Amphibian Estivation and Hibernation



Lecture Outline

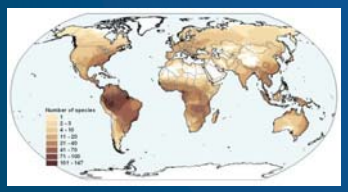
I. Introduction

II. Estivation

III. Hibernation

IV. Future Research

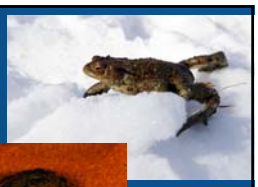
Amphibians range widely over globe



Why?

- Ability to withstand harsh conditions
- Life history needs met in short periods when conditions favorable

- Main challenges:
  1) Starvation
  2) Cold **Hibernation**
  3) Drought **Estivation**



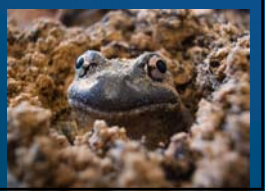
- Solution: conserve resources as much as possible until next active period

Estivation

Allows survival in extreme desert conditions:
- Some species can survive for several years without rain

Metabolic reduction – conserve energy

Many reduce H_2O loss by:
- Burrowing into moist soil
  OR
- Forming cocoon



Characteristics of Estivators

- Inhabit desert-like environments
  – Seasonal / variable rainfall
- Most highly terrestrial
  – Return to water to breed (some exceptions)
- Many nocturnal

Boutilier et al 1979: Bufo marinus (non estivator in nature)
- estivation induced in lab

Suggests: All fossorial amphibians may have metabolic reduction capability

Estivators – Life History

- Opportunistic Breeders
  - Triggered by rain
  - Lay eggs in ephemeral pools
  - Larvae develop quickly
  - After rains, subadults burrow into loose soil
- May spend most of life estivating

Estivators – Life History Example

- Some Myobatrachidae:
  - Lay eggs in dry depressions
  - Don't hatch until flood occurs
    - Arrested development of embryos
    - Slow rate of O_2 consumption
    - Withstand up to 90% H_20 loss from egg
    - Can last several weeks if air is humid
  - Larvae also can reduce metabolic rate
    - Survive several days without rain

Aquatic Estivators

(small group)

- Includes:
  - Ambystoma
  - Siren
  - Amphiuma
- Burrow into mud after water dries up
- Remain encased in hardened mud until rainy season
- Some shelter under loose debris or in other animals' burrows

Estivation: Cues for Emergence

- Rain
  - May extend active season if rain continues
- Photoperiod
  - Semour (1973): Toads kept in constant light will come to surface
- Temperature
  - May not emerge during rains if temp too high or low

Burrow Microenvironment

- Important variables
  - Temperature
  - Soil H_2O tension
    (Affinity of soil for H_2O)
  - Conc. of respiratory gases

Determined by depth, soil type, climate

Temperature:
Determines Metabolic rate (fuel usage)
Adjust by digging deeper – loose soils only

Constraints to Estivation Time

- Starvation
  - Accumulate resources during feeding period
- Water loss
  - Adapted to function when dehydrated
  - Conserve / Store water
    - Absorb H_2O from soil
    - Waterproof cocoons

Cocoons

- Prevent evaporation
- 2 Types:
  1) Single / multiple layers of shed skin (stratum corneum)
  2) Layer of secreted mucous
     - *Siren intermedia*

Estivation – Withstanding Water Loss

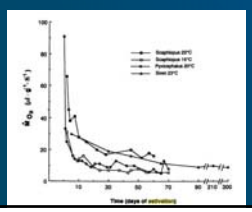
- Water storage
  - Amphibian body: 77 – 83% water (mammals 70%)
  - Desert anurans: Store water in bladder to absorb later
- Take up H_2O from soil – permeable skin
  - Some species accumulate urea
    - Increases osmolarity of body fluids
    - Also assists in metabolic reduction (Muir et al 2007)

Estivation - Electrolyte Balance

- Problem: Buildup of urea is dangerous
  - Product of metabolism
  - Denatures proteins, disturbs enzyme function
- How do amphibians deal with this?
  - Elasmobranch fishes produce solutes such as methylamines to counteract
    - Has not been found in anurans
  - Possible modifications to protein structure

Estivation - Metabolism Reduction

- Allows prolonged estivation without food
- Regulated by changes in
  1) Enzyme / protein activity
  2) Subcellular location of enzymes
  3) Anabolic uses of carbohydrates



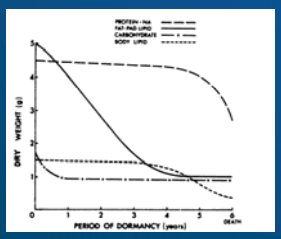
Within 3 hrs, O2 uptake decreases to 30% of resting

Estivation -Triggers for metabolism reduction

- Poorly understood
- Possible physiological triggers
  - pH change: acidosis common but more likely a result than a cause
  - Hormonal control
  - Opiates
    - May maintain dormancy in *Bufo marinus*

Estivation - Fuel Reserves

- Lipids: from body fat and organs
  - Primary energy source during estivation
  - *Scaphiopus*: 72% (Jones, 1980)
- Carbohydrates
  - *Scaphiopus*: 5%
- Protein
  - Last resort (only when other sources used)
  - *Scaphiopus*: 23%



Estivation - Gas Exchange

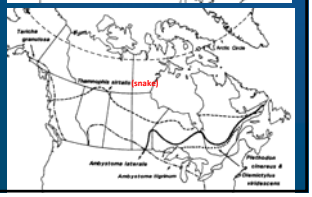
- Respiration necessary to use fuel efficiently
- Difficult in mud or cocoons

1) Cutaneous (*Scaphiopus*)

2) Pulmonary (*Pyxicephalus adspersus* – cocoon forming)

Hibernation – adaptation to extreme cold

- Frogs are northernmost ectothermic tetrapods
- Salamanders also reach high latitudes



Distribution limits – hypotheses

- Ability of larvae to overwinter
  - Limits salamanders
  - Frogs more tolerant of low oxygen than salamanders
  - Generally, only larvae of aquatic adults can overwinter
    - Frogs: Ranids only
- Other factors:
  - Food availability
  - Cold tolerance of adults
  - Length of breeding season

Hibernation - Responses to cold and starvation

- Reduce metabolism
  - Result of temp decrease
  - **Not always dormant**: some move and feed
- Accumulate lipid reserves before winter
  - Depend on lipid oxidation for fuel during hibernation
- Adjustments to enzymes and proteins produced by organs
  - Optimize low-temp function
  - More efficient metabolism
- Adjust cellular membrane function
  - Change physical properties of membranes for optimal function
  - Permeability, enzyme and transport activities, receptor and neural functions

Hibernation - Site Choice

Factors:

- Temperature
- Moisture
- O_2 level
- Protect from predators
- Supply cues for emergence

1) Submergence under water or ice
   - Prevents: freezing, desiccation
   - Risks: hypoxia, salt loss
2) Hibernate in burrow
   - Prevents: hypoxia, predation
   - Risks: freezing, desiccation
3) Stay on land (rare)
   - Tolerate freezing
   - Disadvantage: requires intracellular changes

Hibernation - Caudates

- Aquatic species
  - Usually overwinter in water
  - Many remain active
- Terrestrial species
  - Hibernate on land
  - Plethodontids:
    - Intolerant of freezing
    - Many burrow to avoid low temps
    - Remain active, feed underground

Hibernation - Anurans

- Bufonidae, Pelobatidae
  - Hibernate underground
  - Not freeze tolerant
- Hylidae
  - Not good at digging
  - Use preexisting burrows, crevices or debris
- Ranidae
  - Hibernate underwater (*R. Sylvatica* exception)

Terrestrial Hibernation

1) Avoid subzero temp (most)
   - Find moist, aerated hibernaculum
   - Use stored fat reserves
2) Tolerate Freezing
   - *Rana sylvatica, Hyla versicolor, H. crucifer, Pseudacris triceriata*
   - Adaptations:
     - Permit extracellular ice formation
     - Regulate cell volume
     - Protect subcellular organization

Hibernation - Cryoprotectants

- Important in amphibians that tolerate freezing
- Solutes that protect cellular structure

1) Colligative: Reduce osmolality of body fluid
   - Prevent too much extracellular ice from forming
   - Prevent intracellular volume from becoming too low
2) Membrane: Protect subcellular organization
   - Trihalose and proline: stabilize membrane
   - Glucose or glycogen: stabilize protein structure
   - Costanzo and Lee (2005): Urea acts as a cryoprotectant

Video: http://www.youtube.com/watch?v=Fjr3A_kfspM

Aquatic Hibernation

Anaerobic conditions

- Cutaneous O_2 Exchange impaired by boundary layers
  - Immobile layer of water next to skin
  - Amphibians can break with body movement
- Affects cardiovascular function
  - Decrease in heart rate, plasma volume
- Changes osmotic concentration
  - Increases body water
- Boutilier 2001: Low O_2 causes reduced cell membrane permeability in *Rana temporaria*
  - Reduces energy requirements

Hibernation – Emergence Cues

- Temperature
  - Most important
  - Evidence: re-emerge on warm days in winter
- Rain
  - Especially important for terrestrial caudates
  - Necessary for migration without desiccation
  - Increases hibernaculum temperatures, melts frost

Future Research

- Microenvironments of estivators and hibernators
- Control systems
  - Mechanism for metabolic reduction
  - Estivators: alteration of ventilation and effect of CO_2
  - Aquatic hibernators: control of fluid and ion balance, cardiovascular control in hypoxic conditions
- Formation of urea
- Formation of cryoprotectants
- Internal signals for emergence
- Reestablishing body function after thawing