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:
- Gotthard and Nylin 1995. Oikos 74: 5-17

Supplemental readings:
- Gotthard and Nylin 1995. Oikos 74: 5-17

Required readings for class discussion:

Lecture roadmap
- Basics of phenotypic plasticity
- Metamorphosis and paedomorphosis
- Cannibalism
- Predation
- Competition
- Class discussion (next Tuesday)
Phenotypic variation is the basis of biology

Genetic variation leads to phenotypic variation

Environmental variation also leads to phenotypic variation

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

Genetic variation for plasticity

Environment

Phenotype

Gene expression depends on the type of food
Escherichia coli
Stem elongation is sensitive to wind
Arabidopsis thaliana
Sex is determined by temperature
Alligator mississippiensis

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

Environmental heterogeneity
Phenotypic trade-offs
Reliable cues
Heritable variation

How would you empirically test for phenotypic plasticity?
Decisions about metamorphosis

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

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

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

Wilbur and Collins 1973. Ecological aspects of amphibian metamorphosis

The effects of resources & temperature

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
Let’s summarize these results

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

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

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

Does this support the Wilbur and Collins model?

Effects on performance

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

Bufo terrestris; Beck & Congdon 2000

Sprint Speed

Endurance

Explanation?

Why consider these variables?
Pond drying & metamorphosis

Does pond drying affect the decision to metamorphose?

Tadpoles were reared in pens within ponds

Ponds differed in duration

What cues are tadpoles using to detect pond drying?

Pond drying & metamorphosis

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

Interpretation?
Paedomorphosis in salamanders

Like anurans, salamanders 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

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

Interpretation?

Gut contents

Diet composition

Ambystoma tigrinum nebulosum, Whiteman et al. 1996

Costs and benefits

Two families of larvae were used

Hatching time was manipulated

Proportion surviving

Which morph can reproduce sooner?

Ambystoma talpoideum; Ryan & Plague 2004

Cannibalism

Consumption of conspecifics - occurs in many groups

Observed in frogs and salamanders

Ambystoma, Dicamptodon, Triturus

Rana, Hyla, Spea, Scaphiopus

Alternative tadpole phenotypes

Omnivore morph

Carnivore morph

Patterns are seen in jaw muscles

Gut
Cannibalism in Spadefoot toads

Environmental heterogeneity
Proximate mechanism or cue

Your ideas

Cannibalsm in tadpoles

Does the addition of exogenous thyroxine induce the carnivorous morph?

Distribution in nature

Thyroxine added

(Pfennig 1992)

(Storz 2004)

Cannibalism in tadpoles

Phenotypic trade-offs

Your ideas

Time to metamorphosis

Post-metamorphic survival

Carnivore

Carnivore

Classified: < 146 days

Crossed: 146 - 358 days

Days after hatching

% Survival

Fig. 4. Phenotypic variation in larval tadpoles, classified as either crossed or normal. 

Carnivore: Cannibalism

Carnivore: Cannibalism
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.

Cannibalism and Kin

How would kin relationships affect cannibalism? If reared with siblings, spadefoots are less likely to form cannibalistic morph.

Spadefoot toad species can coexist

Plains spadefoot: S. bombifrons only

Mexican spadefoot: S. multiplicata only

Both species: Abundant shrimp, Abundant detritus

Playa lake: Abundant shrimp, Reduced detritus

Reduced shrimp, Abundant detritus
Spadefoot toad species can coexist

How do the species partition morphological space?

Tadpoles must consider:
- Resource levels
- Resource types
- Competitive ability

Character displacement in the expression of resource polyphenism

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?

(From 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?

Predation
Predators are ubiquitous in terrestrial and aquatic habitats
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?
Responses to snakes

Egg hatching video

What is the environmental cue of predation?

Snake attack (day 5)

Snake attack (day 6)

Control

Are there trade-offs?

Predator-induced plasticity in larvae

Aquatic predators are diverse in form and abundance

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

Responses to wasps

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

- Attacked by wasps
- Undisturbed

Predators also 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?

We will talk more about this later.

Designing experiments

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

By caging predators, we can make use of chemical cues released during predation events

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

The larvae can then 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

Morphological responses to predators

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

Recently discovered in anurans and salamanders

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

No predator   Anax   No predator   Anax

Benefits of the responses

Larvae were exposed to 3 caged predator treatments
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.

Interpretation?

Dissecting alarm 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
Reversibility of defenses
Predators may colonize or emigrate from ponds over tadpoles lifetime
Given the costs associated with defenses, tadpoles should track changes in predation risk
However, tadpoles may not be infinitely plastic

Competitor-induced plasticity
These results lead to questions about how tadpoles respond to competitors
When the abundance of predators is low, competition is usually high
Generally, competitors induce higher activity, larger bodies, and smaller tails
Environmental variation in predator and competitor abundance favors plasticity

Fine-tuned phenotypes
How do tadpoles balance the risk of predation and the presence of competitors
Simple experiment that manipulates the number of caged predators and the density of competitors
Topics for class discussion

The importance of plasticity within communities

Predators and metamorphosis

Phylogenetic patterns of plasticity


Important books