Amphibian Foraging Ecology (Part I)

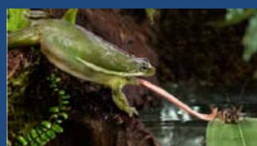


Photo Credit: Ellen Lucy

Goal of Lecture

To familiarize students with the basic principles and evolution of amphibian foraging ecology

To familiarize students with the different foraging strategies, resource selection, prey detection, and feeding mechanisms of terrestrial amphibians

Reading Assignments
Zug: pp. 249-256
Pough: pp. 395-397, 400-405
Duellman: pp. 238-240

Supplemental Reading
Toft Foraging Ecology Lecture

Lecture Road Map

I. Evolution of Foraging Techniques
II. Energetics
III. Foraging Movement and Habitat Selection
IV. Foraging Modes
V. Prey Selection & Diet
VI. Prey Detection
VII. Feeding Mechanisms

Foraging vs. Feeding?

Feeding: A physiological and morphological process that involves consuming and digesting food

Foraging: A behavioral process which includes searching for resources and the decision-making involved in how, when and where to *search*

(Toft 2002)

Foraging Ecology in the Light of Evolution

- Foraging behavior is evolutionarily plastic
  - feeding strategies and mechanisms have evolved in response to natural selection
- If different strategies lead to a difference in fitness, then natural selection occurs
  - Difference in energy gain
  - Quality of shelter

Optimal Foraging Theory

Explains the evolution of foraging strategies

“Animals that harvest resources the best are at a selective advantage. Thus natural selection should favor the fine tuning of resource acquisition (optimal foraging)” – Zug

Obtain the most from available resources while expending the least amount of energy

Factors that Influence Foraging Behavior

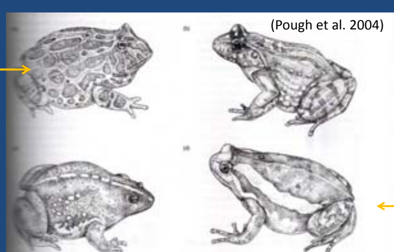
External
- Resource availability, predation risk, social interactions, etc.

Evolutionary history
- Morphological (size of mouth)
- Physiological (bursts of movement)
- Anatomy (shape)
- Very noticeable in tadpoles

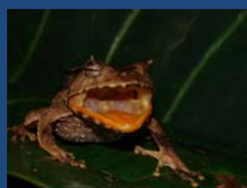
Internal
- Hunger, age, reproductive state, etc.

Example: Morphological Constraint

Size of Gape in ant-eating specialists vs. generalist feeders



(a) *Ceratophrys ornata* (b) *Leptodactylus pentadactylus* (c) *Rhinophrynus dorsalis* (d) *Kaloula pulchra*



Energetics

"There's no such thing as a free lunch." – Barry Commoner

- What determines how an animal acquires its resources?
- **Cost-benefit analysis**
  - **Cost** – use of energy in searching and obtaining resources (such as food)
  - **Benefit** – energy acquired to survive, grow, and reproduce
- **Energy Budget:** the balance of energy income against energy outcome

Optimal Diet

Diet which maintains positive energy budget

What does an amphibian consider when making it's shopping list?

1.) Prey abundance
2.) Energy spent handling prey
3.) How often predator eats

Plethodon cinereus switches from generalist to specialist as prey abundance increases

Habitat and Home Range

Salamandra salamandra was recaptured in the same home range after 7 years

Habitat

- Population level
- Series of resource patches
  - Depletable resource: Food
  - Nondepletable resource: Shelter

Home Range

- Individual level
- Area within habitat occupied by animal during normal activities (foraging)
- Most amphibians have small home ranges
- High fidelity

What determines size of home range?

Movement

Homing Behavior

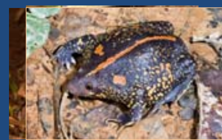
Daily movements for amphibians are short and brief (usually)

Sit and wait predators move from refuge to feeding station (*Hyla chrysoscelis)*

Active predators move from refuge and alternate between bouts of searching to rest (*Plethodon cinereus*)

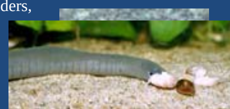
Foraging Modes

Sit-and-wait
- Most anurans
- Energetically conservative, low capture rate
- Short bursts of movement
- Well developed vision
- Cryptic coloration
- Specialists



Leptodactylus pentadactylus

Active
- Some anurans (Dendrobatids), most salamanders, caecilians
- Energetically expensive, high capture rate
- Well developed chemical senses
- Sustained amounts of activity
- Generalists



Plethodon cinereus (red-backed salamander)

*Foraging modes usually exist as a continuum

Zug 1993

How Did Foraging Modes Evolve?

Two hypotheses of evolution of foraging modes:
- Selection-based
- Phylogeny-based

Gastrophryne carolinensis

Family Microhylidae

Dendrobates pumilio

Family Dendrobatidae

Diet and Prey Selection

- In general, adult anurans, salamanders, and caecilians are **opportunistic carnivores**
- Eat insects and small invertebrates (and anything else that fits in mouth)
- Eat prey whole, do not chew

Zug 1993

Video

Prey Detection

Three main sensory cues used by terrestrial amphibians for prey detection

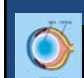
1.) Visual
2.) Auditory
3.) Chemosensory

These are often combined during foraging

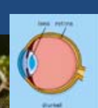
Visual Prey Detection

Fire Salamander Foraging

- Sit-and-Wait Predators
- Anurans and caudates
- Use vision to determine, size, speed, and location of prey
- Large, well-developed eyes



Agalychnis callidryas



Dendrobates granuliferus

Auditory Prey Detection

Use of airborne sounds to detect prey poorly documented

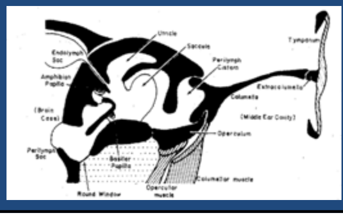
- *Bufo marinus* moves towards calling *Physalaeumus postulosus*

Active foragers (mostly caudates and caecilians)

Opercularis system transmits seismic vibrations (as low as ~200Hz) to inner ear

Opercularis System

- Transmits vibrations from forelimb to inner ear through opercularis muscle
- create fluid movement in inner ear cavity
- Vibrations stimulate neurorecetprs
- These low frequencies are usually made by digging insects
- Caecilians use mechanoreceptors

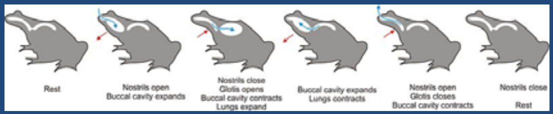


Chemosensory Prey Detection

- Three main chemical senses:
  - Olfactory – airborne odors
  - Vomerolfactory – surface odors
  - Gustation – tasting
- Olfaction and vomerolfaction used in prey location and identification, gustation used to accept or reject prey once captured

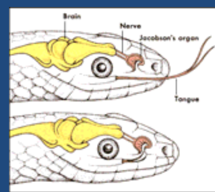
Olfaction

- Airborne odors
- Long-distance detection
- Olfactory epithelium sensitive to volatile compounds
- Buccal pumping – lunged amphibians



Vomerolfaction

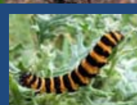
- Surface odors – high molecular weight compounds
- Short-range odor detection
- Picked up by tongue or snout and transported to vomerolfactory organ (Jacobson's organ)
- Common in active foragers (salamanders)



Hydromantes italicus – hunts in total darkness

Gustation

- Not used to locate prey
- Accepts or rejects based on chemical (taste) or mechanical (spines) stimuli

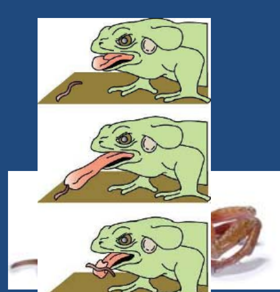


Terrestrial Feeding Mechanisms

- Two broad classes of terrestrial feeding mechanisms in amphibians

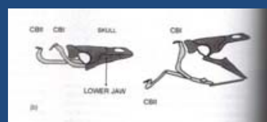
1.) Akinetic – move lower jaw only

2.) Projectile – use tongue to capture prey



Akinetic Feeding Mechanism

- Simplest tetrapod feeding system
- Caecilians
- Rigid skull and hinged lower jaw
- Many lineages with akinetic skulls have evolved projectile feeding mechanisms

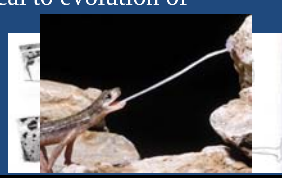


Caecilians Feeding

(Pough et al. 2002)

Projectile Feeding Mechanisms in Caudates

- Lingual Prehension
- Less derived salamanders - large fleshy tongue
- Evolved independently in several lineages multiple times (Plethodontids)
- Absence of lungs critical to evolution of tongue projection



Different tongue projections in Plethodontidae (Pough et al. 2002)

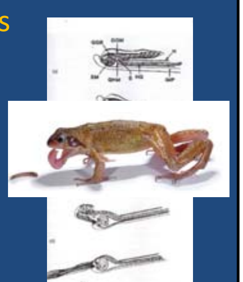
Projectile Feeding Mechanisms in Anurans

Mechanical pulling

- Basal frogs (Ascaphidae and Discoglossidae)
- Muscles attached to front of mandible draws tongue slightly forward
- Accompanied by lunging

Inertial elongation

- Tongue “flipped” out of mouth
- Smaller prey



Intertial elongation in *Bufo marinus* (Pough et al. 2002)

Overview

- Be able to differentiate feeding and foraging
- Know the evolutionary process of foraging ecology
- Be able to explain the Optimal Foraging Theory
- Know which factors influence foraging behavior
- Know the different types of terrestrial foraging modes among amphibians
- Know how terrestrial amphibians detect their prey
- Know the different terrestrial feeding mechanisms of amphibians

Texts Used

Pough, F. Harvey., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. *Herpetology*. 3rd ed. Upper Saddle River, NJ: Prentice Hall, 1998. Print.

Zug, George R., Laurie J. Vitt, and Janalee P. Caldwell. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. 2nd ed. San Diego, CA: Academic, 2001. Print.

Duellman, William Edward, and Linda Trueb. *Biology of Amphibians*. New York: McGraw Hill, 1986. Print.

Foraging ecology

Part II

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Road map

I. Adaptations of amphibians to foraging on water
   i. Caecilians
   ii. Caudata
   iii. Anura

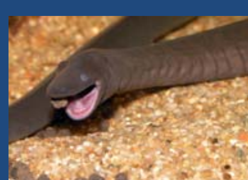
II. Foraging ecology of tadpoles

Amphibians that feed under water

- ❖ Several amphibian families have adapted to aquatic life
- ❖ Mostly opportunistic
- ❖ Both active hunters or sit and wait

Caecilians

- Genus Thyphlonectes
  - Active hunters
  - Poor vision
  - Smell and tact
- Opportunistic
- Generalists



Typhlonectes compressicauda diet

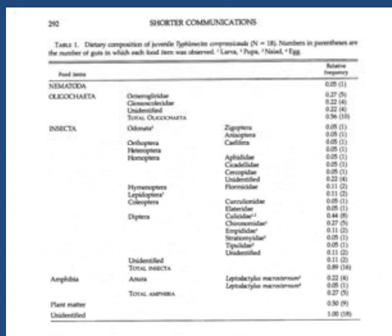


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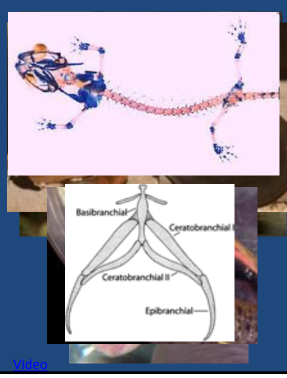
TABLE 1. Dietary composition of juvenile *Typhlonectes compressicauda* (N = 18). Numbers in parentheses are the number of guts in which each food item was observed. [1] Larva, [2] Pupa, [3] Naiad, [4] Egg.

Food items			Relative frequency
NEMATODA			0.05 (1)
OLIGOCHAETA	Ocnerodrilidae		0.27 (5)
	Glossoscolecidae		0.22 (4)
	Unidentified		0.22 (4)
	TOTAL OLIGOCHAETA		0.56 (10)
INSECTA	Odonata[3]	Zygoptera	0.05 (1)
		Anisoptera	0.05 (1)
	Orthoptera	Caelifera	0.05 (1)
	Heteroptera		0.05 (1)
	Homoptera	Aphididae	0.05 (1)
		Cicadellidae	0.05 (1)
		Cercopidae	0.05 (1)
		Unidentified	0.22 (4)
	Hymenoptera	Formicidae	0.11 (2)
	Lepidoptera[1]		0.11 (2)
	Coleoptera	Curculionidae	0.05 (1)
		Elateridae	0.05 (1)
	Diptera	Culicidae[1,2]	0.44 (8)
		Chironomidae[1]	0.27 (5)
		Empididae[1]	0.11 (2)
		Stratiomyidae[1]	0.05 (1)
		Tipulidae[2]	0.05 (1)
		Unidentified	0.11 (2)
	Unidentified		0.11 (2)
	TOTAL INSECTA		0.89 (16)
Amphibia	Anura	*Leptodactylus macrosternum*[1]	0.22 (4)
		Leptodactylus macrosternum[4]	0.05 (1)
	TOTAL AMPHIBIA		0.27 (5)
Plant matter			0.50 (9)
Unidentified			1.00 (18)

(Verdade, 2000)

Caudata

- Several families adapted to aquatic life
  - Salamandridae
  - Cryptobranchidae
  - Sirenidae
  - Amphiumidae
  - Proteidae
- Hyobranchial apparatus
  - Support and move gills
  - Expand and contract the buccal cavity during feeding



Amphiuma

Video

Caudata

- Use suction to capture the prey
  - Just with buccal expansion
  - Rapid strike
  - Manipulate prey with teeth
- Diet
  - Fish
  - Aquatic invertebrates
  - Worms
  - Crustaceans
- Aquatic salamanders respond to odor, movement or touch; terrestrial ones respond to movement

Diet of *Hynobius retardatus* larvae

Food item	Wet weight (mg)	Body length (mm)
Terrestrial invertebrates		
Araneae	23.20	5.50
Collembola	0.36 (0.02)	0.94 (0.04)
Lepidoptera	23.42 (3.79)	6.30 (0.37)
Coleoptera	30.10 (4.40)	5.50 (1.00)
Dermaptera	11.20	3.50
Hymenoptera	0.51 (0.02)	2.94 (0.06)
Isopoda	7.62 (2.30)	2.58 (0.74)
Diptera	0.58 (0.15)	2.38 (0.24)
Aquatic invertebrates		
Diptera larvae	0.27 (0.03)	2.70 (0.34)
Ephemeroptera	0.16 (0.02)	3.60 (0.33)
Trichoptera	6.33 (1.86)	4.50 (0.76)
Cyclopoida	0.10	0.57 (0.09)

TABLE 1. Results of ANOVAs for diet proportion of *Hynobius retardatus*.

Source	df	MS	F	p*
Terrestrial invertebrates	1, 42	[illegible]	[illegible]	[illegible]
Diptera larvae	1, 42	[illegible]	[illegible]	[illegible]
Ephemeroptera	1, 42	[illegible]	[illegible]	[illegible]
Trichoptera	1, 42	[illegible]	[illegible]	[illegible]
Copepoda (Cyclopoida)	1, 42	[illegible]	[illegible]	[illegible]
Salamander	1, 42	[illegible]	[illegible]	[illegible]
Detritus	1, 42	[illegible]	[illegible]	[illegible]

* Reduced alpha level [illegible]

Kohmatsu and Yukihiro (2001)

Predators

- Salamanders prey on other salamanders
- Can be cannibals
- Scavengers

Salamander larvae

- Same as adults: opportunistic predators
  - Aquatic invertebrates
  - Tadpoles
  - Other salamanders

Aquatic Frogs

- Predators
- Sit and wait
- Use camouflage or hiding places

Xenopus Video

Xenopus borealis diet

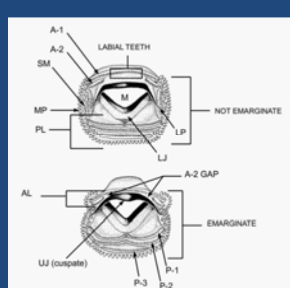
Order	DP1	DP2	PP	Total	%FO
Aranaea	0	2	4	6	9.4
Blattodea	2	4	3	9	14.1
Coleoptera	6	2	4	12	15.6
Odonata	5	3	5	13	20.3
Hymenoptera	3	7	1	11	17.2
Hemiptera	3	0	5	8	12.5
Isoptera	0	0	1	1	1.6
Isopoda	0	0	3	3	4.7
Ephemeroptera	1	0	1	2	1.6
Orthoptera	0	1	4	5	7.8
Diptera	3	1	9	13	20.3
Trichoptera	4	0	8	12	15.6
Annelida	0	1	2	3	4.7
Mollusca	2	1	0	3	4.7
Fish	0	1	0	1	1.6
Amphibian eggs	9	0	3	12	18.8
Tadpoles	3	0	0	3	4.7
Bait	2	5	3	10	
Plant material	2	3	22	27	
Empty stomach	2	2	0	4	
Non identified prey item	0	2	0	2	

DP1, disturbed pond 1; DP2, disturbed pond 2; PP, permanent pond.

(Bwong and Measey, 2010)

Tadpoles

- Most have:
  - Keratinized jaw
  - Rows of labial teeth
  - Papillae
- Food transport by buccal pumping
- Food particles catch by branchial filaments and branchial mucus

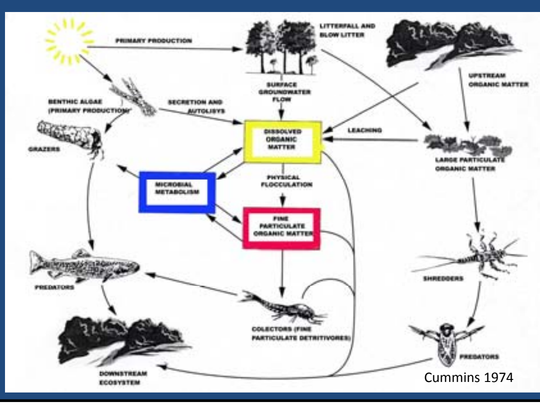


Adults and tadpoles have different Diets

- Carnivorous
  - Insectivorous
- Little selection

- Herbivores
  - Scarpers
  - Filters
  - Grazers
- Carnivores
- Oophagous

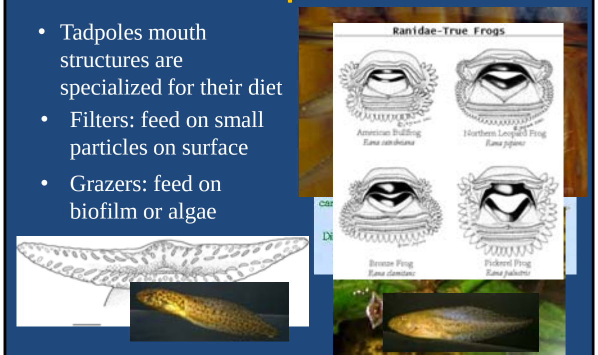
Classical stream ecosystem



Multiple functional roles of tadpoles

Tadpoles

- Tadpoles mouth structures are specialized for their diet
- Filters: feed on small particles on surface
- Grazers: feed on biofilm or algae



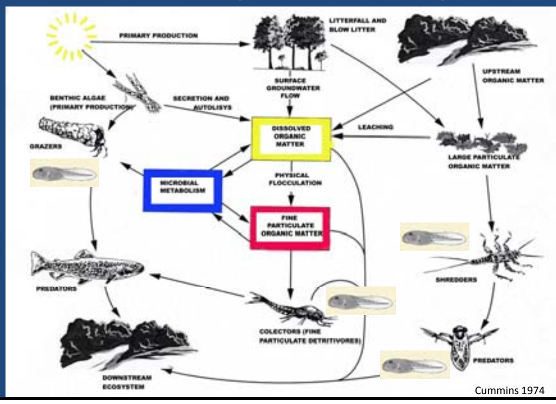
Tadpoles

- Stream grazers: feed from algae in fast moving streams
- Oophagus: feed eggs
- Detriti... particl...

Tadpoles

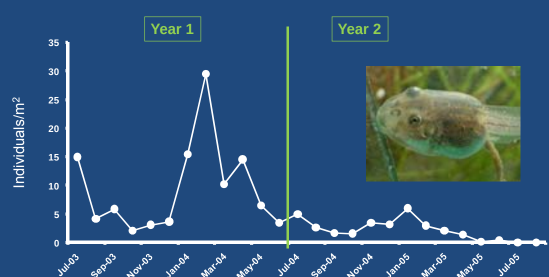
- Carnivores: Feed on animals
- Cannibals: Feed on their own species
- Gatherer: Feed par...s from th...

Classical ecosystem with tadpoles

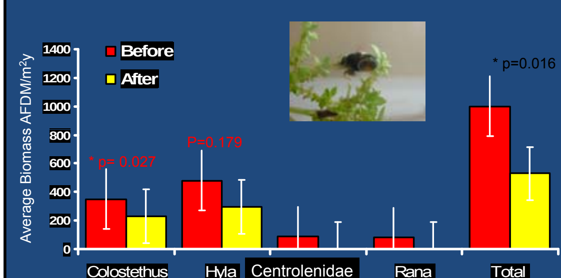


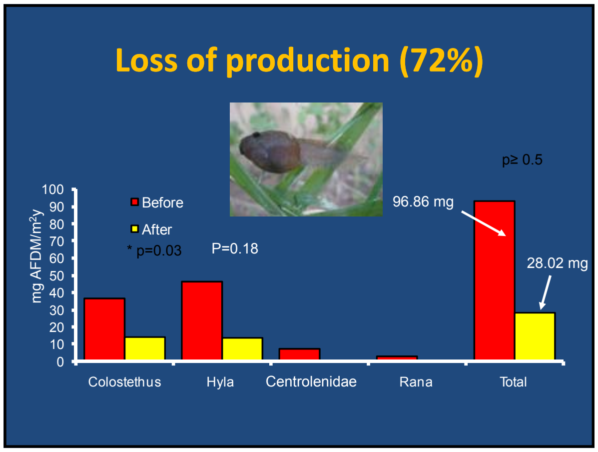
Cummins 1974

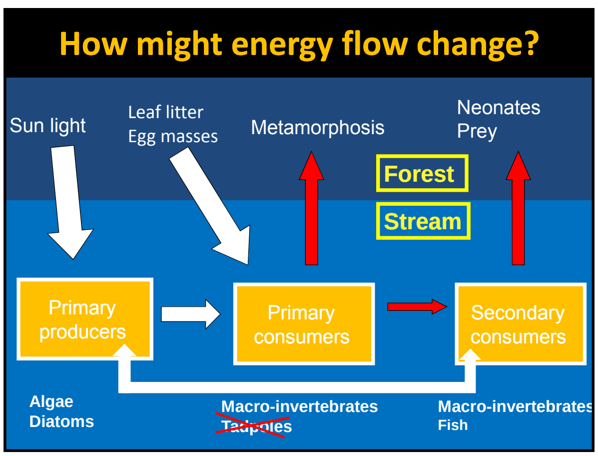
Tadpole declines

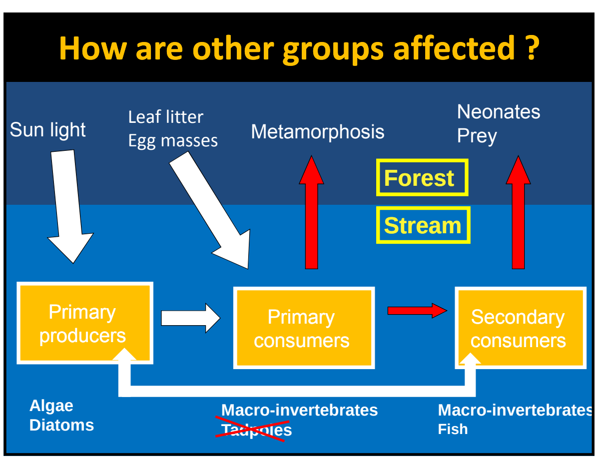


Loss of Biomass (47%)

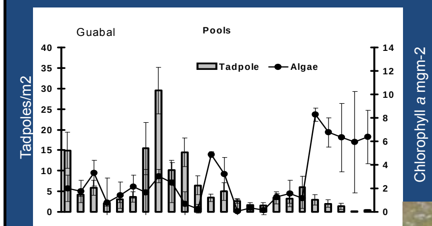


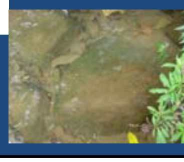

Loss of production (72%)
p≥ 0.5
96.86 mg
28.02 mg
Before
After
* p=0.03
P=0.18
mg AFDM/m²y
100
90
80
70
60
50
40
30
20
10
0
Colostethus
Hyla
Centrolenidae
Rana
Total


How might energy flow change?
Sun light
Leaf litter
Egg masses
Metamorphosis
Neonates
Prey
Forest
Stream
Primary producers
Primary consumers
Secondary consumers
Algae
Diatoms
Macro-invertebrates
Tadpoles
Macro-invertebrates
Fish


How are other groups affected ?
Sun light
Leaf litter
Egg masses
Metamorphosis
Neonates
Prey
Forest
Stream
Primary producers
Primary consumers
Secondary consumers
Algae
Diatoms
Macro-invertebrates
Tadpoles
Macro-invertebrates
Fish

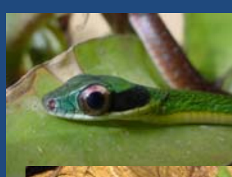
Algae Bloom

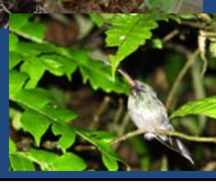




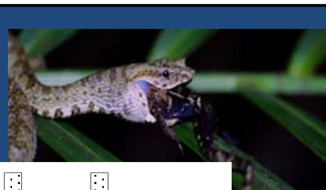
Connelly et al. *in press*

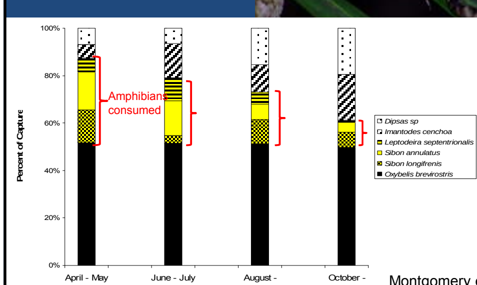
What is going to happened in the Forest





Reduction in amphibians as prey

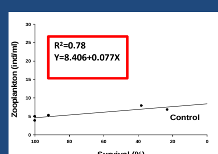


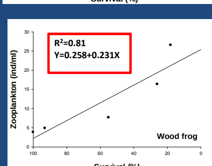


Montgomery et al. *in press*

Trophic cascades caused by ranavirus

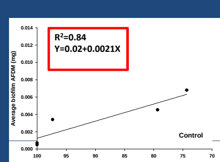
- Decline in number of individuals resulted in an increased in the abundance of the zooplankton community

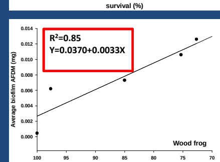




Trophic cascades caused by ranavirus

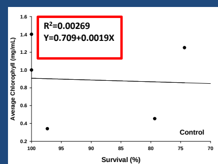
- Decline in number of individuals resulted in an increased in the biofilm layer of the pools

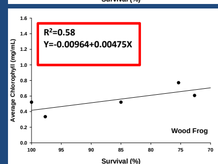




Trophic cascades caused by ranavirus

- Decline in number of individuals resulted in an increased of phytoplankton





Summary

- Aquatic amphibians are mostly predators
  - Opportunistic
  - Non selective
- Salamander larvae and caecilians can be active hunters
- Aquatic anurans are ambush predators
- Tadpoles have mouth parts adapted to the niche they inhabit
- Tadpoles are an important part of the ecosystem

Questions

- What is the function of the hyobranchial apparatus in caecilians and aquatic salamanders
- What is/are the major difference/s on foraging strategies between aquatic anuras, Caecilians, and aquatic salamanders
- What is/are the major difference/s on foraging strategies between adult anurans and its larvae
- What is the ecological role of tadpoles. What happened if they are removed?