Phenotypic plasticity in amphibians

Goals

- Overview of phenotypic plasticity
- Summary of different types of plasticity
- Discuss costs and benefits of plasticity
- Discuss complexity of plasticity
- Readings
  - Wells: Scattered parts of chapters 13-15
  - Wilbur, H. M., and J. P. Collins. 1973. Ecological Aspects of Amphibian Metamorphosis. Science 182:1305-1314.
  - Denoel, M., P. Joly, and H. H. Whiteman. 2005. Evolutionary ecology of facultative paedomorphosis in newts and salamanders. Biol Rev Camb Philos Soc 80:663-671.
  - Denver, R. J., M. Phillips, and N. Mirhadi. 1998. Adaptive plasticity in amphibian metamorphosis: Response of Scaphiopus hammondii tadpoles to habitat desiccation. Ecology 79:1859-1872.
  - Relyea, R. A. 2002. Local population differences in phenotypic plasticity: predator-induced changes in wood frog tadpoles. Ecol Monographs 72:77-93.
  - Warkentin, K. M. 1995. Adaptive plasticity in hatching age: a response to predation risk trade-offs. PNAS 92:3507-3510.

Phenotypic variation

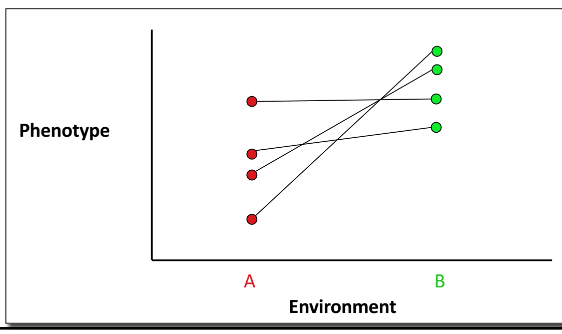
Genetic variation leads to phenotypic variation

The influence of environment

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

Phenotypic plasticity

When a single genotype can produce different phenotypes under different environmental conditions



Adaptive plasticity

Key factors in the evolution of plasticity

1.
2.
3.
4.

*

The basics of plasticity

Metamorphosis

Paedomorphosis

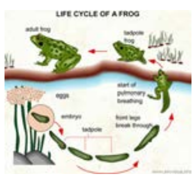
Predation

Competition

Decisions about metamorphosis

Environmental variation

- Temperature
- Hydroperiod
- Resource levels
- Competition
- Predation
- Water quality

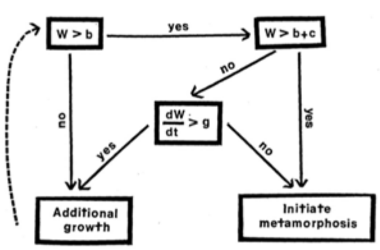


1. Do these factors affect the decision to metamorphose?
2. What cues are used to initiate metamorphosis?
3. What are the costs and benefits of this flexibility?
4. Is it adaptive?

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:

1.
2.

If food resources increase:

1.

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

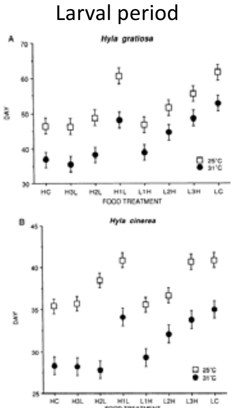
Leips and Travis 1994

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.

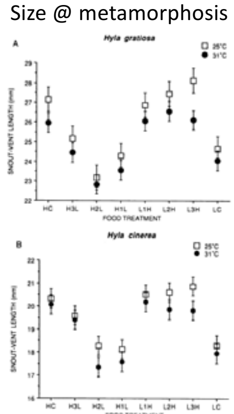
Species	Treatment code*	Food level	Day of switch 25°C	Day of switch 31°C
Hyla gratiosa	LC	L	Never	Never
	L1H	L → H	9	9
	L2H	L → H	21	20
	L3H	L → H	29	28
	HC	H	Never	Never
	H1L	H → L	9	9
	H2L	H → L	21	20
	H3L	H → L	29	28
Hyla cinerea	LC	L	Never	Never
	L1H	L → H	8	7
	L2H	L → H	16	16
	L3H	L → H	22	21
	HC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



Summary

-
-
-

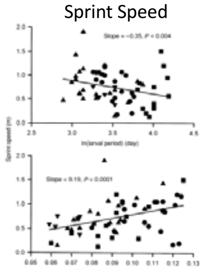
Does this support the Wilbur and Collins model?

Impacts on performance

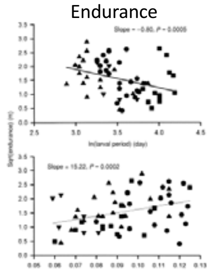
Food ration & temp altered to create variation in larval period & mass

Performance of the metamorphs was tested

Sprint Speed



Endurance

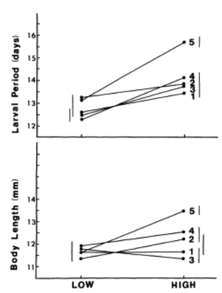


Bufo terrestris; Beck & Congdon 2000

Pond drying & metamorphosis

Does pond drying affect the decision to metamorphose?

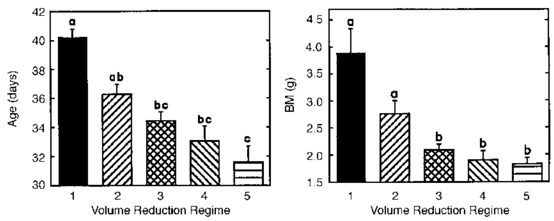
- Tadpoles were reared in pens within ponds
- Ponds differed in hydroperiod
-
- Different families showed different amounts of plasticity -
- What are the trade-offs?



Spadefoot toads; Newman 1988

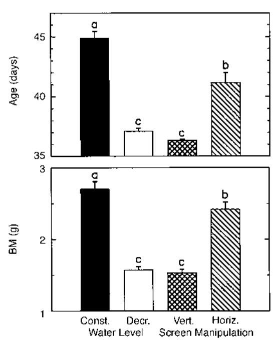
Pond drying & metamorphosis

- 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?

1. Reduction in swimming volume
2. 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 (10%)

- Salamandridae, Ambystomatidae, Dicamptodontidae, Hynobiidae, Plethodontidae

What affects the decision?

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

Key variables

Salamanders might be able to assess:

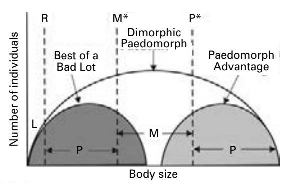
1. Temperature differences that affect growth
2.
3.
4. Predation pressure (e.g., fish)
5.

Possible outcomes

Proposed explanations for paedomorphs

1.
2.
3.

Similar to Wilbur & Collins



Predicted environmental factors that select for paedomorphosis through each alternative mechanism

Whiteman 1994

Mechanism	Aquatic environment	Aquatic parameters: Temp.	Density	Food	Predation	Growth season	Terrestrial parameters: 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

•

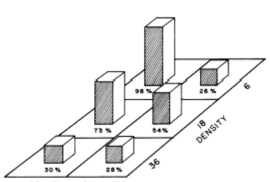


FIG. 1. Mean percentage of individuals becoming paedomorphic from the drying regime (water level) and density treatments. Means were calculated from eight artificial ponds ($n = 4$ from each of the nonsignificant food treatments).

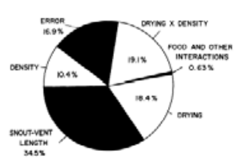
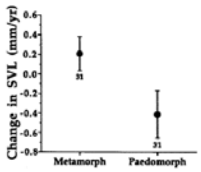


FIG. 3. Proportion of the variance in the percentage of individuals becoming paedomorphic accounted for by each component of the experimental design. Variance was calculated from the Type I sum of squares of each component divided by the total sum of squares, when snout–vent length was the first variable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

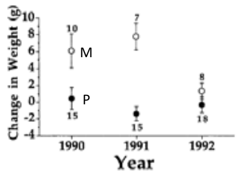
Ambystoma talpoideum; Semlitsch 1987

Costs and benefits

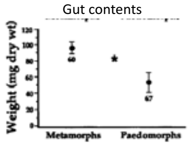
Growth over 2 years



Growth over time



Gut contents



-
-

Ambystoma tigrinum nebulosum, Whiteman et al. 1996

Costs and benefits

Two families of larvae were used

Hatching time was manipulated

Synchronous hatching

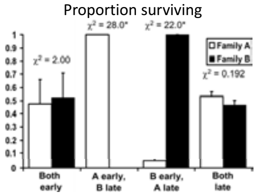
-

Asynchronous hatching

-

-

Proportion surviving



Ambystoma talpoideum; Ryan & Plague 2004

Predation

Great system to explore plasticity

- Common in many systems
- Diversity of foraging modes
- Variable in space and time
- Huge impacts on fitness

Egg hatching plasticity

Many tropical anurans lay eggs on vegetation over ponds
Clumped, stationary, and good sources of protein and energy
Egg predators can dramatically reduce clutch sizes
Is phenotypic plasticity important for these frogs?

Red-eyed treefrog
(*Agalychnis callidryas*)

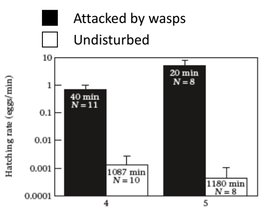
Cat-eyed snake
(*Leptodeira septentrionalis*)

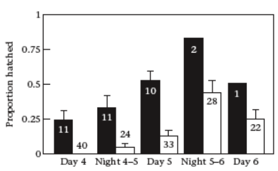
Wasps
(*Polybia rejecta*)

Responses to wasps

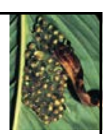
Wasps attack one egg at a time
- Carry off the embryo

Greatest risk =





Responses to snakes



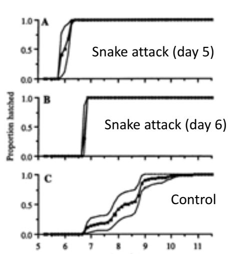
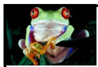
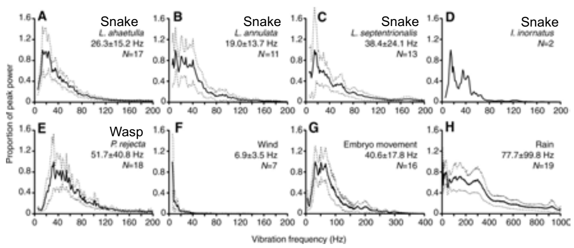


FIG. 2. Hatching of *A. callidryas* clutches with and without snake attack. Experimental clutches were attacked by *L. septentrionalis* at age 5 days (*A*; *n* = 9) or 6 days (*B*; *n* = 5); control clutches were not attacked (*C*; *n* = 14). Data are mean proportion hatched out of total hatch for each 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.



Responses to snakes

Vibrational cues



Caldwell M S et al. J Exp Biol 2009;212:566-575

Responses to snakes

Opens up more questions

- Why not always hatch as fast as possible?
- Is there a cost to hatching too quickly?
-
-

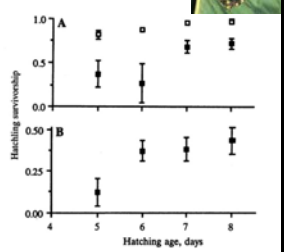


FIG. 4. Survivorship of *A. callidryas* hatchlings with shrimp, *M. americanum* (*A*), and fish, *B. rhabdophora* (*B*), in relation to hatching age. Data are mean proportion of tadpoles surviving (± 1 SE). In *A*, data from small shrimp (open symbols) and large shrimp (closed symbols) are plotted separately.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

Predator-induced plasticity in larvae

Aquatic predators are diverse in form and abundance

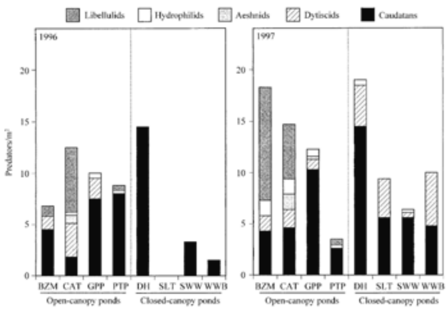
-

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 -
2. Kairomones -

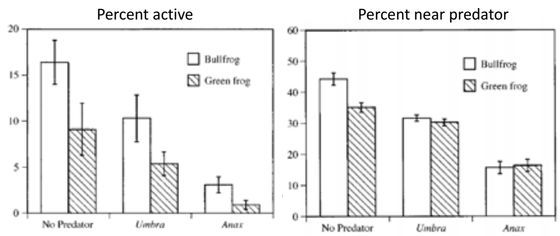
Designing experiments

- If we just put predators and prey together, prey mortality would be extremely high
- With cages we can make use of chemical cues
- Experiments can be conducted in small tubs, mesocosms, or ponds
- Larvae can be observed and measured to assess whether predators induce changes

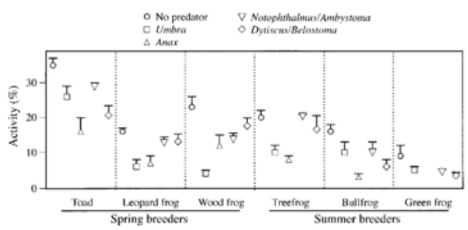
Behavioral responses

Types of responses include:

-
-
-



Behavioral responses

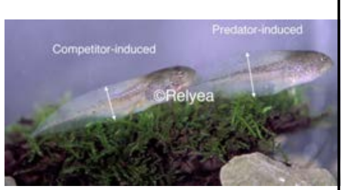


Morphological responses

Types of responses include:

-
-
-

Gray treefrogs (*Hyla versicolor*)

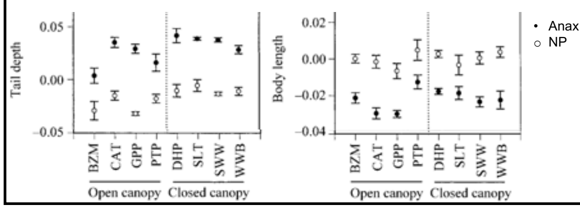


Wood frogs (*Rana sylvatica*)

Morphological responses

Data from common garden experiment using different populations of wood frogs

-
-

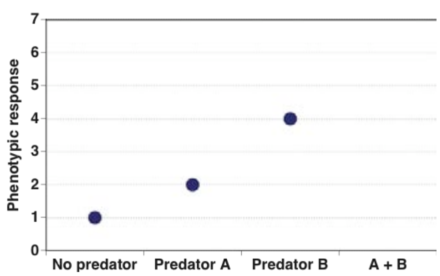


What if multiple predators are present?

Aquatic communities can contain several different predator species

Predators differ in risk posed to tadpoles

How do tadpoles respond to combined predators?

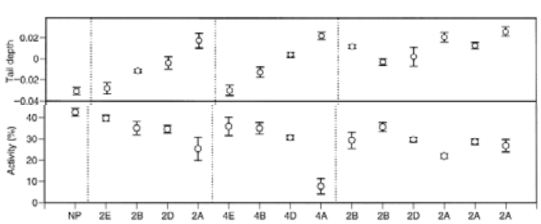


Responses to combined predators

Tadpoles were reared with 4 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

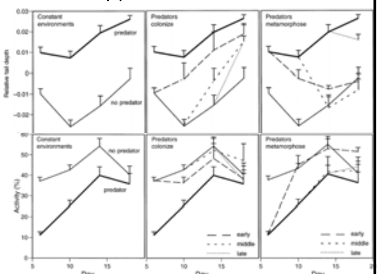


Reversibility of defenses

Predators enter and leave habitats over time

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

However, tadpoles may not be infinitely plastic



Competitor-induced plasticity

- Variation in predators and competitors favors plasticity

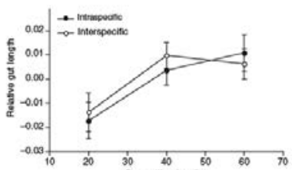
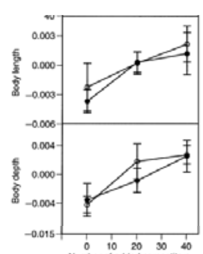
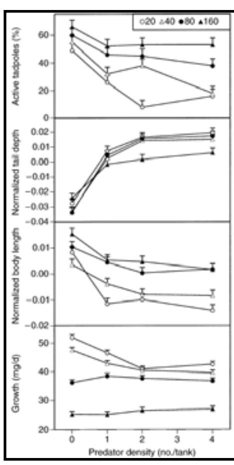


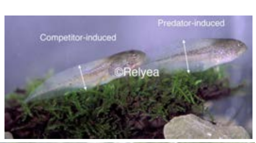
Figure 1 The change in relative gut length of wood frog tadpoles when reared under different densities of intraspecific or interspecific competitors. Gut length was made size independent by regressing log gut lengths against log tadpole mass and saving the residuals. Data are mean ± 1 SE.





Fine-tuned phenotypes

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



Books on plasticity