	L → H	16	16
	L3H	L → H	22	21
	HC	H	Never	Never
	H1L	H → L	8	7
	H2L	H → L	16	16
	H3L	H → L	22	21

* LxH and HxL are treatments in which food level was changed from initial L or H to final L or H level at time x, where x = 1, 2, or 3 for early, middle, or late time of switch.

Larval period



Size @ metamorphosis



Let's summarize these results

Larval period was affected by changes in food ration during first 60% of the larval period, but not the last 40%

Food addition leads to larger size @ metamorphosis while food reduction leads to smaller size

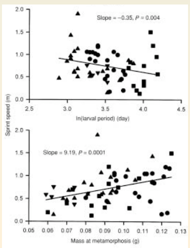
Temperature had minimal effects on size @ metamorphosis, but large effects on larval period

Does this support the Wilbur and Collins model?

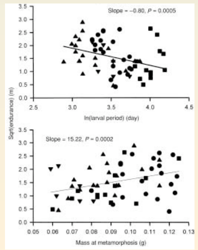
Impacts on performance

Larval period & mass were manipulated by adjusting food ration & temp
Performance of the metamorphs was tested

Sprint Speed



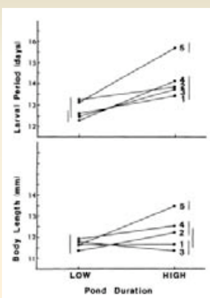
Endurance



***Bufo terrestris*; Beck & Congdon 2000**

Pond drying & metamorphosis

Does pond drying affect the decision to metamorphose?



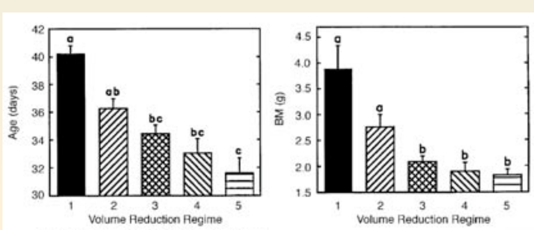
Tadpoles were reared in pens within ponds

Ponds differed in duration

Spadefoot toads; Newman 1988

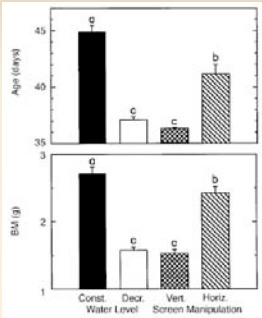
Pond drying & metamorphosis

Lab experiments can be used to assess the effect of water volume on metamorphosis



Spadefoot toads; Denver et al. 1998

Pond drying & metamorphosis



What cues are tadpoles using to detect the pond drying?

Reduction in swimming volume
or
Increased proximity to the surface

Spadefoot toads; Denver et al. 1998

Paedomorphosis in salamanders

Salamanders also must make decisions about metamorphosis

Unlike anurans, some salamanders are facultative paedomorphs

Salamandridae, Ambystomatidae, Dicamptodontidae, Hynobiidae, Plethodontidae

(10% of salamander species)

What affects the decision to metamorphose or become paedomorphic?

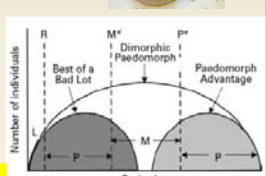
What are the costs and benefits of this flexibility?

Denoël et al. 2005. Evolutionary ecology of facultative paedomorphosis in newts and salamanders. *Biological Review* 80:663-671

Environmental variables to consider

Influences on the metamorphic/paedomorphic decision

Proposed explanations for paedomorphs
1. Paedomorph advantage
2. Best of a bad lot
3. Dimorphic paedomorph



Wilbur & Collins

Predicted environmental factors that select for paedomorphosis through each alternative mechanism

Whiteman 1994

		Aquatic parameters					Terrestrial parameters		
Mechanism	Aquatic environment	Temp.	Density	Food	Predation	Growth season	Humidity	Cover	Predation
Paedomorph advantage	favorable[1]	high	low	high	low	long	low	sparse	high
Best of a bad lot	unfavorable[1]	low	high	low	high	short	suitable	suitable	low

Terrestrial versus aquatic decision

Larvae were reared in pond mesocosms at three densities

Tanks were slowly drained or the water level kept constant

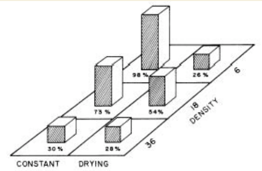


FIG. 1. Mean percentage of individuals becoming paedomorphic from the drying regime (water level) and density treatments. Means were calculated from eight artificial ponds ($n = 4$ from each of the nonsignificant food treatments).

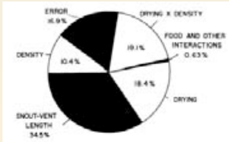
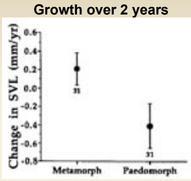


FIG. 3. Proportion of the variance in the percentage of individuals becoming paedomorphic accounted for by each component of the experimental design. Variance was calculated from the Type I sum of squares of each component divided by the total sum of squares, when snout–vent length was the first variable added to the model.

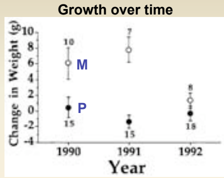
Ambystoma talpoideum; Semlitsch 1987

Costs and benefits

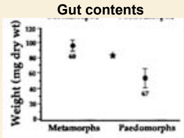
Growth over 2 years



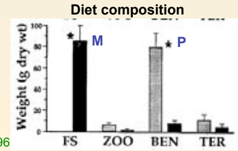
Growth over time



Gut contents



Diet composition



Ambystoma tigrinum nebulosum, Whiteman et al. 1996

Costs and benefits

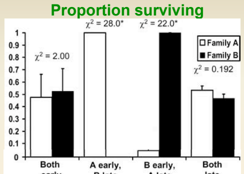
Two families of larvae were used

Hatching time was manipulated

Synchronous hatching

Asynchronous hatching

Proportion surviving

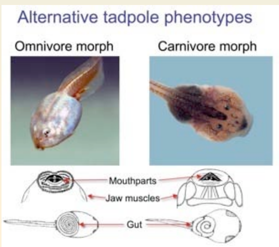


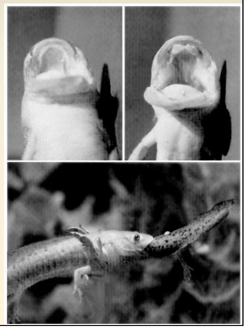
***Ambystoma talpoideum*; Ryan & Plague 2004**

Cannibalistic/carnivore morph

Frogs and salamanders will consume conspecifics

Ambystoma, Dicamptodon, Triturus
Rana, Hyla, Spea, Scaphiopus

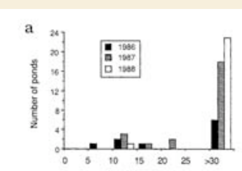




Carnivore morphs in Spadefoot toads

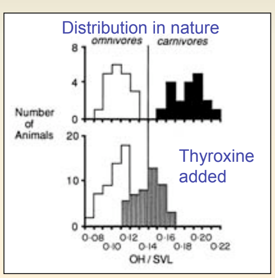
Environmental heterogeneity
Proximate mechanism or cue

Your ideas

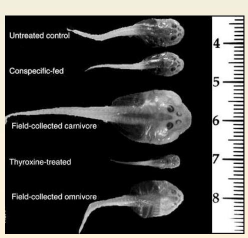


Carnivorous tadpoles

Does the addition of exogenous thyroxine induce the carnivorous morph?



(Pfennig 1992)

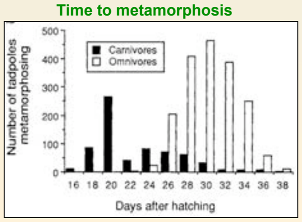


(Storz 2004)

Carnivorous tadpoles

Phenotypic trade-offs → Your ideas

Time to metamorphosis



Post-metamorphic survival

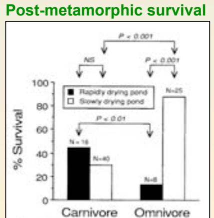


FIG. 4. Postmetamorphic survival for each morph when reared in wading pools designed to mimic ponds of different duration. Sample sizes are above each bar. P determined using a two-tailed Mann Whitney U-test.

Manipulations of morph frequency

Given these phenotypic trade-offs, why do we find both morphs in a pond?

If morph frequency is altered, original frequencies are restored

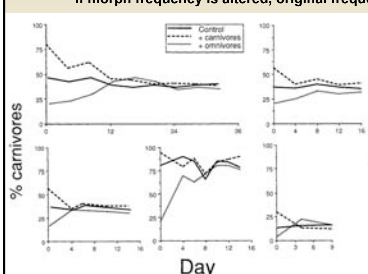
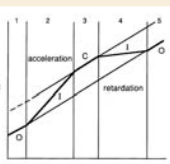


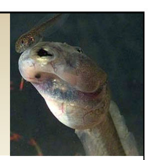
FIG. 5. Morph frequency (% carnivores), as a function of time, for ponds in which morph composition was manipulated differentially in enclosed areas of ponds. Data are mean percent carnivores from two replicates within each pond. For all graphs—solid line: control sections (i.e., sections in which morph frequency was left at the original pond-wide value); dashed line: excess carnivores; dotted line: excess omnivores.

Food availability and morph frequency determine fitness

Alter development of different tissues



Cannibalism and Kin



How would kin relationships affect cannibalism?

If reared with siblings, spadefoots are less likely to form cannibalistic morph

Why?

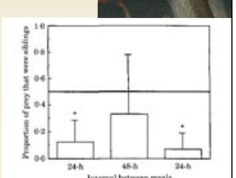


Figure 2. Mean ($\pm$SD) proportion of the prey of five carnivorous tadpoles that were siblings as a function of length of time between meals. The experiment was done sequentially over 96 h, with food withheld for 24 h, 48 h, and then 24 h again. At the end of each fasting period, the carnivore's consumption of kin and non-kin was assessed for 30 min. * Indicates that the observed value was significantly ($P < 0.02$) less than 0.5 (heavy, horizontal line), the value expected if cannibalism were random with respect to kinship.

What if you are really hungry?

Cannibalism in salamanders

Proportionally larger heads or distinct morphs
- Larger vomerine teeth

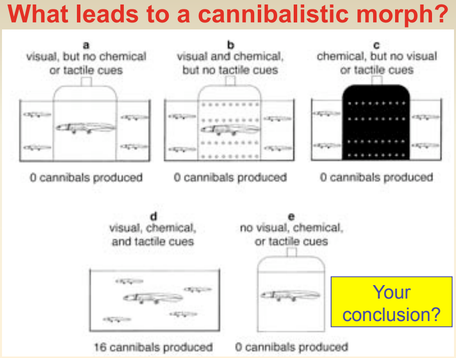
Starts with simple attacks on conspecifics
- Loss of limbs
- Tail nipping

Size disparity leads to full-scale cannibalism
- Feed on larger inverts, fish, tadpoles

Benefits of cannibalism
- Increased growth rate
- Accelerated metamorphosis

Important for temporary pond breeders

What leads to a cannibalistic morph?



(Hoffman and Pfennig 1999; *Ambystoma tigrinum*)

Costs of cannibalism

Cannibalistic salamanders benefit from greater growth rates and shorter larval periods

Why not always be a cannibal?

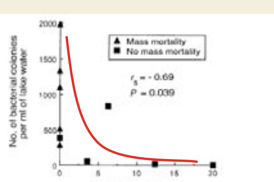


Fig. 3. Frequency of cannibals as a function of bacterial density in ten different natural lakes

(Pfennig et al. 1991; *Ambystoma tigrinum*)

Disease transmission

- 42% die before metamorphosis if a diseased conspecific is eaten
- Growth rate is reduced after a diseased conspecific is eaten

(Pfennig et al. 1998; *Ambystoma tigrinum*)

Predation

Predators are ubiquitous

Predators are variable in space and time

Predators can have huge impacts on fitness

Is phenotypic plasticity important?

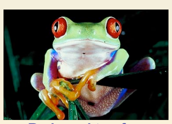
Egg hatching plasticity

Many tropical anurans lay eggs on vegetation over ponds

Egg predators can dramatically reduce clutch sizes

Eggs are clumped, stationary, and good sources of protein and energy

Is phenotypic plasticity important for these frogs?

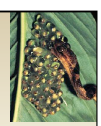


Red-eyed treefrog
(*Agalychnis callidryas*)

Cat-eyed snake
(*Leptodeira septentrionalis*)

Wasps
(*Polybia rejecta*)

Responses to snakes



Egg hatching video

What is the environmental cue of predation?

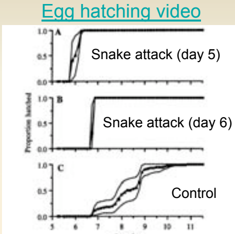


FIG. 2. Hatching of *A. callidryas* clutches with and without snake attack. Experimental clutches were attacked by *L. septentrionalis* at age 5 days (*A*; $n = 9$) or 6 days (*B*; $n = 5$); control clutches were not attacked (C; $n = 14$). Data are mean proportion hatched out of total hatch for each clutch. The 95% confidence intervals are shown by dotted lines. Time is plotted from midnight on the night of oviposition. Experimental clutches hatched rapidly when attacked by snakes; the mean hatching pattern reflects in part the variation in attack times. Embryos that hatched survived, and those that did not were eaten.

Are there trade-offs?

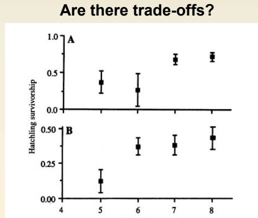


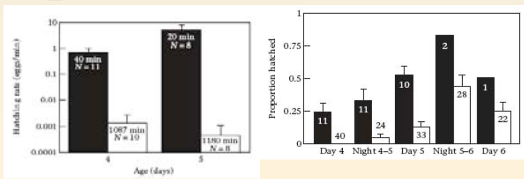
FIG. 4. Survivorship of *A. callidryas* hatchlings with shrimp, *M. americanum* (*A*), and fish, *B. rhabdophora* (*B*), in relation to hatching age. Data are mean proportion of tadpoles surviving (± 1 SE). In *A*, data from small shrimp (open symbols) and large shrimp (closed symbols) are plotted separately. The increase in survivorship with increasing hatching age is significant with both shrimp and fish predators, as is the effect of predator size.

Responses to wasps

Wasps attack one egg at a time (carry off the embryo)

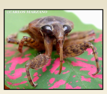
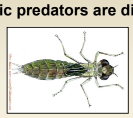
Greatest risk = embryo being attacked + immediate neighbors

■ Attacked by wasps
□ Undisturbed



Predator-induced plasticity in larvae

Aquatic predators are diverse in form and abundance

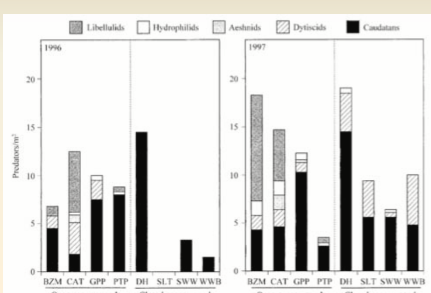
Predators vary in how much risk they pose to different prey species

Predator	Capture efficiency	Palatability	Handling time (min:s)
Toad tadpoles			
Umbra	1.00 ± 0.00 (2)	0.00 ± 0.00 (2)	never ate (13)†
Anax	1.00 ± 0.00 (6)	0.08 ± 0.08 (6)	02:08 ± 00:00 (1)‡
Notophthalmus	0.67 ± 0.09 (10)	0.43 ± 0.11 (10)	00:44 ± 00:10 (8)
Dytiscus	0.48 ± 0.08 (6)	1.00 ± 0.00 (6)	17:24 ± 03:34 (6)
Wood frog tadpoles			
Umbra	0.92 ± 0.04 (7)	0.83 ± 0.09 (7)	00:28 ± 0:07 (7)
Anax	0.63 ± 0.10 (6)	1.00 ± 0.00 (6)	02:34 ± 00:18 (6)
Notophthalmus	0.57 ± 0.06 (7)	1.00 ± 0.00 (7)	00:56 ± 00:12 (7)
Dytiscus	0.40 ± 0.06 (4)	1.00 ± 0.00 (4)	34:35 ± 10:15 (4)
Leopard frog tadpoles			
Umbra	0.82 ± 0.09 (11)	0.49 ± 0.14 (10)	01:49 ± 00:36 (8)
Anax	0.80 ± 0.12 (4)	1.00 ± 0.00 (4)	02:05 ± 00:17 (4)
Notophthalmus	0.45 ± 0.06 (4)	0.95 ± 0.05 (4)	01:09 ± 00:05 (4)
Dytiscus	0.45 ± 0.09 (4)	1.00 ± 0.00 (4)	23:12 ± 02:21 (4)

Note: Sample sizes are in parentheses.
† Only two of 13 *Umbra* struck at toads, and all were spit out.
‡ Only one of the seven *Anax* consumed any of the toads captured.

Predator-induced plasticity in larvae

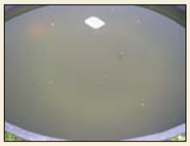
Predators are variable in space and time



Detecting predators

How do larvae detect predators in the water?

For aquatic larvae, which of these cues is most important?



Chemical cues are complex mixtures

1. Alarm cues - released by damaged or consumed prey
2. Kairomones - released by predators

We will talk more about this later

Designing experiments

If we just put predators and prey together, prey mortality would be extremely high

With caged predators we can make use of chemical cues released during predation

Experiments can be conducted in small tubs, pond mesocosms, or natural ponds

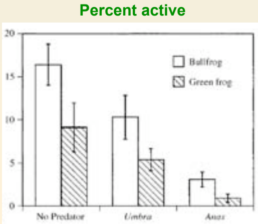
Larvae can be observed and measured to assess whether predators induce changes

Behavioral responses to predators

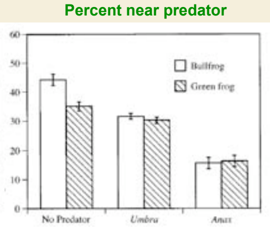
Behavioral responses include:

Reduction in activity level
Increased use of refuges
Avoidance of the predator

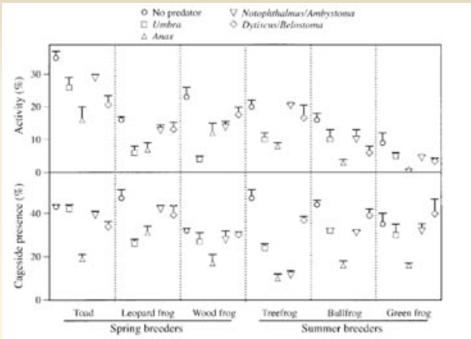
Percent active



Percent near predator



Behavioral responses to predators

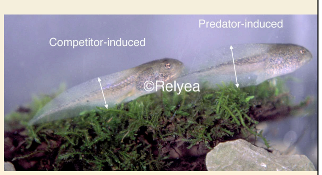


Morphological responses to predators

Recently discovered in anurans and salamanders

Morphological responses include:
Deeper and shorter tails, smaller bodies, greater tail pigmentation

[Video of predator-induced plasticity]



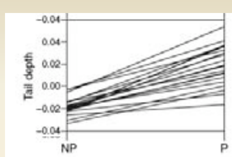
Gray treefrogs (*Hyla versicolor*) **Wood frogs (*Rana sylvatica*)**

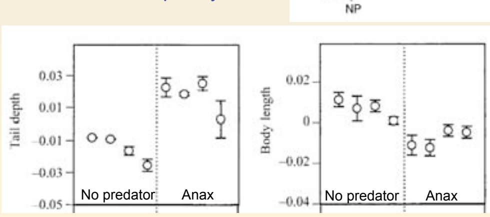
Morphological responses to predators

Data from a pen experiment in natural wetlands using different populations of wood frogs

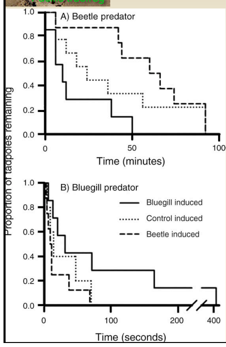
Populations differed in plasticity
Local adaptation

Families also differ in the expression of plasticity
Genetic variation for plasticity





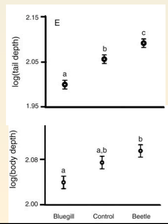
Benefits of the responses



Larvae were exposed to 3 caged predator treatments

Bluegill and beetle larvae induced opposing phenotypes

The larvae were subsequently exposed to lethal predators and survivorship recorded

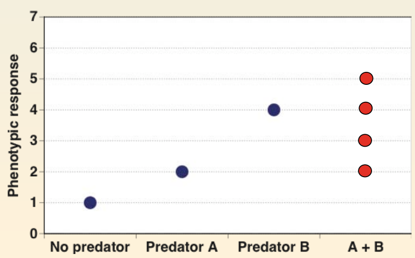


What if multiple predators are present?

Aquatic communities can contain several different predator species

Predators differ in risk posed to tadpoles

How do tadpoles respond to combined predators?

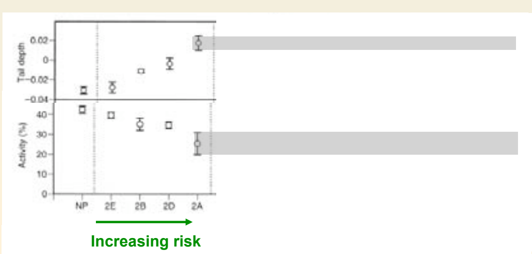


Responses to combined predators

Tadpoles were reared with 4 different predators that varied in risk level

The density of each predator species was doubled to increase risk

All 6 pairwise combinations of predators were made



Dissecting chemical cues

A variety of chemical cues will be 'floating' around the aquatic environment and tadpoles must be able to process this information to form their responses to predators

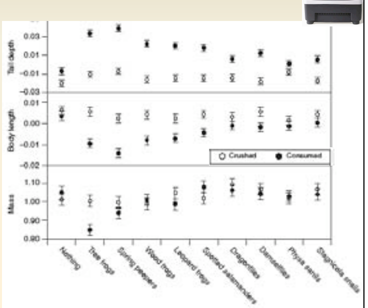
Alarm cues from damaged prey

Are cues from damaged prey enough to elicit a response?

Many predators are generalists

Can tadpoles detect predators when they consume heterospecific prey?

Predators were fed a wide range of diets and these diets were mechanically crushed by the researcher



What are the costs of the responses?

Why not always form the predator-induced phenotypes?

Wood frogs were reared with and without caged predators

The tadpoles were transferred to tubs to assess competitive ability

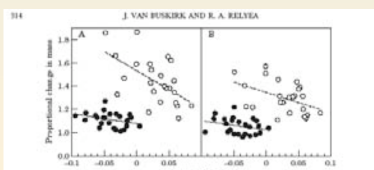


Figure 1. Growth rates of groups of 10 *Rana sylvatica* tadpoles, measured over 7 days in the (A) absence and (B) presence of competing *R. catesbeiana*. Growth rate declined with increasing tail fin depth, especially in the treatment without competitors and for tadpoles originating from tanks with caged dragonflies. Predator-induced tadpoles grew relatively more during the experiment, probably because of their small initial size. (●) no-predator phenotype; (○) predator-induced phenotype.

Predators and metamorphosis

How do predators impact the decision to metamorphose?

Tadpoles should minimize the ratio of mortality rate (μ) to growth rate (g) when comparing the aquatic and terrestrial environment

Given that predators increase the ratio of mortality rate (μ) to growth rate (g), tadpoles should metamorphose earlier and at a smaller size

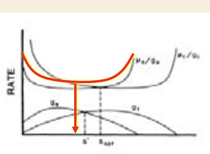


Fig. 7.—Ratios of mortality to growth rates for the μ- and g-curves portrayed in figure 6. The optimal size at metamorphosis (s_{opt}) is delayed to a size larger than the one that maximizes growth rates (s') because of the trade-off between increased growth rate and the risk of mortality.

Werner 1986

Review of 41 studies (Relyea 2007):

95% found metamorphosis at same time or later

86% found metamorphosis at same size or larger

Contradicts the model predictions. WHY?

Reversibility of defenses

Predators may colonize or emigrate from ponds over a tadpole's lifetime

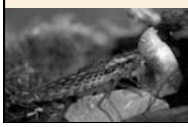
Given the costs associated with defenses,
tadpoles should track changes in predation risk

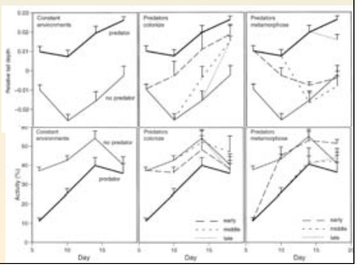
However, tadpoles may not be infinitely plastic

Gray treefrogs were reared in wading pools

Predator cages were moved to different pools over time

Tadpoles were measured every week





Competitor-induced plasticity

When the abundance of predators is low, competition is usually high

Generally, competitors induce higher activity, larger bodies, and smaller tails

Environmental variation in predators and competitors favors plasticity

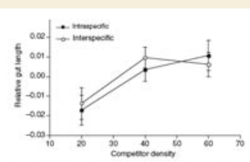
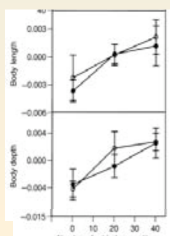
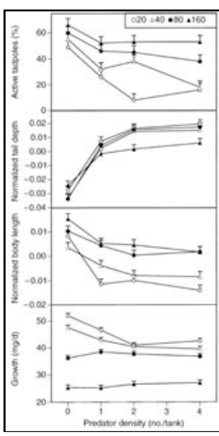


Figure 1 The change in relative gut length of wood frog tadpoles when reared under different densities of intraspecific or interspecific competitors. Gut length was made size independent by regressing log gut lengths against log tadpole mass and saving the residuals. Data are mean ± 1 SE.

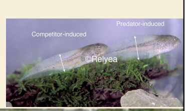




Fine-tuned phenotypes

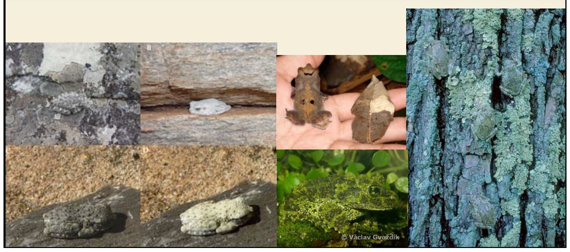
How do tadpoles balance the risk of predation and the presence of competitors?

Manipulate the number of caged predators and the density of competitors



Responses of adults to predation

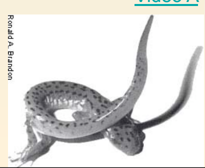
Cryptic coloration - match dorsal coloration/ pattern with surroundings
- When disturbed, seek out habitats they match
- Rapid color change to match background
- Seasonal changes in coloration

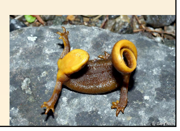


Responses of adults to predation

Behavioral responses
-Avoid cues of predation: *Plethodon cinereus* avoids cues from snakes fed conspecifics but not earthworms (Madison et al. 1999)
-Flee from predators: rapid movement away from threat, rolling down hills, flash colors
-Present glands towards: depend on where the glands are concentrated
-Inflate body and stretch out limbs: appear bigger, harder to swallow
-Tail displays: direct strikes towards the expendable tail (costly?)
-Aggressive displays and screams

Video A Video B Video C



Important books