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

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

\[ W = \text{larval body size} \]
\[ b = \text{min. size to undergo meta} \]
\[ b+c = \text{max. size to remain as larvae} \]
\[ \frac{dW}{dt} = \text{size-specific growth rate} \]
\[ g = \text{current body mass} \]

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

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

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
- 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?


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

Whiteman 1994

Wilbur & Collins
Terrestrial versus aquatic decision
Larvae were reared in pond mesocosms at three densities
Tanks were slowly drained or the water level kept constant

Costs and benefits
Growth over 2 years
Growth over time
Gut contents
Diet composition

Costs and benefits
Two families of larvae were used
Hatching time was manipulated
Synchronous hatching
Asynchronous hatching
Cannibalistic/carnivore morph
Frogs and salamanders will consume conspecifics
*Ambystoma, Dicamptodon, Triturus*
*Rana, Hyla, Spea, Scaphiopus*

Alternative tadpole phenotypes
Omnivore morph  Carnivore morph

Environmental heterogeneity
Proximate mechanism or cue

Carnivore morphs in Spadefoot toads

Carnivorous tadpoles
Does the addition of exogenous thyroxine induce the carnivorous morph?

(Pfennig 1992)  (Storz 2004)
Carnivorous tadpoles

Phenotypic trade-offs

Time to metamorphosis

Post-metamorphic survival

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

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?

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?

- Visual, but no chemical, or tactile cues
- Visual and chemical, but no tactile cues
- Chemical, but no visual or tactile cues
- Visual, chemical, and tactile cues

18 cannibals produced
9 cannibals produced
0 cannibals produced
0 cannibals produced

(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?

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)

(Pfennig et al. 1991; 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?

Are there trade-offs?

Snake attack (day 5)

Snake attack (day 6)

Control
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-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
--- | ---
![Graph showing behavioral responses](image)
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 larvae were 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.

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.

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.

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

Important books